

Factors associated with antler size of white-tailed deer in Iowa

by

Daniel Mark Adams

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Program of Study Committee:
Julie A. Blanchong, Major Professor
Stephen J. Dinsmore
Jesse A. Randall

The student author, whose presentation of the scholarship herein was approved by the program of study committee, is solely responsible for the content of this thesis. The Graduate College will ensure this thesis is globally accessible and will not permit alterations after a degree is conferred.

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ABSTRACT

Antler size of an individual cervid is a result of age, genetic, and environmental factors. Antlers are physiologically costly to produce and dependent upon condition, as nutritional requirements for body maintenance and growth take precedence over antler growth, indicating only individuals with access to adequate nutrition and in good health can afford to allocate resources for maximum antler growth. Therefore, biologists and managers are interested in antlers as possible indicators of condition of individuals and populations. To date, most studies of relationships between environmental factors and antler size have been conducted in the Southeastern U.S., but findings from these studies may not be generalizable to deer elsewhere in North America where environmental conditions are different. In order to identify associations between antler size and environmental factors in the Midwest U.S., I sampled hunter-harvested white-tailed deer in the row-crop dominated state of Iowa. I collected antler measurements, age, and location for 1,575 deer harvested between 2012–2018 to identify relationships between environmental factors and antler size. The first component of this thesis was an evaluation of methods for aging white-tailed deer. Because of the close relationship between antler size and age, controlling for the influence of age is important when attempting to identify environmental factors associated with antler size. I examined the congruence of age estimates obtained from two different methods for aging white-tailed deer: tooth replacement-and-wear (TRW) and counting cementum annuli (CA). I also examined the precision of the CA method using paired CA age estimates from two incisors from the same deer. Congruence rates of CA and TRW ages differed among age classes (80% congruence in yearling TRW age classification, 65% with 2-year-olds, 78% with ≥ 3 -year-olds) and the precision of CA aging was influenced by the level of certainty assigned to the age estimate as well as the batch in which the teeth were aged. These

findings suggest managers are best served by using TRW to age adult deer as yearlings or ≥ 2 -years-old, as the TRW method does not accurately age deer ≥ 2 -years-old to a single age. If additional ages are required, CA aging is likely to be more, but not perfectly, accurate. The second component of this thesis was to, after controlling for age, identify environmental factors associated with antler size of Iowa white-tailed deer and quantify variation in antler size across Iowa. Age was the most important factor explaining variation in antler size of white-tailed deer in Iowa. The amount of agricultural area in the area (typically $\approx 23.3 \text{ km}^2$) the deer was harvested and the average summer temperature the year the deer was born both had a positive influence on antler size, while the amount of forested area and the winter severity while the deer was *in utero* both had a negative influence. I observed regional differences in antler size among older age classes where, generally, deer from the southwestern part of Iowa had larger antler sizes than deer from the northern regions of Iowa. Environmental influences and aging error were among the possible explanations for these differences. However, the magnitude of the differences was smaller than previously observed in other studies examining differences in antler size metrics between physiographic regions (e.g., $< 1\text{--}13\%$ differences between landform regions in Iowa compared to $3\text{--}31\%$ for deer sampled in Mississippi). Through the sampling of harvested deer, I identified that the primary factor responsible for the antler size of an individual white-tailed deer in Iowa is age, with small, but statistically significant, influence from environmental factors. These environmental factors may partially explain regional differences in antler size across Iowa. The third component of this thesis was an analysis of spatial and temporal trends in the Iowa Department of Natural Resources' Iowa Trophy Deer record book that included entries from 1939–2017. While I did not identify any temporal trends within the records, negative latitudinal trends were observed within a category of the records. These trends are similar to the

regional differences in antler size from my contemporary sample. Although I observed some interesting trends from the record book data, biases associated with record books, such as their reliance on self-reporting by hunters, lack of age information for the submitted specimen, and focus on larger deer, may limit their usefulness for making inferences about a population.

Monitoring a more representative sample of a population may better serve managers looking to observe trends in antler attributes of a population. Overall, the environmental factors I identified influenced antler size of white-tailed deer in Iowa. However, antler size, when controlling for age, did not vary as greatly across the state compared to previous studies conducted outside of the Midwest. These findings suggest the Iowa landscape offers deer adequate nutritional resources for antler growth, such that age is the primary factor explaining antler size in Iowa white-tailed deer.

CHAPTER 1. GENERAL INTRODUCTION

White-tailed deer (*Odocoileus virginianus*) are a highly adaptable game species occurring across much of North America and into Central and South America. Because of this widespread distribution, white-tailed deer can be found in many different habitats occurring within those latitudes. Living in the diverse landscapes of forests, mountains, swamps, and areas of heavy agriculture results in phenotypic, and sometimes significant genotypic, variation throughout the white-tailed deer's range (Heffelfinger 2011). Deer are one of the most recognizable animals in North America due, in part, to antlers that occur within males of the population. The hunting of deer for food resources and their antlers, along with wildlife watching, allow deer to provide a large amount of economic revenue, resulting in the white-tailed deer being one of North America's most managed large game species.

Antlers are bone-like structures that protrude from the top of the skull. They are cast and reproduced each year based on testosterone levels (Lincoln 1992). Testosterone levels in white-tailed deer are regulated by the photoperiodic cycle (Goss 1969). Antler regeneration begins in early spring after the previous year's set is cast and testosterone levels are low (Lincoln 1992). Antler growth continues through late summer until testosterone levels begin to rise in preparation for mating season. At this point, the antler begins to calcify and the overlying, protective skin begins to die and fall off and that set of antlers will accompany the buck throughout the mating season until testosterone levels begin to wane in late winter (Lincoln 1992).

There has long been speculation as to why deer have antlers. The most widely accepted explanation for deer having antlers (Geist 1966, Clutton-Brock 1982) is that they are used during intraspecific male-male combat in establishing dominance for mating rights. Males lock antlers with each other, pushing and wrestling each other, to determine the stronger deer of the pair, thus

establishing dominance (Geist 1966, Clutton-Brock 1982). However, antlers may also be a phenotypic indicator of male quality, age, and condition (Andersson 1986, Ditchkoff et al. 2001, Kodric-Brown and Brown 1984, Kruuk et al. 2002, Malo et al. 2005, Vanpé et al. 2007), which may influence mate selection by females (Morina et al. 2018). Antlers seemingly serve as dual-purpose structures, weapons and ornaments.

Antler size and characteristics are highly variable among individuals and are a result of an individual's age, genetic background, and environment (Demarais 1998). White-tailed deer grow their first set of antlers after their first birthday, and antler size increases with age until approximately 5.5 years of age (Strickland and Demarais 2000, Monteith et al. 2009, Hewitt et al. 2014). Age, body size, and antler size are all positively correlated with one another until asymptotic body size is reached around 5.5 years of age (Strickland and Demarais 2000). Therefore, accurate age classification is important to managers using body or antler metrics as condition indicators for individuals and populations (Hamlin et al. 2000, Strickland and Demarais 2000). The two most-widely utilized techniques for aging deer are the tooth wear-and-replacement (TRW; Severinghaus 1949) and cementum annuli (CA; Low and Cowan 1963) methods.

The genetic influence on antlers is not well understood. It is understood that an individual's genetic makeup contains the information for potential size and conformation (Demarais & Strickland 2011). Multiple studies of white-tailed deer surveyed the heritability of antler traits of offspring from their sire with results ranging from little to no heritability (0.00-0.25) to many antler traits being very heritable (0.49-0.80) (Williams et al. 1994, Lukefahr and Jacobson 1998, Michel et al. 2016). Foley et al. (2012) investigated repeatability (the variance of growth of antler traits in unique individuals over time) of antler traits in eight different locations

in Texas and found that all traits were at least moderately repeatable (≥ 0.42), but that more variable environments (more variable rainfall and nutrition) decreased repeatability from year to year. It seems that there is still more research to be done on the influence of environmental conditions on the genetic expression of antler traits (Foley et al. 2012).

Beyond the genetic influence, nutrition has a positive relationship with antler growth and characteristics, as evidenced by studies showing differences in antler characteristics as a function of diet. Groups of deer that were fed a more nutritiously-optimal diet (16% protein content) grew larger antlers than other groups (<10% protein content) (French et al. 1956, Harmel et al. 1989). Antlers are physiologically costly to produce and dependent upon condition, as nutritional requirements for body maintenance and growth take precedence over antler growth, indicating only individuals with access to adequate nutrition and in good health can afford to allocate resources for maximum antler growth (French et al. 1956, Ullrey 1983, Andersson 1986, Foley et al. 2012). Therefore, environmental factors (e.g., land use, population densities, weather) that impact available nutritional resources can influence not only body size and condition, but antler size as well (Ashley et al. 1998, Strickland and Demarais 2008, Freeman et al. 2013). Further, environmental conditions experienced prenatally and after birth by mother and offspring can affect phenotype in the offspring and throughout its life (Mech et al. 1991, Monteith et al. 2009, Michel et al. 2016).

Antlers are of interest to biologists and managers as possible indicators of condition and health of individuals and populations (Kodric-Brown and Brown 1984, Andersson 1986) and to hunters due to their popularity in hunting culture (Knox 2011). The widespread interest in antlers has led to record-keeping of antler measurements with the most notable record book being the Boone and Crockett Club's *Records of North American Big Game*. The Boone and Crockett

Club, founded by Theodore Roosevelt and his friends in 1887, was created to promote conservation of North America's big game animals and later began collecting measurements from them to ensure information was available about these animals should they ever disappear (Wright and Nesbitt 2003). In 1950, the Boone and Crockett Club implemented what became the standard for measuring all of the big game species of North America, taking measurements of antlers, horns, or skulls (Wright and Nesbitt 2003). The scoring system takes measurements of lasting characteristics of the specimen, antlers in the case of deer. These measurements are used to arrive at a numerical score that can be ranked relative to other specimens (Wright and Nesbitt 2003).

Up until the 2016 hunting season, Iowa had held the Boone & Crockett Club's world record hunter-harvested non-typical white-tailed deer (Boone and Crockett Club 2017). That record was quite a feat for a state that had virtually extirpated deer from the landscape just over 100 years ago (Stone 2003). Populations of deer were reintroduced through planned releases as well as escapes from captive herds in the early 1900's, expanding across the state until hunting seasons were opened in 1953 (Stone 2003). Deer hunting, including the pursuit of trophy deer, now provides a great economic boost to the state. In 2011, deer hunting in Iowa, alone, generated over \$196 million in retail sales and \$21 million in state and local tax revenues, with both figures being approximately 45% of the total economic revenue generated by all hunting activities in Iowa, combined (Southwick Associates 2012). The economic value provided by deer hunting in Iowa makes understanding factors that influence white-tailed deer characteristics in Iowa a point of interest in order to continue effective management for future enjoyment and economic revenue.

Studies of white-tailed deer antler characteristics have not been conducted in Iowa. Therefore, the results and recommendations may not be directly applicable to Iowa deer because of differences in many attributes including land use, soil type, deer densities, and weather in Iowa compared to areas where other antler studies have taken place (e.g., Ashley et al. 1998, Strickland & Demarais 2008, Quebedeaux et al. 2019). Another reason for this study was antler size's relationship with condition. Since antler size is dependent upon an individual's condition, obtaining statewide antler metrics across Iowa may provide insight into the condition of the Iowa deer population (Kodric-Brown and Brown 1984, Andersson 1986). While I was unable to evaluate the influence of genetics on antler size, age and a multitude of environmental factors (i.e., land use, deer density, weather, etc.) were examined to identify factors affecting antler size in Iowa white-tailed deer.

The goals of this study were to, first, evaluate two aging methodologies for white-tailed deer and then, using information gathered from the evaluation of the two aging techniques, identify environmental factors associated with antler size in Iowa white-tailed deer. Lastly, I aimed to identify spatial and temporal trends in historical antler records. My objectives were to:

1. Identify and assess factors affecting precision of paired cementum annuli age estimates of white-tailed deer as well as evaluate congruence between cementum annuli and tooth replacement-and-wear age estimates (Chapter 2).
2. Quantify variation in antler size of white-tailed deer across the state of Iowa and identify factors associated with that variation (Chapter 3).
3. Assess both temporal and spatial trends in antler score of white-tailed deer within the Iowa Department of Natural Resources' Iowa Trophy Deer record book (Chapter 4).

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CHAPTER 2. PRECISION OF CEMENTUM ANNULI METHOD FOR AGING MALE WHITE-TAILED DEER (*Odocoileus virginianus*)

Modified from a manuscript to be submitted to Wildlife Society Bulletin

Abstract

The most common method used to estimate ages of harvested white-tailed deer (*Odocoileus virginianus*) and other cervids is a criterion based on tooth replacement-and-wear (TRW). Previous studies have shown this method is prone to considerable error because TRW is partially subjective. A presumably more accurate, but more labor intensive and expensive, method to estimate age involves the counting of cementum annuli (CA) of cross-sectioned incisors. Quantifying rate of error of the CA aging method is not possible without known-aged specimens, but precision of duplicate CA age estimates for two teeth may be related to accuracy if identical factors influence both CA accuracy and precision. The objective of this research was to identify and assess factors affecting precision of paired CA ages as well as evaluate congruence between TRW and CA age estimates. I obtained paired CA age estimates from 473 adult (≥ 1 year old), male white-tailed deer harvested in Iowa (USA; 2014–2018). Not all CA age estimates of paired incisors agreed with one another and probability of agreement between the paired CA ages decreased as the certainty level of the CA ages decreased and was dependent upon the batches in which they were aged by the laboratory. I also estimated the age of 1,292 adult, male deer using both TRW and CA methods and compared the congruence between the TRW and CA age estimates. Congruence rates of CA and TRW ages differed among age classes (80% congruence in yearling TRW age classification, 65% with 2-year-olds, 78% with ≥ 3 -year-olds). My results showed that CA aging is imperfect and that the certainty code is an important factor to consider with CA ages, as shown in previous research, as is the batch the teeth were aged in. I also confirmed previous studies' findings that CA and TRW ages for adult deer are not

always congruent, particularly in age classes other than the yearling age class. My results suggest managers are best served by using TRW to age adult deer as yearlings or ≥ 2 -years-old. If additional age classes are required, CA aging is likely to be a better tool than TRW as CA is likely more, but not perfectly, accurate.

Key Words age estimation, cementum annuli, Iowa, logistic regression, tooth replacement-and-wear, *Odocoileus virginianus*, white-tailed deer

Introduction

Estimating the age structure of a population is a key component of many wildlife management programs, as demographic parameters (e.g., survival and fecundity) that are important to population modeling are typically age-specific (Ditchkoff et al. 2001, Schroeder and Robb 2005, DelGiudice et al. 2007). Furthermore, age-specific prevalence rates of highly-transmissible diseases (e.g., chronic wasting disease) have been of recent concern (Edmunds et al. 2016, Samuel and Storm 2016). The age structure of harvested animals is typically used to reconstruct a population's age structure, especially in cervid populations (Williams et al. 2002, Millspaugh et al. 2009). Inaccurate estimates of a population's age structure could lead to potential downstream impacts on demographic and epidemiological models (Leberg et al. 1989, Millspaugh et al. 2009).

The most common method used to estimate age of white-tailed deer (*Odocoileus virginianus*) and other cervids is the tooth replacement-and-wear (TRW) criterion. Severinghaus (1949) developed the TRW aging criterion for white-tailed deer based on unique teeth arrangements at younger ages and the wear and degradation of the same premolars and molars of the lower jaw at older ages. TRW aging is popular among management agencies because it can be conducted quickly in the field at little to no cost (Storm et al. 2014). Previous studies have shown the TRW method is prone to considerable error because it is partially subjective,

especially at older age classes (Roseberry 1980, Jacobson and Reiner 1989, Hamlin et al. 2000, Gee et al. 2002, Storm et al. 2014). Error in the TRW method at older ages has led to recommendations to implement TRW aging categories for adult white-tailed deer that bin older age classes together: either suggesting the binning of all deer ≥ 2 years of age together (Roseberry 1980, McCaffery 2001, Gee et al. 2002, Meares et al. 2006, Storm et al. 2014) or differentiating deer 2 years of age from deer ≥ 3 years of age (Jacobson and Reiner 1989, Hamlin et al. 2000, Elliott and Edwards 2012), with both points-of-view suggesting an independent age class for deer 1 year of age (yearlings), since a unique tooth should almost unmistakably identify the age class (Severinghaus 1949).

A more labor-intensive and expensive, but more accurate, option for aging deer is cementum annuli (CA) aging, which involves the counting of annual rings, the CA, in the roots of cross-sectioned incisors. Seasonal rates of cementum deposition in the root tips that coincide with body growth produce alternating light and dark bands, with the dark bands representing the CA (Low and Cowan 1963, Gilbert 1966). The CA method has been established as a more accurate method than TRW through the comparison of known-age individuals, especially at northern latitudes (Sauer 1971, Roseberry 1980, Hamlin et al. 2000). While CA is more accurate than TRW, with the exception of a sample of 97 known-aged deer by McCaffery (2001) in Wisconsin that were aged 100% accurately by the CA method, error has been documented with CA aging in relation to known-age individuals with error rates ranging from 15–28% in northern latitudes (Sauer 1971, Roseberry 1980, Hamlin et al. 2000). While assessing error rates of CA age estimates in comparison to known-age individuals is the only method to identify the accuracy of CA aging for certain, obtaining known-age individuals is difficult outside of captive facilities and capture-recapture studies. In response to the challenges of obtaining actual

accuracy rates of CA aging, evaluating the precision between the CA age estimates of multiple incisors from the same deer is an option for samples from wild populations of unknown ages because if factors known to affect CA accuracy can also be shown to be related to the precision of CA aging, the measurement of precision can provide insight related to accuracy of the CA method (Storm et al. 2014). Few studies, however, have evaluated the precision of CA ages in white-tailed deer (Roseberry 1980, DeYoung 1989, Storm et al. 2014). While Roseberry (1980) and Storm et al. (2014) extracted paired incisors from individual deer after harvest, DeYoung (1989) extracted separate incisors one or two years apart from live deer. Precision of CA age estimates has also been examined in other cervids such as mule deer (*Odocoileus hemionus*; Asmus and Weckerly 2011) and moose (*Alces alces*; Boertje et al. 2015). Storm et al. (2014), along with Asmus and Weckerly (2011), have examined factors influencing the precision of paired CA ages. Factors included the sex of the individual, precipitation during the individual's life, the level of certainty assigned to the CA age estimates, as well as the age of the CA age estimates, themselves (Asmus and Weckerly 2011, Storm et al. 2014).

The first objective of this study was to evaluate the precision of the CA aging method of paired incisors from wild white-tailed deer in Iowa. I hypothesized that precision would decrease as the age of the CA age estimate increased, the level of certainty of the estimate decreased, and that precision would be dependent upon the batches in which the teeth were aged. My second objective was to evaluate factors influencing the level of certainty assigned to CA age estimates. I hypothesized that the level of certainty in the age estimates would decrease with age and be influenced by the batch in which the age estimates were aged. My third objective was to assess congruence between the age estimates from the CA and TRW methods. I hypothesized that congruence between the two aging methods would be greatest within the yearling age class

because the TRW criteria within that age class mostly relies on the presence or absence of a tooth rather than a subjective assessment of tooth wear.

Study Area

Iowa is located in the Midwestern U.S. between the approximate latitudes of 40.4–43.5 decimal degrees. Highly-fertile Mollisol soils cover much of Iowa (Griffith et al. 1994). Cultivated crops compose 72% of the landscape, with pasture and forested land composing the next-largest land use percentages at 9% and 7%, respectively (United States Department of Agriculture, 2015). The climate is humid continental, with hot summers ($\bar{x} = 22.0^{\circ}\text{C}$), cold winters ($\bar{x} = -5.5^{\circ}\text{C}$), and an average of 89.6 cm of annual precipitation (Kottek et al. 2006, H. Hillaker, Iowa Climatology Bureau, unpublished data).

Methods

Staff from the Iowa Department of Natural Resources (DNR), Iowa State University (ISU) technicians, and I extracted incisors as well as assigned ages, using the TRW method, to antlered, male deer that were harvested from 2014–2018 in Iowa. I submitted I1, and rarely I2, incisors to Matson’s Lab (Manhattan, MT) for age estimation, to the year of age, by the CA method. The I1 incisors are the standard teeth preferred to be aged by Matson’s Lab for ungulates but aging of I2 incisors is possible when the lab is made aware (Matson’s Lab, unpublished cementum annuli age report). Matson’s Lab assigned each age estimate a certainty code describing the lab’s certainty in the accuracy of the estimate ranging from highest (“A”) to lowest certainty (“C”). Certainty codes may be partly subjective because assignment of them to an age is based on the similarity of cementum characteristics of the individual tooth with the standardized model used by the lab (e.g., “A” certainty code indicates near identical matches between histological evidence of tooth and standardized model, “B” indicates close resemblance, “C” indicates a poor match; Matson’s Lab, unpublished cementum annuli age report). For a

subset of the deer aged, both I1 incisors were removed and submitted independently with unique identification numbers so Matson's Lab was unaware they were aging two teeth from the same deer. I submitted four batches of incisors to Matson's Lab in total (one after the 2016 deer hunting season, two after the 2017 season, one after the 2018 season) and the number of teeth per batch ranged from 297–582.

Most deer were harvested during deer hunting seasons in late autumn (Oct–Dec), with some harvest occurring in other deer hunting seasons in September and January. Deer were assigned ages using the TRW method in the field during the Iowa DNR's chronic wasting disease (CWD) surveillance and ISU's efforts at deer meat processors. Specimens were also obtained from taxidermists and were assigned ages in a laboratory setting, as taxidermists extracted and provided mandibles for sampling. Deer were assigned to one of three age classes: yearling (1 year of age), 2 years of age, ≥ 3 years of age. Deer were harvested approximately six months between birth days, so the age classes represented age at the time of their last birthday. According to Severinghaus' (1949) TRW aging criterion, yearlings were identified by the presence of a deciduous tricuspid P4 premolar or, if the tricuspid premolar had already been lost, the emergence of the permanent, bicuspid P4 premolar that was relatively unstained when compared to other cheek teeth. By 2 years of age, deer contain all permanent teeth and age classes are distinguished by the amount of tooth wear and degradation (e.g., exposed dentine increases with tooth degradation and age). Deer at 2 years of age were distinguished from older deer by the lack of exposed dentine and wear on the lingual crests of the M1 molar and by identifying a slope towards the lingual side of the jaw by the posterior cusp of the M3 molar. I assumed that rates of tooth replacement and wear were consistent in deer within the sample.

As indicated above, incisors were submitted for aging in several batches. Preliminary exploration of the data indicated lower congruence between TRW and CA age estimates of yearlings from the first batch of teeth sent to Matson's Lab compared to the second and third batch (i.e., batches for which I had paired ages; Table 1) and also lower than reported in the literature (e.g., Storm et al., 2014). Further, a higher percentage of paired CA ages agreed when a pair did not contain a tooth aged in the first batch than paired CA ages that did contain a tooth aged in the first batch. I suspected that there might be higher error in the CA age estimates in the first batch than in the second and third batches and that these preliminary findings were caused by human-associated (i.e., cementum laboratory employee examining teeth) error. Based on these preliminary findings, I used logistic regression to investigate the relationship between probability of agreement with models containing a two, three, or four-category batch letter coding system. To determine the impact of batch on probability of agreement between paired incisors I began by coding each pair of incisors with an identifying code indicating in what batch each tooth of the pair was aged. For example, if one tooth was aged in the first batch and the paired tooth was aged in the second batch, I assigned it code "1-2". The remaining letter codes included "2-3", "1-3", and "3-3". The fourth batch is not included in these classifications because none of the paired incisors were aged in that batch.

Similar to Storm et al. (2014), I also used logistic regression to assess the relationship between CA age estimate and batch code (based on the best model determined above) on the probability of at least one of the paired ages having a lower certainty code (i.e., not "A"). Age estimates with lower certainty codes of "B" or "C" were combined because of there were very few "C" code teeth in the dataset.

I used logistic regression to evaluate factors influencing the probability of agreement of paired CA ages (Storm et al. 2014). My predictor variables were CA age estimate, certainty code (“A” vs. not “A”), and batch code (based on the best model determined above). For all regression analyses described here, I used Akaike’s Information Criterion corrected for small sample size (AIC_c ; Burnham and Anderson 2002) to identify the best models. Models within 2 AIC_c of the highest-ranking model were considered to have equivalent support (Burnham and Anderson 2002). I also produced a cross-classification table illustrating probabilities of agreement between the paired CA age estimates. I estimated the probability of receiving a CA age estimate from a second aged incisor, given the age of the initial paired CA age estimate by assembling a cross-classification table of cell counts of each classification possibility, then dividing each cell count by the marginal total of the age class of the corresponding initial CA age estimate.

Lastly, I produced a cross-classification table of the probabilities of receiving a CA age estimate, given its corresponding TRW age estimate to assess congruence between the CA and TRW methods (Storm et al. 2014). Before estimating probabilities, I binned CA ages into age classes identical to the TRW age classes to produce a symmetric table. I estimated probabilities of receiving a CA age estimate, given its corresponding TRW age estimate by dividing cell counts by the marginal total of the corresponding TRW age class. In order to include deer that had paired ages in this analysis, I assigned the first CA age estimate received from Matson’s Lab as the CA age estimate based on the assumption that managers using the CA method to age deer will typically have only one incisor aged by a lab.

Results

I obtained TRW and CA age-estimates for 1,292 deer, including paired CA ages from 473 deer. The models evaluating the effect of the batches on agreement between the paired age data were all within 2 AIC_c units (Table 2). The model containing the two-category batch

variable differentiating between pairs that included an age from the first batch and pairs that did not was the top-ranked model (Table 2). The batch effect in this model, however, was not statistically significantly related to the probability of the paired CA age estimates being assigned the same age ($\beta_{\text{batch}} = 0.38$, $P = 0.11$, $\text{OR}_{\text{batch}} = 1.47$, 95% CI = 0.92–2.35). The only statistically significant effect in any of the three models was in the four-category model where batch code “2-3” significantly increased the probability of the paired CA age estimates being assigned the same age compared to batch letter code “1-2”. Since, according to AIC_c, the models were considered equal, I chose to use the simplest, two-category batch variable in subsequent analyses.

The number of paired ages that contained at least one tooth with a certainty code that was not “A” was 104 of 473 (22%). The highest-ranking model describing the probability of at least one tooth from a deer receiving a certainty code that was not “A” contained only an age effect, and the model containing both an age and batch effect was within 2 AIC_c units (Table 3). In the model containing only the age effect, the probability of at least one tooth receiving a certainty code that was not “A” increased with CA age ($\beta_{\text{age}} = 0.24$, $P = 0.004$, $\text{OR}_{\text{age}} = 1.27$, 95% CI = 1.08–1.49; Table 4). In the model containing both an age and batch effect, the probability of at least one tooth from a deer receiving a certainty code that was not “A” increased with CA age but was not statistically related to batch.

Of the 473 paired CA ages, most ($\approx 95\%$) were estimated in ages 1–4 and, as illustrated in the cross-classification table of the paired CA age estimates (Table 5), agreement between the first and second CA ages within those four age classes ranged from 77–89%. Eighty-nine of the 473 paired ages disagreed (19%) but of the 89 that disagreed, 95% differed by only one year (two pairs differed by two years, two by three years, and one pair by four years). The top-ranked model describing probability of agreement between the paired CA ages contained the CA age,

certainty code, and batch code terms, as well as an interaction between certainty code and batch. Two models were within 2 AIC_c units of the top model (Table 6). Both of these models contained an interaction between certainty code and batch code and one also had an interaction between certainty code and CA age. In the top-ranking model, probability of agreement was not statistically significantly related to age ($\beta_{\text{age}} = -0.16$, $P = 0.09$, $\text{OR}_{\text{age}} = 0.85$, 95% CI = 0.71–1.02), but was greater for high certainty teeth regardless of batch (Fig 1). Among high certainty teeth, agreement was statistically significantly greater for pairs in which neither of the paired ages were aged in the first batch sent to Matson’s Lab (Batch B) than for pairs in which one of the ages was aged in the first batch sent to Matson’s Lab (Batch A) ($\beta_{\text{cc*batch}} = -1.13$, $P = 0.04$; Fig 2). The interaction between certainty code and batch code was also statistically significant in the model containing an interaction between certainty code and CA age, which was not a significant interaction in that model.

The congruence between TRW and CA age estimates was greatest for yearlings and lowest for the 2-year-old age class (Table 7). For younger ages (i.e., 1 or 2 years of age), in the majority of instances of disagreement, the TRW age estimate was younger than the CA age estimate (Table 7).

Discussion

Precision of paired CA age estimates was influenced by an interaction between the level of certainty of the CA age estimate and the batches in which the CA age estimates were aged by Matson’s Lab. For high certainty teeth, specifically, the probability of agreement differed between batches. However, when at least one of the ages in a pair received a lower certainty code the batches the pairs were aged in was not important (Fig. 2). These results are consistent with findings of higher aging error rates for lower certainty teeth in a study of known-age deer (Roseberry 1980) as well as harvested deer (Asmus and Weckerly 2011, Storm et al. 2014). Our

results further suggest that certainty in the age estimate is a more important factor than batch on the probability that paired CA ages will agree. Therefore, managers receiving age estimates with certainty codes that are not “A” should consider having another incisor aged by CA or use the age cautiously, acknowledging a higher likelihood of error.

I was surprised that I failed to find a statistically significant association between CA age and CA precision. The mean effect of CA age that I observed ($OR_{age} = 0.85$) was nearly equal to that observed by Storm et al. ($OR_{age} = 0.87$; 2014). In Storm et al.’s (2014) analysis, their data contained paired CA age estimates from both males and females that exceeded 15 years of age, whereas my dataset was limited to male deer up to 8 years of age and $\approx 95\%$ of the deer were estimated in age classes 1–4. It is possible that my dataset did not span a wide enough age distribution or did not contain enough samples in the upper age classes to discern an effect of CA age on precision. While Hamlin et al. (2000) observed proportionally more errors occurring in older deer (≥ 5 years old; 12 samples) than in deer that were younger (< 5 years old; 62 samples), they were unable to detect an age effect on the accuracy of CA aging on known-aged white-tailed deer. Increased difficulty in aging older deer using CA has been noted due to annuli from older ages appearing very close together and less-distinguishable, apparently caused by a lessening in cementum production (Gilbert 1966, Lockard 1972). Incidence of these particular cementum characteristics possibly coincides with deer reaching asymptotic body size at 4–5 years of age (Goss 1983, Strickland and Demarais 2000), indicating peak maturity. Therefore, an effect of age on the probability of agreement between paired CA age estimates may only be apparent with deer of older ages, as CA become increasingly difficult to distinguish.

Matson’s Lab is the foremost histological lab specializing in cementum aging and has been used in many previous studies (Hackett et al. 1979, Roseberry 1980, DeYoung 1989,

Jacobson and Reiner 1989, Hamlin et al. 2000, Asmus and Weckerly 2011, Storm et al. 2014). According to Matson's Lab (2019), typical accuracy of the CA method for white-tailed deer is 80-85% but is higher in deer from northern populations that are not supplementally-fed, which encompasses deer in Iowa. Inconsistencies within the cementum, such as the occurrence of split, compound, or false annuli or the thinning of annuli at older ages can affect the accuracy of CA age estimates (Lockard 1972, Boertje et al. 2015) and may be related to the factors I explored in my study (e.g., age). The occurrence of these irregular structures is not consistent between paired incisors (Rice 1980) and likely affects the precision of CA estimates as well as accuracy.

Another factor influencing CA accuracy is human error, which can be related to the experience of the person counting the annuli or poorly-prepared incisor cross-sections (Rolandsen et al. 2008). The differences in precision related to different pairs of batches of incisors sent to Matson's Lab that I observed may be at least partially explained by human error. Matson's Lab was sold and moved to a new location in 2015 with mostly-new personnel, so the skill-level of observers may have improved from the first batch (aged in 2017) to the second and third batches (both aged in 2018). Other factors, such as age and certainty of a CA estimate, that have been shown to be related to the accuracy of CA aging (Roseberry 1980, Rolandsen et al. 2008, Boertje et al. 2015) have also been demonstrated to influence the precision in CA aging (Asmus and Weckerly 2011, Storm et al. 2014). The established impact of these factors on both accuracy and precision of the CA method has allowed researchers to draw inferences about CA accuracy from precision rates of paired CA ages (Asmus and Weckerly 2011, Storm et al. 2014).

Asmus and Weckerly (2011) attempted to quantify error rates of the CA method using the precision of paired CA ages. They argued that since most paired CA ages that disagreed differed by only one year, it was likely that only one of the CA age estimates was incorrect, so the error

rate of CA aging was half of the proportion of paired CA ages that disagreed (e.g., if 34% of paired CA ages disagreed, the error rate of CA was 17%; Asmus and Weckerly 2011). Following this methodology, since 19% of my paired CA ages disagreed, the observed error rate of CA aging would be 9.5%. Unfortunately, this approach could underestimate the error rate of CA aging when converting from precision of paired CA ages, as in some cases, neither age estimate may be accurate. Obtaining true accuracy rates of CA age estimates from the precision of paired age estimates alone is unlikely. Furthermore, Storm et al. (2014) highlighted that precision, as well as accuracy, may be age- and sex-specific, rendering a single measurement of error uninformative.

Because CA age estimates are not always accurate, it is not possible to definitively evaluate accuracy of the TRW method using CA aging though comparisons between the two methods can be useful to identify the age classes for which each method might be strongest. The rates of congruence I found between the TRW and CA aging methods in the different age classes were similar to recent findings for deer in Illinois and Wisconsin (Storm et al. 2014). I expected poorer congruence for older deer because, with the exception of yearlings, the TRW method is generally not as accurate classifying older deer (Jacobson and Reiner 1989, Hamlin et al. 2000, Gee et al. 2002). In addition, the low congruence in the 2-year-old age class may be related to the fact that the Iowa DNR uses a two-age classification system (yearling, ≥ 2 years of age) for adult deer during CWD surveillance (T. M. Harms, Iowa DNR, personal communication). As a result, Iowa DNR personnel may not have been as effective at distinguishing 2-year-olds from deer ≥ 3 years of age. The higher congruence of the ≥ 3 -year-old age class than the 2-year-old age class likely was a result of the binning of multiple age classes into one, allowing for obviously older deer to be placed in this broad age class more accurately. As expected, I observed a high

congruence between the two aging methods for the yearling age class likely because TRW is considered very accurate at that age as a unique, deciduous tooth or the partial eruption of the permanent tooth is expected to almost unmistakably identify yearlings (Severinghaus 1949). However, the congruence for yearlings was not perfect. The observed incongruence could have been caused by personnel erroneously aging yearlings with a newly-erupted permanent tooth in late fall/early winter as an older deer because of the identification of the permanent tooth. The incongruence between aging methods in the yearling age class was also perhaps due to error within the CA age estimates, as we observed non-perfect precision with CA aging in the former part of this research as well as congruence rates within the yearling age classes unexpectedly fluctuated among batches aged by Matson's Lab (Table 1). Studies that have examined the accuracy of the CA method for known-age yearlings have found some error in this age class. Using CA, 76% of a sample of 34 known-age white-tailed deer in Mississippi were aged correctly, whereas all 34 deer were aged correctly using TRW (Jacobson and Reiner 1989). Hamlin et al. (2000) had their only known-age yearling white-tailed deer in their sample aged incorrectly by CA (aged as 3-year-old with "B" certainty code) in Montana, although all seven of their yearling mule deer were aged correctly by CA.

Management Implications

Due to the potential for misclassifications at older age classes with the TRW, my results suggest that managers that want to age deer using the TRW method should use a two-age classification system (yearling, ≥ 2 years of age) because the subjectivity of estimating older ages based on TRW can lead to bias in a reconstructed age structure (DeYoung 1989, Hamlin et al. 2000, Gee et al. 2002, Storm et al. 2014). The two-age classification system serves managers in scenarios where fecundity and survival rates are assumed to only differ between yearlings and deer ≥ 2 -years-old (Chitwood et al. 2015). If more age classes are desired, managers should

utilize CA aging for deer ≥ 2 years of age. Managers should be aware that the level of certainty and batch of a CA age estimate influence the probability of agreement between paired CA ages, which are therefore also related to accuracy of CA age estimates. Options for dealing with lower certainty level CA age estimates include having another incisor from the individual deer aged, taking TRW age into consideration, or statistically-modeling the possibility of ± 1 -year-error in analyses as most errors have been demonstrated to be within one year of age.

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Tables and Figures

Table 1. *Probability of cementum annuli (CA) age estimate matching tooth replacement-and-wear (TRW) age estimate for TRW age classes of harvested male deer in Iowa, 2014–2018, based on different batches of incisors aged by CA by Matson’s Lab.*

	Estimated Age Class		
	1	2	≥3
Batch from Matson’s Lab			
1	0.74	0.72	0.83
2	0.89	0.54	0.78
3	0.85	0.57	0.79
4	0.77	0.68	0.76

Table 2. *Summary of three models for analysis of influence of batch coding of paired cementum annuli (CA) ages on probability of agreement between paired CA ages of male white-tailed deer in Iowa, 2014–2018. Models are ordered by ΔAIC_c .*

Model	ΔAIC_c^a
Prob. of Agreement ~ Two-Category Batch Variable ^b	0.00
Prob. of Agreement ~ Four-Category Batch Variable ^c	0.75
Prob. of Agreement ~ Three-Category Batch Variable ^d	1.01

^a $AIC_c = 452.96$

^bTwo categories: 1) Paired batches 1-2 & 1-3; 2) Paired batches 2-3 & 3-3

^cFour categories: 1) Paired batch 1-2; 2) Paired batch 1-3; 3) Paired batch 2-3; 4) Paired batch 3-3

^dThree categories: 1) Paired batches 1-2 & 1-3; 2) Paired batch 2-3; 3) Paired batch 3-3

Table 3. Summary of three models for analysis of influence of cementum annuli (CA) ages and batches in which the teeth were aged by Matson's Lab on probability that at least one of the paired CA ages of male white-tailed deer in Iowa, 2014–2018, would receive a certainty code from Matson's Lab other than "A". Models are ordered by ΔAIC_c .

Model ^a	ΔAIC_c^a
Prob. of Certainty ~ CA Age	0.00
Prob. of Certainty ~ CA Age + Batch	1.17
Prob. of Certainty ~ Batch	7.03

^a $AIC_c = 494.22$

Table 4. Frequency of certainty codes assigned to cementum annuli (CA) ages by Matson's Lab for CA ages of individual incisors of male white-tailed deer in Iowa, 2014–2018.

Estimated Age	Certainty Code ^a		
	A	B	C
0	1	1	0
1	476	44	0
2	522	60	0
3	337	54	1
4	130	32	0
5	49	9	1
6	31	7	0
7	5	2	0
8	6	1	0
9	2	0	0
Total	1559	210	2

^aCertainty codes by Matson's Lab: "A" age estimates indicate high confidence in the estimate and that cementum characteristics closely match those of standardized CA model; "B" age estimates are supported by cementum characteristics, although error is possible; "C" age estimates indicate that cementum characteristics do not match those of standardized CA model and that error is probable.

Table 5. Probability of a cementum annuli (CA) age class for a second aged incisor, given the first CA age class from the initial incisor from the same individual for harvested male deer in Iowa, 2014–2018. Cell values in bold indicate agreement of classifications between the paired CA ages. Sample size (N) indicates number of individuals placed within each CA age class from the incisor aged initially.

First CA Age Class	Second CA Age Class									N
	0	1	2	3	4	5	6	7	8	
1	0.01	0.89	0.09	0.00	0.01	0.00	0.00	0.00	0.00	121
2	0.00	0.15	0.77	0.07	0.01	0.00	0.01	0.00	0.00	163
3	0.00	0.00	0.08	0.86	0.06	0.00	0.00	0.00	0.00	119
4	0.00	0.02	0.00	0.11	0.78	0.09	0.00	0.00	0.00	46
5	0.00	0.00	0.00	0.00	0.20	0.70	0.10	0.00	0.00	10
6	0.00	0.00	0.00	0.00	0.00	0.50	0.50	0.00	0.00	8
7	0.00	0.00	0.00	0.00	0.00	0.33	0.33	0.33	0.00	3
8	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00	3

Table 6. Summary of nine models for analysis of influence of *cementum annuli* (CA) ages, certainty code (CC), and batches in which the teeth were aged by Matson's Lab on probability of agreement between paired CA ages of male white-tailed deer in Iowa, 2014–2018. Models are ordered by ΔAIC_c .

Model ^a	ΔAIC_c^b
Prob. of Agreement ~ CA Age + CC*Batch	0.00
Prob. of Agreement ~ CC*Batch + CA Age*CC	0.50
Prob. of Agreement ~ CC*Batch	0.81
Prob. of Agreement ~ CC + Batch	2.44
Prob. of Agreement ~ CA Age + CC + Batch	2.45
Prob. of Agreement ~ Batch + CA Age*CC	3.02
Prob. of Agreement ~ Batch*CA Age*CC	3.56
Prob. of Agreement ~ CA Age + CC	4.60
Prob. of Agreement ~ CA Age + Batch	39.32

^aIf interactive effect is included in model, it is assumed additive effects of interaction are included as well.

^b $AIC_c = 410.14$

Table 7. Probability of *cementum annuli* (CA) age class, given the tooth replacement-and-wear (TRW) age class for harvested male deer in Iowa, 2014–2018. For deer where paired ages were available, the initial CA age was included. Cell values in bold indicate agreement of classifications between the CA and TRW methods. Sample size (N) indicates number of individuals placed within each TRW age class.

TRW Age Class	CA Age Class				N
	0	1	2	≥ 3	
1	<0.01	0.80	0.18	0.02	422
2	0.00	0.11	0.65	0.24	403
≥ 3	0.00	0.01	0.21	0.78	467

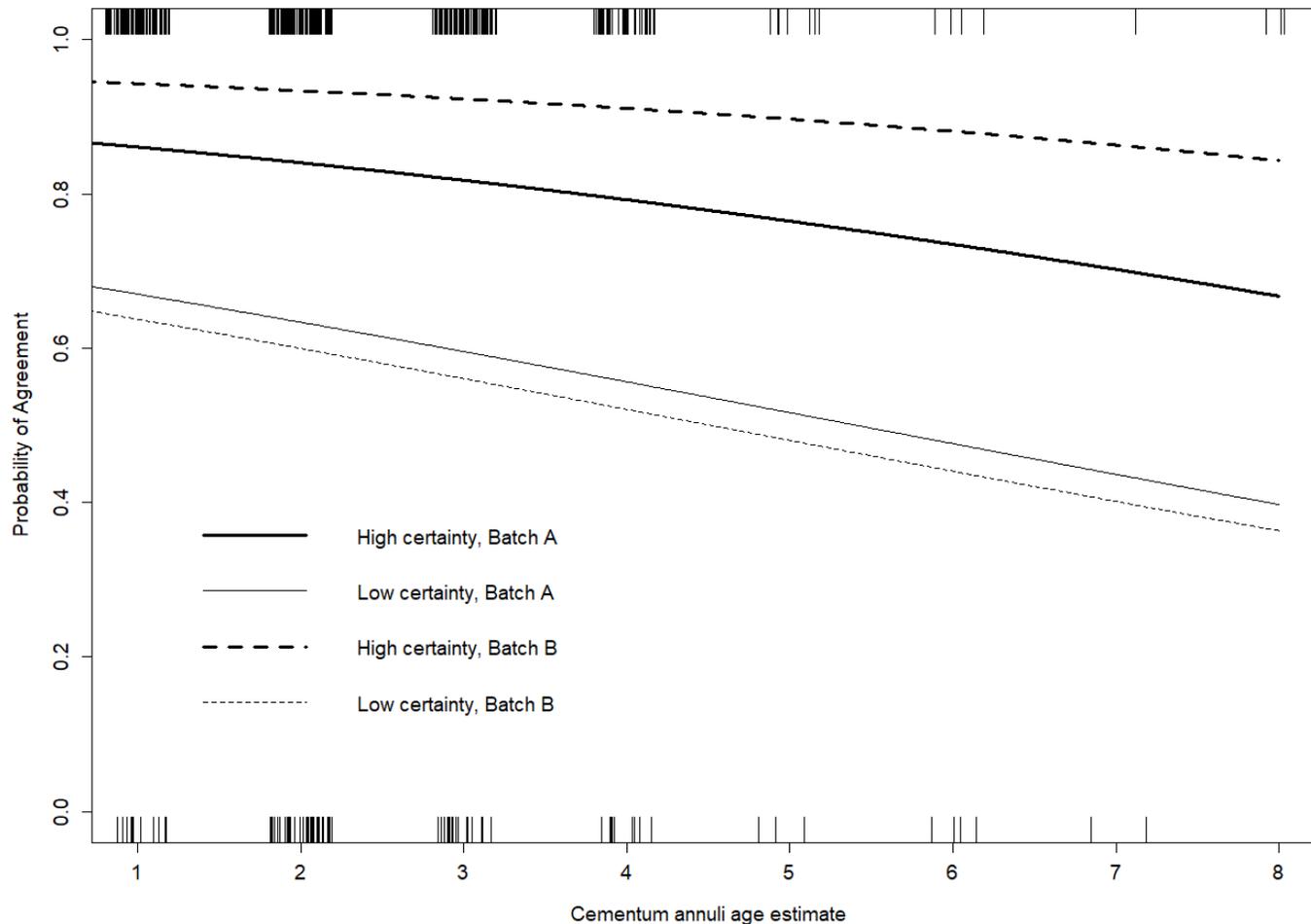


Figure 1. *Predicted probability of agreement of paired cementum annuli (CA) age estimates of male white-tailed deer in Iowa, 2014–2018, explained by CA age, certainty code (CC) of the age estimates, and the batch in which the paired incisors were aged. “High certainty” denotes paired incisors that both received a CC of “A” and “low certainty” denotes paired incisors in which at least one age received a CC that was not “A”. “Batch A” denotes paired incisors where one of the age estimates was received from the first batch of incisors aged by Matson’s Lab within my dataset and “batch B” denotes paired incisors where neither of the age estimates were from the first batch from Matson’s Lab. Hash marks on the x-axes illustrate sample size of paired ages that agreed (top) and disagreed (bottom). Plot adapted from Storm et al. (2014).*

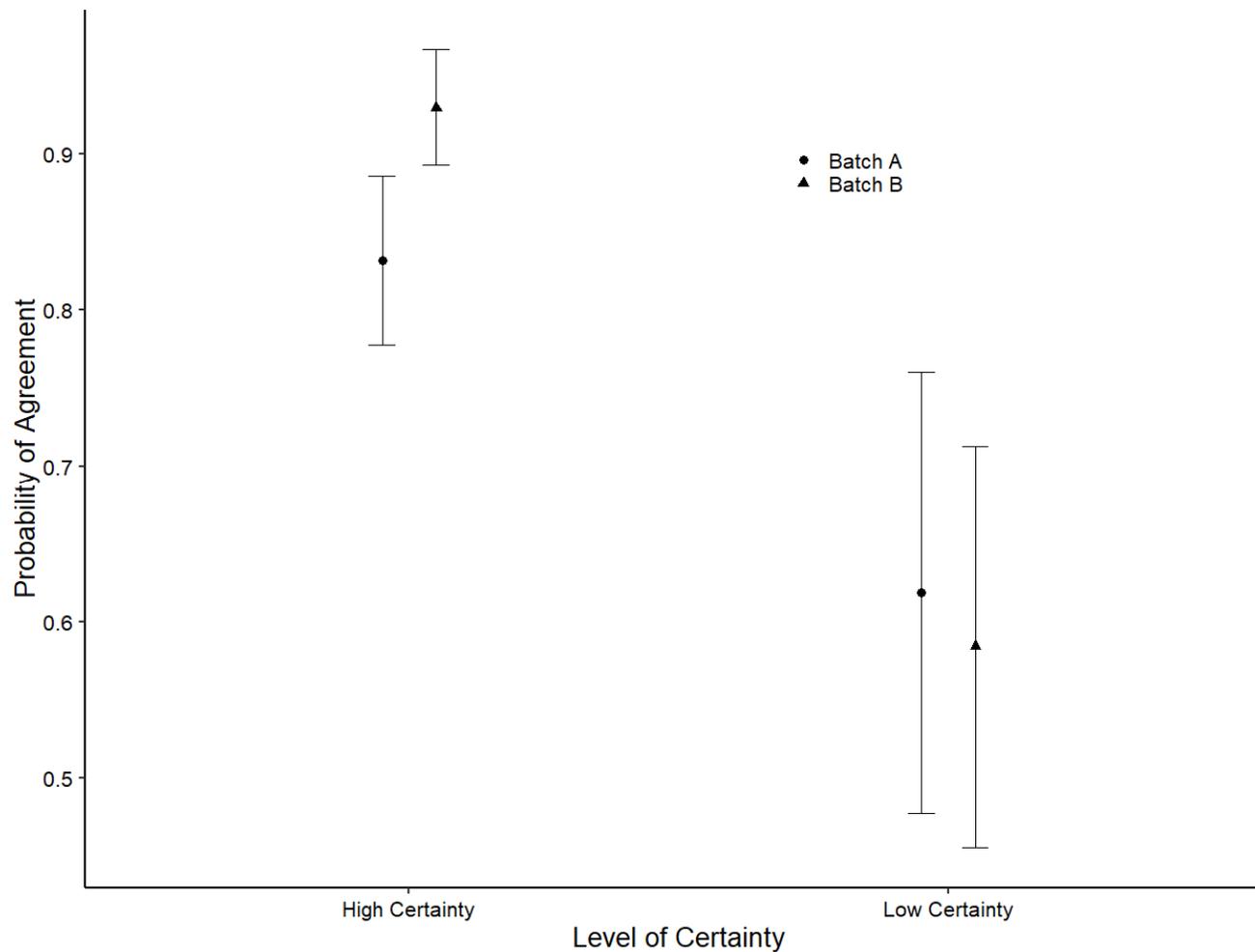


Figure 2. *Interaction plot depicting probability of agreement of paired cementum annuli (CA) age estimates of male white-tailed deer in Iowa, 2014–2018, explained by certainty code (CC) of the age estimates and the batch in which the paired incisors were aged. “High certainty” denotes paired incisors that both received a CC of “A” and “low certainty” denotes paired incisors in which at least one age received a CC that was not “A”. “Batch A” denotes paired incisors where one of the age estimates was received from the first batch of incisors aged by Matson’s Lab within my dataset and “batch B” denotes paired incisors where neither of the age estimates were from the first batch from Matson’s Lab. Error bars depict 95% confidence intervals.*

CHAPTER 3. ENVIRONMENTAL FACTORS INFLUENCING WHITE-TAILED DEER (*Odocoileus virginianus*) ANTLER SIZE IN AN AGRICULTURE-DOMINATED LANDSCAPE

Modified from a manuscript to be submitted to The Journal of Wildlife Management

Abstract

Identifying the influence of environmental factors on white-tailed deer antler size is of interest to biologists using antler size as an indicator of condition. Previous work evaluating the relationships between environmental factors and white-tailed deer antler size have occurred in locations much different from the Midwestern U.S., where nutritional resources for white-tailed deer are not typically considered limited due to the prevalence of row-crop agriculture on the landscape. My objectives were to 1) model the influence of age and environmental factors, including landscape composition, deer densities, and weather, and 2) to identify regional differences in antler size of 1,575 white-tailed deer harvested in Iowa. I hypothesized that, due to the dominance of row-crop agriculture across Iowa, I would be unable to detect significant influences from environmental factors and that age (determined through cementum annuli and/or tooth replacement-and-wear) would be the primary factor responsible for variation in antler size. As expected, age explained the greatest amount of variation in antler size in my models. In addition, I identified several environmental factors that were statistically significantly associated with antler size. Specifically, antler size was positively and negatively associated with agriculture and forested areas, respectively, consistent with previous research indicating forested areas offer comparatively less forage than row-crop agriculture. I also documented significant associations between antler size and weather conditions during the birth year of the animal, suggesting an influence of maternal condition. Specifically, winter severity while *in utero* had a negative effect on antler size while the average summer temperature had a positive effect. The

effect sizes of these environmental factors, however, were small compared to age and their addition did little to improve the fit of the models. When controlling for age, I did observe some regional differences across the state of Iowa, perhaps partially explained by the environmental factors I identified. Overall, while I identified significant variation in antler size associated with environmental factors, age was the primary factor explaining variation in antler size of harvested white-tailed deer across Iowa. Managers and hunters across Iowa should expect that the primary factor responsible for the antler size of an individual deer will be the age of the animal.

Key Words age, agriculture, antlers, Iowa, land use, *Odocoileus virginianus*, weather, white-tailed deer

Introduction

Antler size of an individual cervid is a product of three main determinants: its age, where antler size increases with age to coincide with body growth (Goss 1983); its genetic background, which contains the potential for antler size and shape (Demarais and Strickland 2011); and its environment, where the necessary nutrition for growth is obtained (Ullrey 1983). Antlers are physiologically costly to produce and dependent upon condition, as nutritional requirements for body maintenance and growth take precedence over antler growth, indicating only individuals with access to adequate nutrition and in good health can afford to allocate resources for maximum antler growth (French et al. 1956, Ullrey 1983, Andersson 1986, Foley et al. 2012). Therefore, environmental factors (e.g., land use, population densities, weather) that impact available nutritional resources can influence antler size (Ashley et al. 1998, Strickland and Demarais 2008, Freeman et al. 2013) and provide evidence related to the health of individuals and populations (Kodric-Brown and Brown 1984, Andersson 1986). In regions where row-crop agriculture is abundant, such as the Midwestern U.S. (hereafter, Midwest), identifying environmental factors that are affecting antler size may be of interest to biologists, managers, and

hunters, alike, attempting to obtain a measure of condition and health of deer. Quality nutritional resources for white-tailed deer (*Odocoileus virginianus*) are considered nearly unlimited in the Midwest due to the abundance of row-crop agriculture that comprises much of white-tailed deer diets in the region (Nixon et al. 1991).

The type and amount of forage (i.e., nutrition) available can influence antler size (Brown 1990). For example, the amount of agricultural area on the landscape has been shown to have a positive effect on white-tailed deer antler size, while forested areas have been documented as negatively related (Strickland and Demarais 2008, Jones et al. 2019, Quebedeaux et al. 2019). Along with the types of land use classes available, the configuration of these land use classes on the landscape may also affect available nutrition as heterogeneous landscapes may provide additional forage along habitat edges and may influence home range shape and size (Kie et al. 2002, Miyashita et al. 2007). The length of forest edge was shown to have a positive relationship with fecal nitrogen levels, an indicator of forage quality, in sika deer (*Cervus nippon*), perhaps explained by the increased availability of forbs and understory vegetation at habitat edges (Miyashita et al. 2007). However, edge density was not related to white-tailed deer antler size in other studies (Strickland and Demarais 2008, Quebedeaux et al. 2019). Soil productivity, or the capacity of a soil to produce plant biomass based off a soil's chemical, physical, and biological properties (Karlen 2005), has also been shown to have a positive relationship with antler size in white-tailed deer in Mississippi (Jacobson 1984). Although, the effects of soil productivity may be confounded with the associated land use and deer density impacts on available forage (Jones et al. 2010, Lashley et al. 2015). With respect to density, a negative relationship between population densities and antler size of white-tailed deer has been documented previously (Ashley et al. 1998, Miranda and Porter 2003, Keyser et al. 2005). This effect may be a result of

competition for resources whereby higher densities of deer on the landscape equates to a decrease in available forage per capita (Ashley et al. 1998).

Because antlers are cast and regrown annually, they can be affected by annual variation of environmental conditions, specifically weather (Mysterud et al. 2005). Although an effect of winter severity on antler size has not been previously documented in white-tailed deer, negative effects of winter severity on other phenotypic characteristics known to be correlated with antler size (i.e., body size; Goss 1983, Strickland & Demarais 2000) have been observed (DelGuidice et al. 2002, Garroway and Broders 2005). Deer at northern latitudes must endure the cold temperatures and accumulation of snow during winter. Thermoregulation needed to mitigate the cold temperatures as well as a decrease in available forage and increased energy expenditure caused by deep snows create a drain on energy reserves during winter months (Verme 1968). Male deer exiting winter in poor condition may be at a disadvantage when it comes to growth of the proceeding year's set of antlers, as they may allocate nutritional resources away from antler size in favor of body maintenance and growth (French et al. 1956). In addition, extreme weather (i.e., increased temperatures, lack of precipitation) in summer months, during antler growth, has been shown to affect nutritional quality of deer forage through accelerated plant senescence (Marshall et al. 2005, Lashley and Harper 2012). Attributing their findings to a decline in nutritional quality due to plant senescence, negative relationships between summer temperature and antler size have been documented in numerous cervids (Schmidt et al. 2001, Weladji et al. 2005, Thalmann et al. 2015). Conversely, warmer summer temperatures were documented to have a positive relationship with elk (*Cervus Canadensis*) and mule deer (*Odocoileus hemionus*) by Freeman et al. (2013). Higher amounts of summer precipitation had a positive effect on antler

size of red deer (*Cervus elaphus*; Kruuk et al. 2002) and caribou (*Rangifer tarandus*; Weladji et al. 2005).

Although cast and regrown annually, antlers of mature deer can be influenced by the condition of a male's mother while the male was *in utero* or while dependent upon its mother as a fawn, known as maternal effects (Bernardo 1996, Monteith et al. 2009). Environmental conditions experienced prenatally and after birth by mother and offspring have been shown to be associated with cohort-specific differences in offspring birth mass, body growth, expected survival, as well as antler size later in life in white-tailed deer and other cervids (Mech et al. 1991, Ginnett and Young 2000, Schmidt et al. 2001, Monteith et al. 2009, Campbell and Wood 2013, Freeman et al. 2013, Duquette et al. 2014, Hurley et al. 2017, Warbington et al. 2017, Michel et al. 2018). Mech et al. (1991) observed negative relationships between the birth mass of white-tailed deer fawns and the severity of winter experienced by the mother while the fawn was *in utero* as well as the grandmother while the mother was *in utero* in northeastern Minnesota. A negative effect on white-tailed deer fawn birth weight associated with winter severity was also documented in Michigan (Duquette et al. 2014). Schultz and Johnson (1995) demonstrated a positive relationship between birth mass and adult body mass of white-tailed deer and further, Schmidt et al. (2001) also found that antler size increased with birth mass in red deer. Freeman et al. (2013) found a negative correlation between the winter severity while male mule deer and elk were *in utero* to antler size later in life and observed summer temperatures the year of birth positively affected antler size. Michel et al. (2018) observed a positive relationship between temperatures and precipitation in June with survival of white-tailed deer fawns in the upper Midwest. The authors suggested that warmer temperatures do not induce the stress of thermoregulation that cold temperatures do and the increased precipitation provides the mother

with adequate amounts of quality forage to meet lactation requirements. A positive relationship between warmer temperatures and daily survival was also observed in Wisconsin (Warbington et al. 2017). Although, Warbington et al. (2017) also found a negative relationship between precipitation and daily survival of fawns, arguing that while the precipitation may provide an enhancement to forage for the mother, the effect is operating under a lag between the rainfall and a response from the vegetation, so the immediate effects of colder conditions endured by the fawn may decrease survival. An increase in summer precipitation was shown to promote heavier fawns heading into the winter in Virginia however (Campbell and Wood 2013). An interaction may exist between summer temperatures and precipitation such that when both temperature and precipitation are higher, conditions favoring both fawn and mother are created (Michel et al. 2018). Weather conditions favoring forage availability for the mother seem to be very important for the survival and growth of the fawn and the effects, related to maternal condition, passed on to the fawn may have life-long implications on phenotype (Bernardo 1996, Monteith et al. 2009).

Identifying associations between antler size and environmental conditions in white-tailed deer in the Midwest is of interest for several reasons. First, previous research examining the relationships between white-tailed deer antler size and environmental factors has mostly been conducted in the Southeastern U.S. (Jacobson 1984, Keyser et al. 2005, Strickland and Demarais 2008, Jones et al. 2019, Quebedeaux et al. 2019), so conclusions drawn from their research may not be directly applicable to the Midwest, specifically Iowa. Iowa contains more agricultural lands and less forested area than the Southeastern U.S. (Bigelow and Borchers 2017). Iowa also experiences colder average temperatures and lower amounts of annual precipitation than the Southeastern U.S. does (Kunkel et al 2013a). Therefore, the effects of environmental factors related to antler size in Iowa and the Midwest may vary from the effects previously observed in

the Southeastern U.S. Further, identifying weather-based effects on antler size may provide insight into future phenotype reaction to a changing climate in the Midwest (Kunkel et al. 2013*b*, Weiskopf et al. 2019). Lastly, since antler size is dependent upon an individual's condition, obtaining statewide antler metrics across Iowa can provide insight into the condition of the Iowa deer population (Kodric-Brown and Brown 1984, Andersson 1986).

The objective of my study was to investigate and identify associations between environmental factors, such as landscape composition and configuration, deer density, and weather, and antler size in white-tailed deer in Iowa. I hypothesized that, due to the predominance of row-crop agriculture in Iowa that provides an abundance of quality nutrition, age would be the primary factor explaining variation in observed antler size with no significant effects from environmental factors. Although, if significant effects of environmental factors on antler size were detected, I hypothesized that effects would be consistent with those previously observed. For summer temperatures during antler growth and summer precipitation the year of birth, where conflicting evidence among studies on their effects existed, I hypothesized that warmer summer temperatures would have a negative effect on antler size and summer precipitation the year of birth would have a positive effect on antler size. A secondary objective was to quantify statewide variation in antler size across two different geographic scales based on geologic histories (landform regions; Prior, 1991) and on the structure of deer management within the Iowa Department of Natural Resources (Iowa DNR; Wildlife Management Districts) that may be of interest to hunters and wildlife managers. I hypothesized that, when accounting for age, there would be no regional differences in antler size across the state of Iowa.

Study Area

Iowa is located in the Midwestern U.S. between the approximate latitudes of 40.4–43.5 decimal degrees with elevations ranging between 146–509 meters above sea level (Prior 1991).

Highly-fertile Mollisol soils cover much of Iowa (Griffith et al. 1994), which partly explain the high density of cultivated crops found across the landscape. Cultivated crops composed 72% of the landscape, while pasture/grassland and forested land composed the next-largest land use percentages at 9% and 7%, respectively (U.S. Department of Agriculture 2015). The climate was humid continental, with hot summers ($\bar{x} = 22.0^{\circ}\text{C}$), cold winters ($\bar{x} = -5.5^{\circ}\text{C}$), and an average of 89.6 cm of annual precipitation (Kottek et al. 2006, H. Hillaker, Iowa Climatology Bureau, unpublished data).

The Iowa DNR divides Iowa into five Wildlife Management Districts (WMD), roughly dividing the state into northeastern, southeastern, southwestern, northwestern, and central zones (Fig. 1). The WMDs are delineated along county line boundaries for deer management purposes (e.g., harvest quotas, allotment of antlerless tags, etc.). WMDs also resemble conglomerates of the former deer management zones that were phased out in favor of county deer management in 1992 (Stone 2003).

Iowa can also be represented by eight physiographic regions demarcated based on appearance and the geologic makeup of the landscape. These physiographic regions are referred to as landform regions (Fig. 2; Prior 1991). Some of these landform regions are associated with historical glacial extents and are reflected in the topography (Prior 1991). Previous studies in other states have observed differences in antler size of white-tailed deer across physiographic regions (Gill 1956, Strickland and Demarais 2000, Quebedeaux et al. 2019).

Deer management goals in Iowa are achieved almost exclusively through hunter harvest. With low predator densities and little or no winter mortality, hunting is the main source of mortality of white-tailed deer in Iowa (Harms 2018). Annual harvest has remained consistent

since 2013 with most local populations either stable or slightly increasing (Harms 2018). The Iowa DNR does not employ antler point restrictions.

Methods

Staff from the Iowa DNR, Iowa State University (ISU) technicians, and I sampled harvested white-tailed deer from 2015–2018 in Iowa. A few (< 10) deer harvested before 2015 were also sampled from hunters who had aging information available (i.e., still possessed lower jaw of the deer or had previously had cementum annuli aging conducted). Data collected were harvest date, location of harvest (see below), estimated age based on the tooth replacement-and-wear method (TRW; 1.5, 2.5, \geq 3.5 years of age; Severinghaus 1949, Hamlin et al. 2000), one or both I1 incisors for cementum annuli (CA) aging (Low and Cowan 1963), and various antler measurements (main beam length, basal circumference, number of typical and non-typical points \geq 2.54 cm). Antler measurements were taken with a flexible tailor's tape to the nearest 0.32 cm. To represent antler size in my analyses, I used a model produced by Strickland et al. (2013) to predict gross, non-typical Boone and Crockett (B&C) score from the collected antler metrics, as B&C score is correlated to antler mass, a more accurate measure of antler size (Strickland et al. 2013). While the model by Strickland et al. (2013) was not developed using deer 1.5 years of age or deer with smaller antlers (i.e., spike- or fork-antlered), the model has been used previously to estimate B&C score of yearling deer (Cohen et al. 2016). Deer that did not have all required antler measurements were censored from the dataset. For 80% of deer, one or two incisors were submitted to Matson's Lab (Manhattan, MT) for age estimation by the CA method.

Most samples were obtained from across the state in conjunction with the Iowa DNR's chronic wasting disease (CWD) surveillance program (e.g., hunter-harvested, roadkill, targeted for disease testing). Sample collection involving ISU technicians and me was conducted mainly at deer processors (11 total across three years in Bremer, Calhoun, Cedar, Clayton, Muscatine,

Palo Alto, Sioux, Story, Union, and Warren counties) during the shotgun seasons (first three weeks in December), at taxidermists (6 total across three years in Henry, Montgomery, Sac, Warren, and Woodbury counties), and opportunistically when hunters contacted me. Most animals were sampled shortly after harvest except for samples from taxidermists. I worked with taxidermists to recruit samples from hunters submitting their deer for taxidermy. Hunters electing to participate provided the location of harvest and allowed me to measure the antlers and collect the lower jaw (including incisors) for TRW and CA aging.

Location of harvest was recorded as the section the deer was harvested in (typically ≈ 2.6 km²). The section the deer was harvested in and the surrounding eight sections (SOH; typically ≈ 23.3 km²) were used to quantify examine landscape composition, configuration, and soil productivity metrics associated with each individual deer. This scale was chosen because an individual deer's summer home range may not have been in the section it was harvested due to seasonal movements caused by rutting activity or crop harvest (M. E. Nelson and Mech 1981, Nixon et al. 1991, VerCauteren and Hygnstrom 1998, Brinkman et al. 2005), and to mitigate possible uncertainty of locations provided by hunters who were unsure of the exact location of harvest.

I used ArcMap 10.4.1 (ESRI, Redlands, CA, USA) and the Iowa DNR's 2009 3-m High Resolution Land Cover dataset (Iowa DNR, <https://geodata.iowa.gov/dataset/high-resolution-land-cover-iowa-2009>) to quantify the percent land area within a deer's SOH composed of agriculture, grassland, and forest. Using FRAGSTATS (ver. 4.2; McGarigal et al. 2012), I calculated three landscape configuration metrics: edge-density, interspersion-juxtaposition index (IJI), and Shannon's diversity index (McGarigal 2015). Also within the SOH, I calculated the weighted-average (by area) of Corn Suitability Rating 2 (CSR2) values using the Iowa Soil

Survey Geographic database (U.S. Department of Agriculture, <https://geodata.iowa.gov/dataset/soils-iowa>) as a means of representing soil productivity. The CSR2 rating system was developed to rate soils in Iowa based on corn productivity and is the most detailed soil productivity metric available in Iowa (Fenton et al. 1971, Burras et al. 2015). CSR2 values are assigned to soil mapping units, areas classified by soil components and location on the landscape (Soil Science Division Staff 2017). For deer for which I did not have SOH information but township of harvest was recorded, I calculated these same metrics at the township scale (typically $\approx 93.2 \text{ km}^2$). I considered this justifiable, rather than censoring these animals from the dataset, because each of the three land use categories (i.e., agriculture, grassland, forest) within my sampled sections were highly correlated with the land use of the township they were in ($r \geq 0.71$).

I used reported antlered deer harvest densities per county from the Iowa DNR's annual Trends in Iowa Wildlife Populations and Harvest reports (Harms 2018) as a surrogate for deer density. Antlered deer densities served as reliable estimates of annual deer abundance at the county-level for Snow et al. (2018) across multiple states in the Midwest.

I obtained weather metrics for months preceding and during antler growth the year the deer was harvested as well as weather metrics from the year the deer was born, based on its assigned age, given its CA and/or TRW age estimates. Because the year of birth (YOB) was estimated based on estimated age, this may have been a source of error in the YOB covariates. One aspect of weather I chose to investigate was winter severity and to do that I used the Accumulated Winter Season Severity Index (AWSSI; Mayes Boustead et al. 2015). AWSSI is calculated from commonly available weather metrics (e.g., maximum/minimum temperature, snowfall, and snow depth) to depict daily scores of winter severity that accumulate throughout

the winter season. AWSSI includes separate temperature and snow components that culminate into a single winter severity metric. AWSSI data were obtained from 18 weather stations across the state of Iowa (Fig. 1; S. D. Hilberg, Midwestern Regional Climate Center, unpublished data). Since there were so few weather stations with winter weather data available across the state, I calculated average annual AWSSI scores across Iowa's nine Climate Divisions (CD) delineated by the National Oceanic and Atmospheric Administration. The number of counties and weather stations per CD ranged from 9–12 and 1–3, respectively. My weather metrics included the Snow Score of the Accumulated Winter Season Severity Index (AWSSI; Mayes Boustead et al. 2015). Because I suspected the snow component of AWSSI would be more related to antler size than the temperature component (DelGuidice et al. 2002, Garroway and Broders 2005), I tested, using simple linear regression, the relationships of the temperature component of AWSSI, snow component of AWSSI, and the composite snow/temperature AWSSI metric to antler size. Preliminary evaluation of the data indicated the snow component of AWSSI (AWSSI Snow Score) had a stronger effect than the temperature and composite snow/temperature components, so AWSSI Snow Score was used as the metric to represent winter severity for the winters preceding birth and harvest. DelGuidice et al. (2002) as well as Garroway and Broders (2005) both also found a stronger effect of snow depth than temperature when examining the effects of winter severity on deer survival in Minnesota and on body condition on deer in Nova Scotia, Canada, respectively. My other weather metrics represented summer temperature and precipitation. I obtained data for the centroid of each county from the Parameter-elevation Regressions on Independent Slopes Model (PRISM) Climate Group (PRISM Climate Group, <http://www.prism.oregonstate.edu>). PRISM is a climate analysis system that uses point climate data from local weather stations, a digital elevation model, and other spatial data to produce

gridded weather estimates (Daly et al. 2000). For YOB, I assigned the average temperature and total precipitation for the summer (May-August) the fawn was born based on the county of harvest. Mean parturition date of white-tailed deer in Iowa is the end of May (Huegel et al. 1985, McGovern 2018). For the year of harvest (YOH), I assigned the average temperature and total precipitation of the summer (May–July) preceding harvest. The month of August was not included because while most velvet shedding in the Midwest occurs in late August/early September, antler growth is mostly complete by the end of July with antlers beginning to calcify in early August (Hawkins et al. 1968, Schmitz and Jenks 2001, Demarais and Strickland 2011).

Using Program R (R Core Team 2018), I developed linear regression models to examine the effects of 14 environmental variables on antler size (i.e., estimated B&C score) of Iowa deer, while accounting for age (Table 1). I needed to control for age in the analyses because antler size increases with age (Goss 1983, Strickland and Demarais 2000, Monteith et al. 2009, Hewitt et al. 2014). I scaled all environmental variables to allow comparison of effect size among variables by subtracting the mean and dividing by the standard deviation of each variable vector. Because several of my variables were correlated, I could not include them in the same model. Therefore, all combinations of possible models that included up to three environmental variables were created, excluding models where at least one pair of explanatory variables were highly correlated ($r \geq 0.4$). Models were limited to a maximum of three to reduce the likelihood of inclusion of insignificant parameters and avoid difficulty of parameterization (Jackson et al. 2000). I used Akaike's Information Criterion corrected for small sample size (AIC_c ; Burnham and Anderson 2002) to identify the best models. Models within 2 AIC_c of the highest-ranking model were considered to have equivalent support (Burnham and Anderson 2002). Modeling and model selection were performed on two datasets. One dataset included deer for which I was extremely

confident of their ages. This dataset consisted of deer that had two incisors assigned the same age by CA aging (Dataset 1). All deer aged ≥ 3.5 years were binned into a single category for purposes of comparison with the second dataset. The second dataset included over four times as many deer but my confidence in the accuracy of the ages of some of these deer was lower (Dataset 2). Specifically, this second dataset included all of the deer from Dataset 1 as well as deer that only had one CA age (which in that case was assumed to be true), had CA ages that disagreed (if one of the CA ages was estimated with lesser certainty, I used the CA age with higher certainty; if both CA ages were estimated with high certainty and the TRW age matched one of the CA ages, I used the CA age that agreed with the TRW age; if both CA ages were estimated with high certainty and neither or both CA ages matched the TRW age, the second CA age was used because the paired CA ages were aged in separate batches in later batches had higher agreement between CA and TRW batches and greater precision than the first batch of CA ages, indicating later batches were probably more accurately aged [D. M. Adams, unpublished data; see Chapter 3]), or were only aged using TRW. Since our TRW method grouped all deer older than 2.5 into one group (e.g., ≥ 3.5 years old age class), YOB could not be determined for these deer. As a result, deer without an estimated YOB were excluded from models that contained a YOB weather variable.

I performed modeling and model selection on two different datasets because while Dataset 1 likely had little error associated with age, the deer within the dataset did not provide a complete spatial representation of the state and may not have represented the actual distribution of the environmental factors across Iowa. Conversely, Dataset 2 likely contained more error in deer ages, but provided a better spatial representation of deer across the state of Iowa. Consequently, if similar results were observed between Datasets 1 and 2, the results would

suggest that important environmental factors could be detected despite aging errors and that datasets with some aging error were still valid to be used in analyses.

Lastly, to compare variation in antler size across the state of Iowa, I estimated observed mean antler sizes and associated 95% confidence intervals within WMDs and landform regions. Among landform regions, the Mississippi River Alluvial Plain contained fewer than three samples for all age classes and was, therefore, excluded from analysis because I was not confident so few samples represented that landform region.

Results

I collected antler measurements and estimated age using CA and/or TRW methods for 1,575 white-tailed deer (composed Dataset 2). There were 370 deer that had two incisors assigned the same age by CA aging (composed Dataset 1). After accounting for correlations between variables, model selection was performed on 212 models. Variables that were highly correlated included the three land use variables that were correlated not only with each other, but also with soil productivity, deer density, and the landscape configuration variables. Other notable correlations included correlations between weather variables (i.e., winter severity and summer temperatures) the year of harvest and the year of birth, but not between weather variables from the same years (i.e., winter severity YOH and summer temperature YOH).

Environmental effects were identified as significantly influencing antler size in Iowa white-tailed deer, with similar landscape and YOB variables identified in the most parsimonious models for both datasets (Tables 2 and 3). In Dataset 1, the top-ranked model included three environmental variables: soil productivity (+; represented by CSR2), winter severity preceding YOB (-), and average summer temperature YOB (+); while the other model within 2 AIC_c of the top model contained three environmental variables as well: amount of agriculture (+), winter severity preceding YOB (-), and average summer temperature YOB (+) (Table 4). The average

summer temperature YOB had the largest effect in both models, while the landscape variable (CSR2 or Ag) had the smallest effect. All environmental effects, in both models, were statistically significant. The most parsimonious model for Dataset 2 was similar to those identified in Dataset 1, albeit with smaller effect sizes. In Dataset 2, the top-ranked model included three environmental variables: amount of forest (-), winter severity preceding YOB (-), and average summer temperature YOB (+) (Table 5). The average summer temperature of the YOB had the largest effect and winter severity contained the smallest effect in this model. All environmental effects were statistically significant. Age was statistically significant in all models and explained the majority of variation in models of both datasets. R^2 values for models containing only the age variable for Datasets 1 and 2 were both 0.64.

Comparing the results from Dataset 1 and 2, while I did not obtain identical models between datasets, the land use variables present in the top models were highly negatively correlated with one another (agriculture:forest $r = -0.82$, CSR2:forest $r = -0.57$). As a result, the models appear to identify similar relationships between antler size and land use, specifically that antler size increased as the amount of agricultural land use increased. Also of note was that the model containing amount of agriculture, winter severity preceding YOB, and average summer temperature YOB was the second-ranked model from Dataset 2 (similar to Dataset 1), but was > 2 AIC_c from the top model. Because I obtained similar model selection results between datasets and Dataset 2 contained a better spatial representation of the environmental variables and white-tailed deer across Iowa, I felt Dataset 2 would be just as, if not more, representative of regional differences in antler size of Iowa deer than Dataset 1. The larger sample size of Dataset 2 would also produce more precise estimates of regional differences than Dataset 1, even with the possibility of some aging error associated with Dataset 2.

Using Dataset 2 to estimate mean regional differences in antler size, I observed differences among WMDs within the 2.5- and ≥ 3.5 -year-old age classes (Fig. 4). Among deer 2.5 years of age, the average antler size of deer harvested in the Southwest WMD was significantly larger than the Northwest, Northeast, and Southeast WMDs. Among deer ≥ 3.5 years of age, the average antler sizes of deer harvested in the Central, Southeast, and Southwest WMDs were significantly larger than deer from the Northeast and Northwest WMDs. I also observed differences between landform regions within the 2.5- and ≥ 3.5 -year-old age classes (Fig. 5). Among deer 2.5 years of age, the average antler sizes of deer harvested in the Loess Hills (LH) and Southern Iowa Drift Plains (SIDP) regions were significantly larger than deer from the Northwest Iowa Plains region. Deer from the LH region were also significantly larger than deer harvested in the Des Moines Lobe (DML). Among deer ≥ 3.5 years of age, the average antler sizes of deer harvested in the LH and SIDP landform regions were significantly larger than deer from the DML and Paleozoic Plateau regions.

Discussion

My results allowed me to reject my null hypothesis and demonstrated that when accounting for age, there are environmental factors affecting antler size in Iowa white-tailed deer. But, as expected, age was the primary factor responsible for antler size. I found soil productivity, land use, and weather conditions YOB to be the most influential environmental factors and their respective effects were consistent with those previously demonstrated (Jacobson 1984, Strickland and Demarais 2008, Freeman et al. 2013, Jones et al. 2019, Quebedeaux et al. 2019). I also observed significant regional differences in antler size, perhaps partly explained by the identified significant environmental factors.

While regional differences in antler size were detected, these data, first and foremost, further illustrate the importance of age to antler size. Antler size was significantly different

among age classes, which was expected since antler size increases with age until peak maturity is reached around 5.5 years of age (Strickland and Demarais 2000, Monteith et al. 2009, Hewitt et al. 2014). The differences between WMDs and landform regions within age classes may be partially explained by the significant environmental factors identified, as these vary spatially across Iowa (e.g., generally, winter severity decreased and average summer temperatures increased from north-to-south in Iowa and agriculture increased from southeast-to-northwest). However, since yearling antler size has been documented to be a reasonable predictor of antler size in older age classes (Ott et al. 1997, Hewitt et al. 2014, Michel et al. 2016), environmental factors may not be explaining the observed differences in antler size since antler size was not significantly different between regions in the yearling age classes. The origin of the samples, age structure, and aging error may be alternative explanations for my observed differences.

Differences in antler size among regions among deer in the 2.5- and ≥ 3.5 -year age classes may have been the result of the uneven spatial distribution of taxidermists I worked with during this study, as deer obtained at taxidermists may have had larger antler sizes compared to the mean antler size within their respective regions, biasing mean antler size higher. Age distributions may have been different within the ≥ 3.5 -year-old age class among regions. This is important because antler size continues to increase until about 5.5 years (Monteith et al. 2009, Hewitt et al. 2014). If there were differences in the age distribution in the ≥ 3.5 -year-old age class among the regions this may have led to differences in average antler sizes for that group. Lastly, aging error may have occurred for deer aged by TRW, especially among deer ≥ 2.5 years old (Gee et al. 2002), that may have influenced observed mean antler sizes as well.

Nevertheless, the regional disparity I observed among the landform regions among the yearling (< 1 –16% differences) and ≥ 3.5 -years-old (< 1 –11% differences) age classes were

smaller than previously observed in other studies examining differences in antler size metrics between physiographic regions. Strickland and Demarais (2000) observed regional differences in an antler size index in Mississippi that ranged from 5–29% in the yearling age class and 3–31% for deer ≥ 3.5 years old. Similarly, Gill (1956) identified regional disparities in main beam diameter in yearling West Virginia deer ranging from 2–29%. The age-specific antler sizes I documented (158.8 cm mean estimated B&C score using Strickland et al.'s [2013] model for yearlings, 253.0 cm – 2.5-year-olds, 332.5 cm – ≥ 3.5 -year-olds) were also larger than those previously documented in other parts of the U.S. For example, deer in southern Texas averaged B&C scores of approximately 100 cm and 200 cm for the yearling and 2.5-year-old age classes, respectively, while the 3.5–8.5-year age classes approximately ranged from 260–330 cm (Hewitt et al. 2014). Additionally, data from captive deer in Mississippi reported a mean B&C score of 94 cm and 226 cm for the yearling and 2.5-year-old age classes, respectively, and mean B&C scores ranging from 279–361 cm for deer 3.5–7.5 years of age (Jacobson 1995). The larger antler sizes and less regional variation among those antler sizes that I documented may suggest that white-tailed deer in Iowa are in good condition and are not under nutritional limitations (Andersson 1986, Brown 1990). However, because I found some environmental factors to have a negative relationship with antler size, condition and health of deer in Iowa, at least in some parts of the state, could most likely be improved.

Although most deer in Iowa have access to agricultural lands, I found the amount of agriculture available to have a positive association with antler size, similar to previous research from the Southeastern U.S. (Strickland and Demarais 2008, Jones et al. 2019, Quebedeaux et al. 2019). This finding is another validation that the availability of high-quality forage provided by popular cultivated crops (i.e., corn and soybeans) offer white-tailed deer adequate nutritional

resources for antler growth. Soil productivity was also found to have a positive association with antler size in Dataset 1 and had a similar effect size to the amount of agriculture on the landscape in the other competitive model. Soil productivity and the amount of agriculture on the landscape were highly correlated in my dataset ($r = 0.63$). Combined with the findings of Lashley et al. (2015), who found that poor soils do not limit the nutritional quality of forage but rather the quantity of forage, I suspect that the effects of soil productivity were confounded by the type and quantity of forage being produced from those soils which is a function of land use and deer densities (Jones et al. 2010). While investigating habitat parameters to describe deer densities in Illinois, Roseberry and Woolf (1998) found that quality of deer habitat was driven by the availability of agricultural land, which in turn was explained by soil productivity and terrain. While I did not observe an upper threshold in amount of agricultural land that produced a detrimental effect on antler size, other studies suggest that populations cannot sustain high densities when agricultural lands compose more than 75% of the landscape due to the lack of permanent cover after crop harvest that leave deer vulnerable to winter weather conditions, natural predation, and hunting mortality (VerCauteren and Hygnstrom 2011). However, lack of winter cover may be mitigated by seasonal migrations in some populations (Nixon et al. 1991, VerCauteren and Hygnstrom 1998, Brinkman et al. 2005).

Consistent with my findings of a positive relationship with agriculture, in the top-ranked model selected from Dataset 2, I found the amount of forested area negatively influencing antler size, which was also observed by Strickland and Demarais (2008) and Quebedeaux et al. (2019). Forested area and agriculture were highly negatively correlated ($r = -0.82$). While not prevalent across the Iowa landscape, Iowa forests are predominately composed of large diameter (≥ 28 cm in diameter) deciduous forest-types such as oak/hickory and elm/ash/cottonwood stands (M. D.

Nelson and Feeley 2018). Aside from mast, mature, closed-canopy forest stands do not provide great amounts of accessible deer forage in the form of herbaceous plants compared to early-successional forest plots and cultivated crops (Johnson et al. 2005, Diefenbach and Shea 2011). While forested lands in Iowa offer deer forage in the form of browse in the winter as well as year-round cover, during the times of increased nutritional needs of the spring and summer, they offer comparatively less high-quality forage than do agricultural lands. While cultivated crops provide comparatively more forage on the landscape for white-tailed deer than do Iowa forests, like Strickland and Demarais (2008), this is not a recommendation to remove forests from the landscape, but rather to alter the management of forested lands in Iowa by encouraging silvicultural practices that open the overstory canopy and promote growth of an herbaceous understory that is available as deer forage (VerCauteren and Hygnstrom 2011). By reverting to earlier seral stages, the associated vegetative growth provides abundant, year-round forage and cover.

YOB weather conditions also influenced antler size in white-tailed deer in Iowa. These YOB effects culminate from maternal effects, where the condition of the mother influences the condition and phenotype of the offspring (e.g., lack of nutritional resources during gestation or lactation), as well as effects experienced directly by the offspring after birth. I found the severity of winter, specifically related to snowfall and snow depth, endured by the mother while the male was *in utero* to have a negative impact on antler size, while the average summer temperature experienced by mother and fawn in the first months of life had a positive effect. It is unlikely that winter conditions (i.e., snowfall and snow depth) are a limiting factor for white-tailed deer in Iowa (Harms 2018), unlike some regions of the Western U.S. where Freeman et al. (2013) documented winter effects on mule deer and elk antler size. However, that does not indicate that

white-tailed deer in Iowa are not vulnerable to severe conditions that can adversely affect pregnant female deer through increased energy expenditure and a limitation of nutritional resources. Increased energy expenditure and limitation of nutritional resources can divert energy resources away from the fetus and result in smaller fawn birth weights (Mech et al. 1991, DelGuidice et al. 2002, Garroway and Broders 2005, Duquette et al. 2014). A possible limitation in using the specific winter severity metric that I used (AWSSI) is that AWSSI is a cumulative measure of winter severity and does not consider the seasonal timing of weather events, which may not accurately reflect winter weather's impact on deer (i.e., snowfall in early winter may not have the same effect on deer in late winter or early spring).

Forest management can also lessen the effects of winter severity on deer (Reay et al. 1990, Caron 2009). Dense conifer stands, although not common across all of Iowa, provide protection from winter conditions for deer as these stands typically have lower snow depths by intercepting and suspending snowfall above the ground and are insulated from cold temperatures and wind (Ozoga 1968, Kirchoff and Schoen 1987). Because of these qualities, white-tailed deer select for dense conifer stands in the winter to reduce energy expenditure (Telfer 1967, Rongstad and Tester 1969, Telfer 1970, Ozoga and Gysel 1972, Armstrong et al. 1983). Planting or managing for dense conifer stands that also provide accessibility to quality forage could improve maternal condition of pregnant females that could subsequently lessen negative maternal effects passed on to offspring (DelGuidice et al. 2013, Hoving and Notaro 2015).

The average summer temperature experienced as a fawn had a positive relationship with antler size later in life, consistent with the findings of Freeman et al. (2013). Summer is the time of growth for both neonate and adult ungulates, and for neonates, enhanced rates of body growth increase body size heading into the winter which bodes well for survival and condition exiting

winter (Parker et al. 2009). Ungulate neonates that do not need to expend energy after birth thermoregulating from colder temperatures and rain may be able to contribute more resources to body growth, thus increasing survival (Hegel et al. 2010, Michel et al. 2018). Deer can experience and become cold in the summer. Adult white-tailed deer have exhibited physical responses (i.e., shivering) to summer temperatures $\leq 15^{\circ}\text{C}$ in New Hampshire (Holter et al. 1975). Because fawns typically have higher body temperatures than adults (Parker and Robbins 1985), they may be susceptible to cold-related effects at temperatures even warmer than 15°C . Further, rainfall during summer increased energy costs for black-tailed deer in British Columbia at temperatures above those that would typically incite physical response (Parker 1989). In combination with the benefit of not expending as much energy thermoregulating and provided there is sufficient rainfall, the mother is also experiencing increased forage availability that is directly related to meeting lactation requirements that the fawn depends on (Parker et al. 2009, Michel et al. 2018). These YOB effects that persist to maturity can create cohort-specific differences in antler size.

It is unclear how climate change will affect future winter severity related to deer in the Midwest as winter precipitation is projected to increase but increasing temperatures may reduce snowfall or may also increase rain-on-snow events that form crusts on top of snowpacks and create hazardous conditions for traversing deer (Verme 1968, Kunkel et al. 2013*b*, Weiskopf et al. 2019). Increasing temperatures due to climate change may have detrimental effects to deer in terms of maximum summer temperatures as well. Although there appears to be conflicting evidence related to summer temperatures during the year of antler growth and subsequent antler size (Schmidt et al. 2001, Weladji et al. 2005, Freeman et al. 2013, Thalmann et al. 2015), it did not appear as one of the most important factors in my study. The total annual number of days \geq

35°C in the Midwest is projected to nearly double in the future (Kunkel et al. 2013b). The projection of an increase in hot days is important to consider, as temperatures $\geq 35^\circ\text{C}$ have been shown to incite a panting response in adult white-tailed deer in reaction to heat stress (Holter et al. 1975). Silanikove (2000) reviewed the effects of heat stress on domestic ruminants and noted impairment of growth rate and milk production, which could have adverse effects to antler growth by adult males and to body growth of fawns, respectively. While not examined by Holter et al. (1975), fawns may be better able to cope with warmer summer temperatures than adults because of their higher average body temperatures (Parker and Robbins, 1985). This would suggest that there is an upper threshold in summer temperatures that, when crossed, has negative effects on antler size, whether due to physiological reasons or changes in availability or composition of forage (Marshall et al. 2005, Weiskopf et al. 2019).

Management Implications

My results identified landscape and year of birth weather factors associated with antler size in Iowa white-tailed deer. Row-crop agriculture positively influenced antler size, while forested area had a negative impact. The weather factors, via maternal effects, illustrated that antler size is also associated with conditions before and shortly after birth. Age is the leading driver of antler size of white-tailed deer in Iowa and hunters and managers should set their expectations accordingly. Identifying these environmental factors can provide biologists and managers further evidence of factors that may be influencing antler size and condition of male white-tailed deer. My results suggest managers looking to improve age-specific antler size metrics of white-tailed deer should focus on providing habitat that offers both adequate nutrition and appropriate cover not only for antlered deer, but for the mothers of the next generation of antlered deer as well.

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Tables and Figures

Table 1. *Variables considered for model analysis of antler size of male white-tailed deer in Iowa (2012–2018).*

Variable Tested^{a,b}	Description^{a,b,c}
Landscape Composition and Configuration	
Agriculture	Percent land use within SOH defined as agriculture
Grassland	Percent land use within SOH defined as grassland
Forest	Percent land use within SOH defined as forest
CSR2	(Corn Suitability Rating 2; values 5-100) soil productivity metric available for soil mapping units in Iowa; weighted-average (by area) of SOH
Edge Density	(m/ha) total length of edge between land use classes divided by landscape area within SOH
IJI	(Interspersion-Juxtaposition Index; percent) measure of intermixing of land use types and how adjacent land use types are to all other land use types within SOH
SHDI	(Shannon's Diversity Index) measure of diversity of land use classes within SOH
Population Density Indices	
Buck Harvest	(antlered-deer/km ²) harvest of antlered deer in county of harvest the YOH
Weather Indices	
AWSSI Snow Score YOH	cumulative score of winter severity based on daily snowfall and snow depths the winter before harvest
Summer Temperature YOH	average daily temperature May-July YOH (°C)
Summer Precipitation YOH	total precipitation May-July YOH (cm)
AWSSI Snow Score <i>in utero</i>	cumulative score of winter severity based on daily snowfall and snow depths the winter before birth
Summer Temperature YOB	average daily temperature May-August YOB (°C)
Summer Precipitation YOB	total precipitation May-August YOB (cm)

^a*YOH: Year of harvest*

^b*YOB: Year of birth*

^c*SOH: Section of harvest and adjacent sections*

Table 2. Top linear regression models evaluating influence of age and environmental factors on antler size of male white-tailed deer in Iowa for deer for which 2 incisors received the same cementum annuli age estimate ($n = 370$; 2012–2018). Models with $\Delta AIC_c < 2$ are reported.

Model ^{a,b}	-2LL ^c	ΔAIC_c^d	ω_i	R^2
~ Age + CSR2 + Snow <i>in utero</i> + ST YOB	3664.29	0	0.29	0.657
~ Age + Ag + Snow <i>in utero</i> + ST YOB	3665.71	1.42	0.14	0.656

^aAbbreviated Variables: Snow *in utero* – AWSSI Snow Score *in utero*, ST YOB – Summer Temperature YOB

^bSee Table 1 for description of variables

^c-2LL = -2 log likelihood

^d $AIC_c = 3678.62$

Table 3. Top linear regression models evaluating influence of age and environmental factors on antler size of male white-tailed deer in Iowa with cementum annuli and/or tooth replacement-and-wear age estimates ($n = 1,575$; 2012–2018). Models with $\Delta AIC_c < 2$ are reported.

Model ^{a,b}	-2LL ^c	ΔAIC_c	ω_i	R^2
~ Age + Forest + Snow <i>in utero</i> + ST YOB	14905.11	0	0.69	0.636

^aAbbreviated Variables: Snow *in utero* – AWSSI Snow Score *in utero*, ST YOB – Summer Temperature YOB

^bSee Table 1 for description of variables

^c-2LL = -2 log likelihood

^d $AIC_c = 14919.19$

Table 4. Standardized parameter estimates of environmental variables from top linear regression models evaluating influence of age and environmental factors on antler size of male white-tailed deer in Iowa for deer for which 2 incisors received the same cementum annuli age estimates ($n = 370$; 2012–2018).

Model ^{a,b}	Parameter	β	L95 ^c	U95 ^d	P-value
CSR2 + Snow <i>in utero</i> + ST YOB					
	Intercept	161.71	152.24	171.18	<0.001
	Age – 2.5 Years	106.52	93.21	119.82	<0.001
	Age – \geq 3.5 Years	164.56	151.86	177.26	<0.001
	CSR2	6.28	1.39	11.17	0.012
	Snow <i>in utero</i>	-7.37	-13.36	-1.39	0.016
	ST YOB	7.48	1.36	13.61	0.017
Ag + Snow <i>in utero</i> + ST YOB					
	Intercept	160.77	151.28	170.25	<0.001
	Age – 2.5 Years	107.55	94.16	120.93	<0.001
	Age – \geq 3.5 Years	165.19	152.38	178.00	<0.001
	Agriculture	6.04	0.70	11.39	0.027
	Snow <i>in utero</i>	-7.75	-13.76	-1.73	0.012
	ST YOB	7.84	1.70	13.98	0.013

^aAbbreviated Variables: Snow *in utero* – AWSSI Snow Score *in utero*, ST YOB – Summer Temperature YOB

^bSee Table 1 for description of variables

^cL95 = Lower limit of 95% confidence interval for parameter estimate

^dU95 = Upper limit of 95% confidence interval for parameter estimate

Table 5. Standardized parameter estimates of environmental variables from top linear regression model evaluating influence of age and environmental factors on antler size of male white-tailed deer in Iowa with cementum annuli and/or tooth replacement-and-wear age estimates ($n = 1,575$; 2012–2018).

Model ^{a,b}	Parameter	β	L95 ^c	U95 ^d	P-value
Forest + Snow <i>in utero</i> + ST YOB					
	Intercept	158.06	153.19	162.94	<0.001
	Age – 2.5 Years	96.38	89.48	103.28	<0.001
	Age – \geq 3.5 Years	171.88	164.81	178.95	<0.001
	Forest	-4.44	-7.28	-1.59	0.002
	Snow <i>in utero</i>	-3.20	-6.31	-0.09	0.044
	ST YOB	6.70	3.63	9.77	<0.001

^aAbbreviated Variables: Snow *in utero* – AWSSI Snow Score *in utero*, ST YOB – Summer Temperature YOB

^bSee Table 1 for description of variables

^cL95 = Lower limit of 95% confidence interval for parameter estimate

^dU95 = Upper limit of 95% confidence interval for parameter estimate

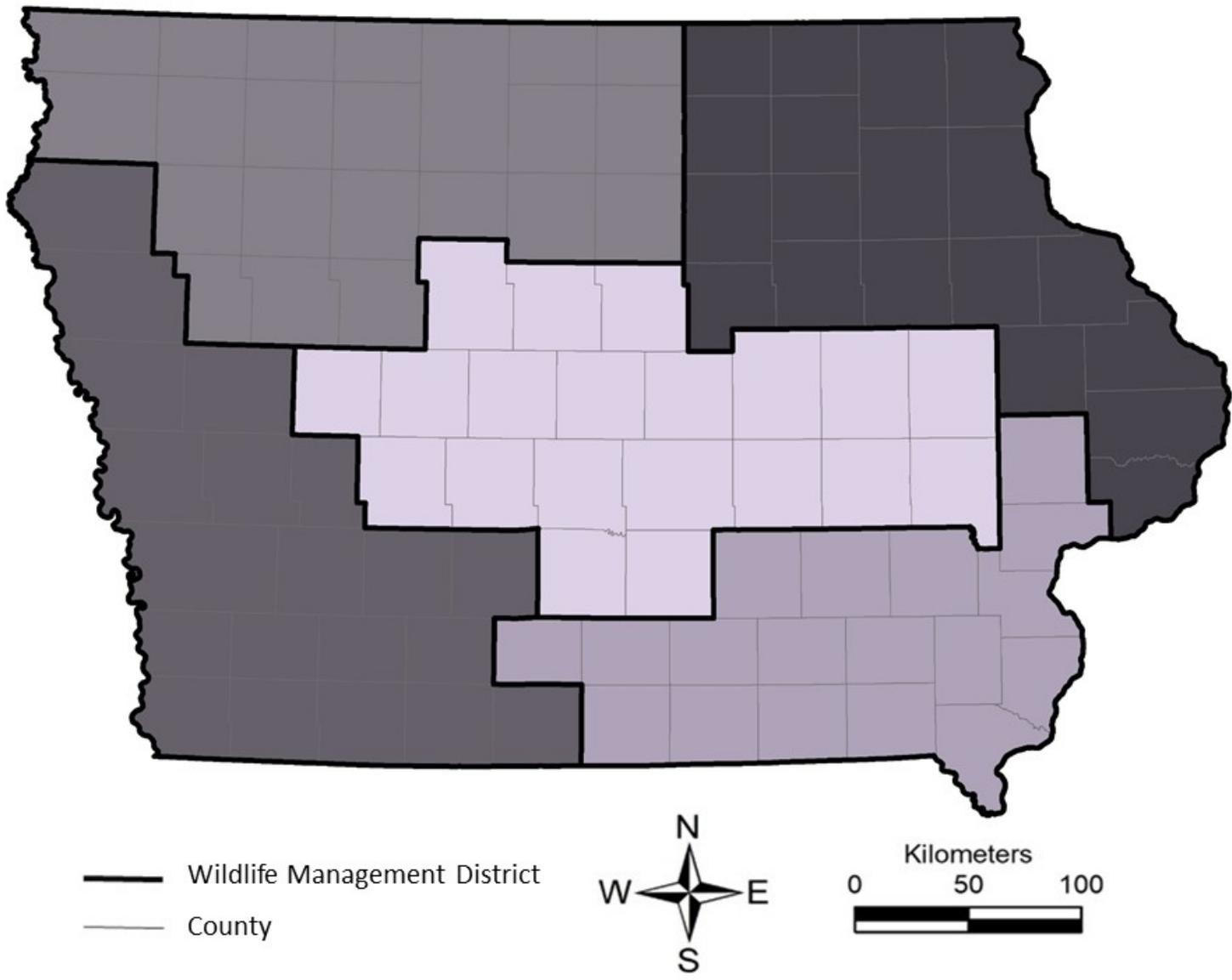


Figure 1. Iowa Department of Natural Resources' Wildlife Management Districts (WMDs) and counties of Iowa.

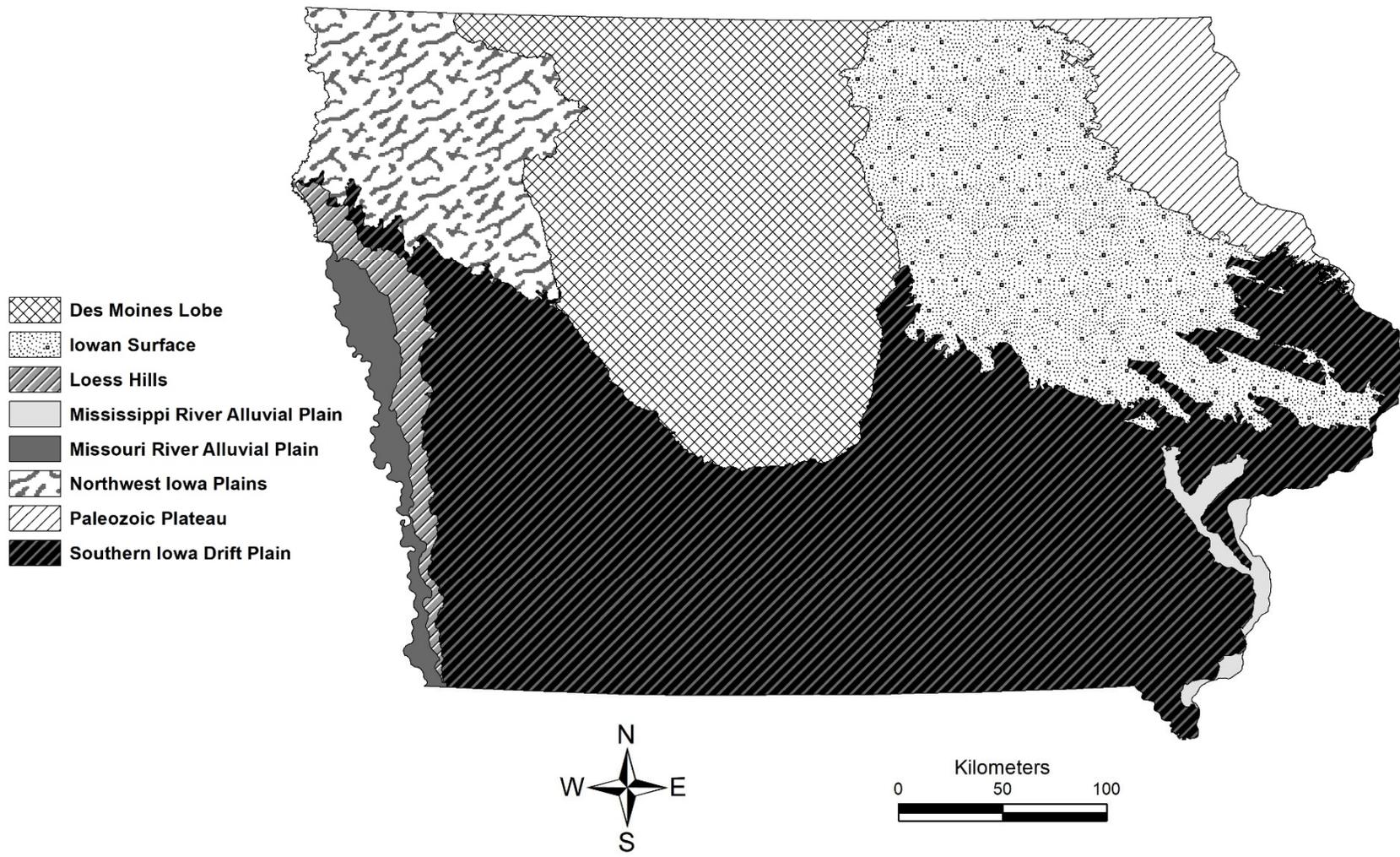


Figure 2. Landform regions of Iowa (Prior, 1991).

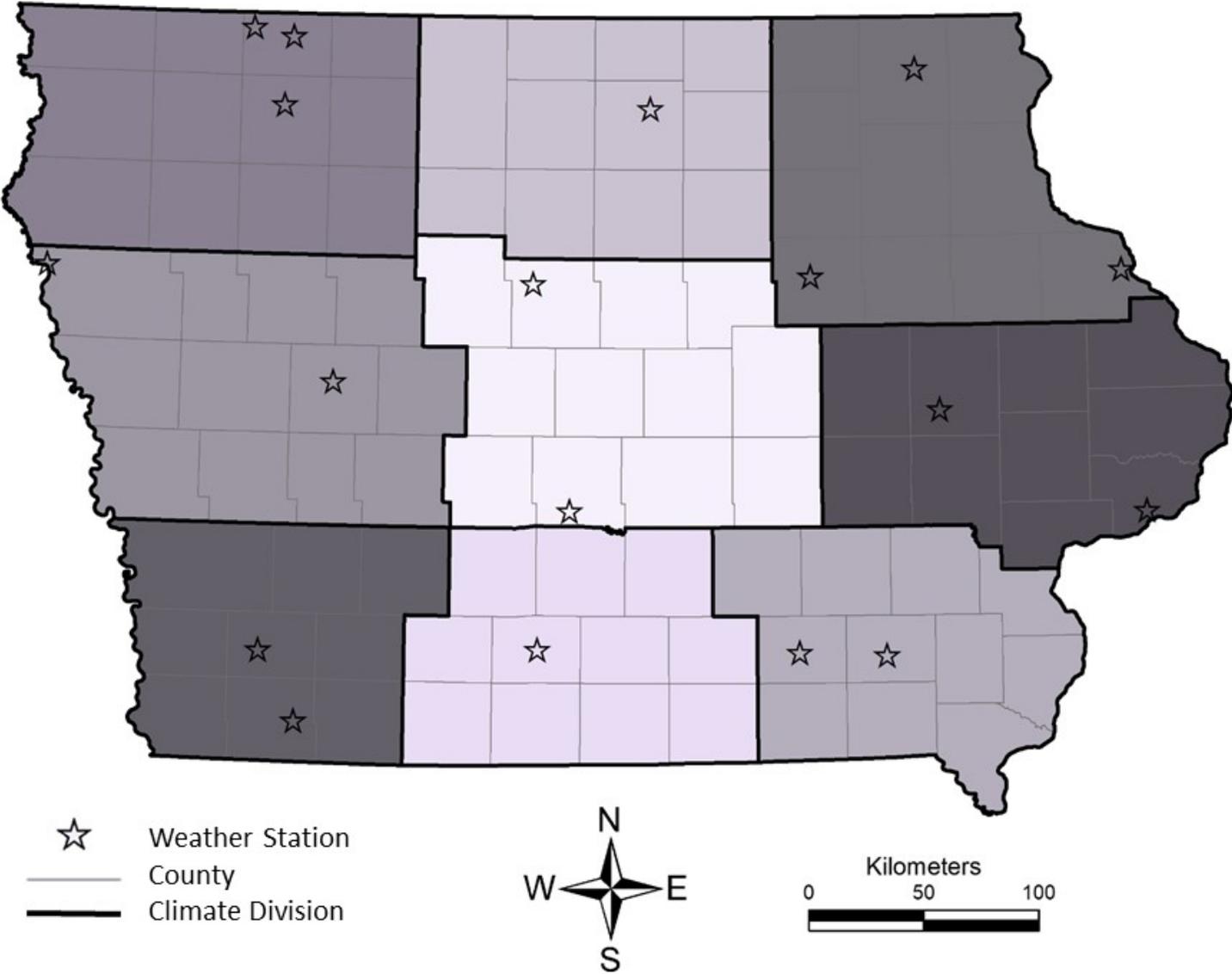


Figure 3. *Weather stations used to calculate Annual Winter Season Severity Index within the National Oceanic and Atmospheric Administration's Climate Divisions of Iowa.*

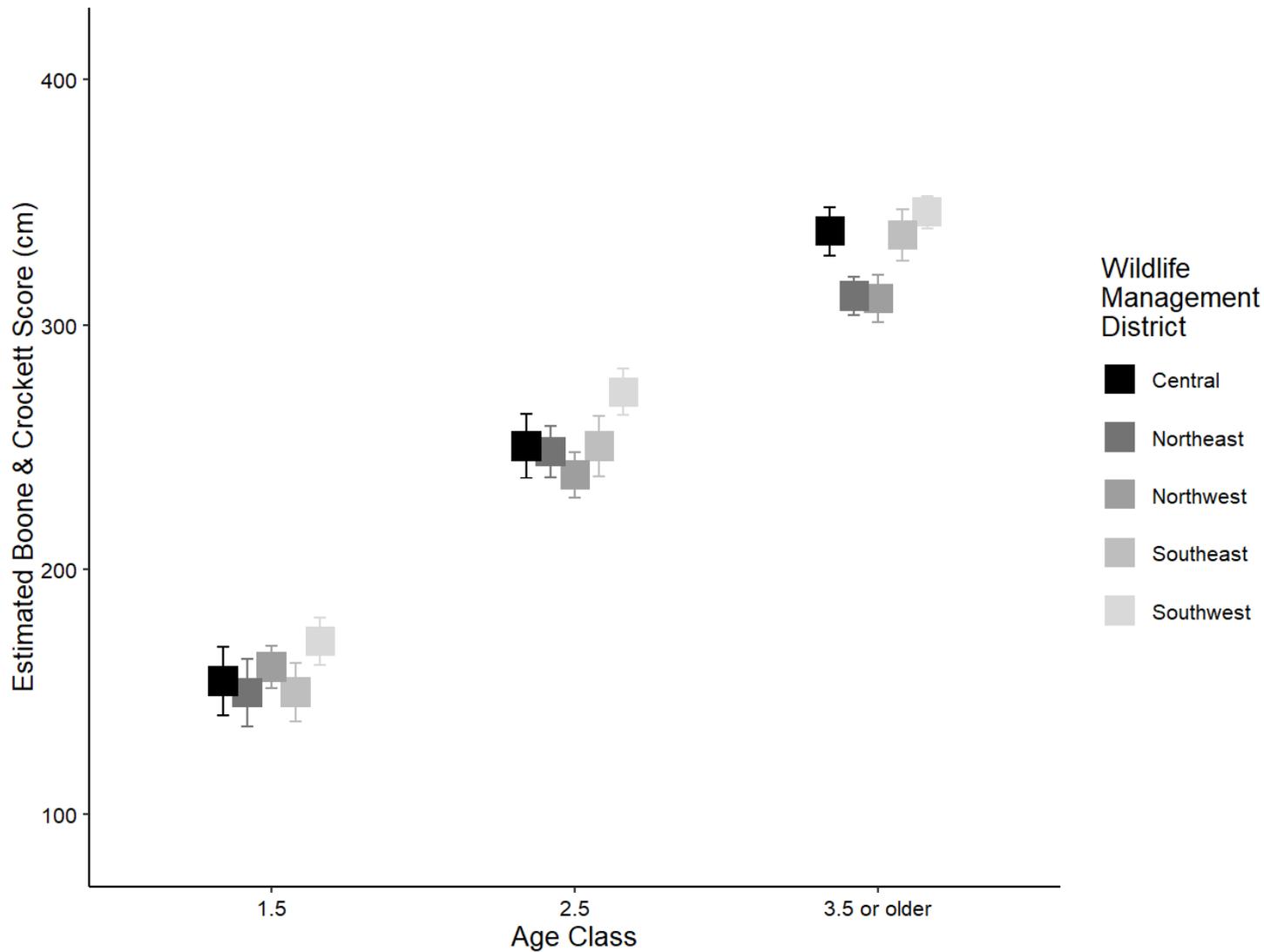


Figure 4. Age- and Wildlife Management District-specific antler size of male white-tailed deer in Iowa with *cementum annuli* and/or tooth replacement-and-wear age estimates ($n = 1,575$; 2012–2018). Data points represent observed means ($\pm 95\%$ CI) depicting differences in antler size relative to age and Wildlife Management District (WMD).

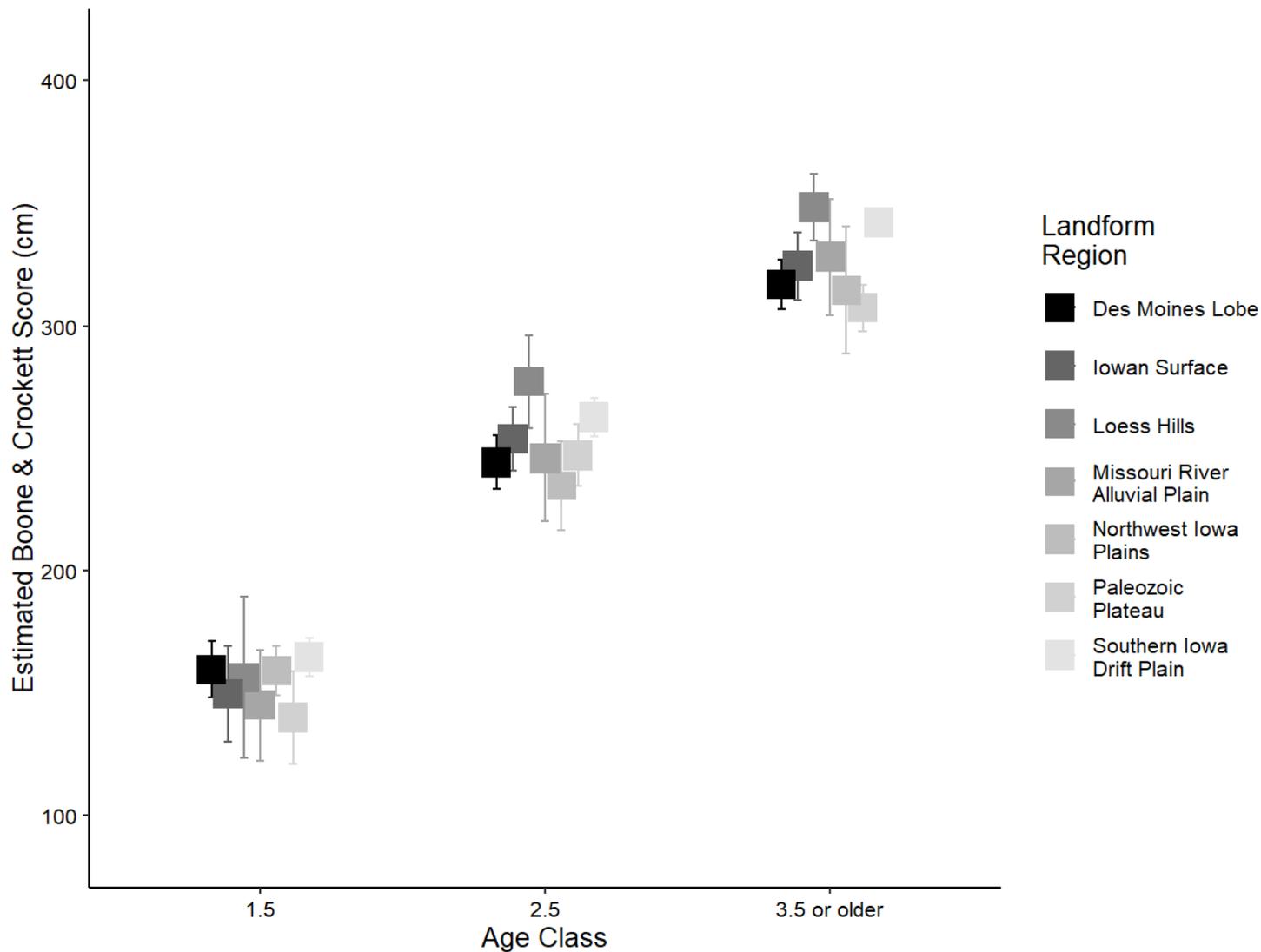


Figure 5. Age- and landform region-specific antler size of male white-tailed deer in Iowa with cementum annuli and/or tooth replacement-and-wear age estimates ($n = 1,575$; 2012–2018). Data points represent observed means ($\pm 95\%$ CI) depicting differences in antler size relative to age and landform region (LR).

CHAPTER 4. TEMPORAL AND SPATIAL TRENDS OBSERVED IN ANTLER SCORES IN AN IOWA WHITE-TAILED DEER (*Odocoileus virginianus*) RECORD BOOK

Abstract

Exploring record books containing historical antler metric data for trends that might be of relevance to management has been of recent interest. I assessed both temporal and spatial trends in antler score of white-tailed deer (*Odocoileus virginianus*) within the Iowa Department of Natural Resources' Iowa Trophy Deer record book. While no temporal trends in antler score were identified, a negative latitudinal trend in antler score was detected within the entire typical category of entries ($\beta = -1.14, P = 0.04$), as well as the largest third of specimens within the typical category ($\beta = -1.72, P = 0.03$). One possible explanation for the trend with latitude may be explained by landscape composition within the Southern Iowa Drift Plain landform region that covers much of the southern portion of Iowa. Although interesting trends may occur in record books, most record books come with biases that may limit their usefulness for making inferences about a population (e.g., truncated segment of population, reliant on self-reporting, lack of specimen's age information). Monitoring a more representative sample of a cervid population may better serve managers interested in temporal or spatial trends in antler size.

Introduction

Iowa is nationally renowned for having a quality white-tailed deer (*Odocoileus virginianus*) herd, along with producing trophy-class antlers within that herd for decades (Helmer 2002, Stone 2003). Historical data regarding antler metrics are sparse, with record books being the main source of these data, but the usefulness of record books in terms of drawing population-level conclusions may be limited (Festa-Bianchet et al. 2015). Yet, there has

been recent interest in attempting to identify trends in metrics found in record books that might be relevant to management (Festa-Bianchet et al. 2015, Monteith et al. 2013).

The most popular record book chronicling historical antler metrics of cervids is *Records of North American Big Game* by the Boone and Crockett Club. The Boone and Crockett Club, founded by Theodore Roosevelt and fellow conservationists in 1887, was created to promote conservation of North America's big game animals and later began collecting measurements from them to ensure information was available about these animals should they ever disappear (Wright and Nesbitt 2003). In 1950, the Boone and Crockett Club implemented what became the standard for measuring big game species of North America, taking measurements of antlers, horns, or skulls (Wright and Nesbitt 2003). The scoring system takes measurements (in inches) of lasting characteristics of the specimen, antlers in the case of cervids, to arrive at a numerical score, the Boone and Crockett (B&C) score, that can be ranked along with other specimens (Wright and Nesbitt 2003). A minimum score, designated by species category, is required for entry into the Boone and Crockett Club's record book, meaning only the largest specimens of a population are eligible for entry. Many state agencies (e.g., Iowa Department of Natural Resources' [DNR] Iowa Trophy Deer) and organizations (e.g., Pope and Young Club's Records Program) have adopted the B&C scoring system and now keep independent record books.

Monteith et al. (2013) examined temporal trends of North American big game species within the Boone and Crockett Club's record book and observed a negative trend in antler size in white-tailed deer submitted to the record book over a period of more than a century (1900-2010). Because antler size increases with age until peak maturity is reached around 5.5 years of age (Monteith et al. 2009, Hewitt et al. 2014,), Monteith et al. (2013) suggested the observed

negative trend may have been the result of increasing harvest of males leading to a younger age structure.

Another hypothesis of Monteith et al. (2013) was that a “sociological effect” could explain trends in antler size of entries in record books, such that an increased rate of smaller, yet eligible, entries into the Boone and Crockett Club’s record book would result in a temporal decrease in average antler size. Monteith et al. (2013) predicted these trends would be most evident when examining the smallest entries in the dataset and less evident within the largest entries, so they examined temporal trends within the largest and smallest thirds of their dataset. Consistent with the negative temporal trend in the entire dataset, Monteith et al. (2013) observed negative temporal trends within the smallest third of their data. They also observed negative trends in antler size within the largest third of white-tailed deer entries, which is not consistent with their hypothesis that a “sociological effect” was responsible for the negative temporal trend in antler size (Monteith et al. 2013). They also explored the hypothesis that entry rate would be related to the negative trend in antler size (Monteith et al. 2013). Although decadal entries to the Boone and Crockett Club’s record book increased by greater than 300% from 1970-2010, this hypothesis was also not supported when examining the direct relationship between annual entry rate and annual mean antler size (Monteith et al. 2013).

Monteith et al. (2013) conducted their study of antler score trends over all of North America. Fewer studies have examined trends in antler metrics at smaller scales such as the scale of a state, though as mentioned above, some states maintain their own record books. It is unclear whether the temporal trends found by Monteith et al. (2013) are likely to be detectable at a smaller scale, perhaps due to differences in state-specific hunting regulations related to harvest of

antlered deer over time and/or differences in data maintained in state record books compared to the Boone and Crockett Club's records.

Prior to the 2016 hunting season, Iowa had held the Boone and Crockett Club's world record hunter-harvested non-typical white-tailed deer (Boone and Crockett Club 2017). That record was quite a feat for a state that had virtually extirpated deer from the landscape by 1900 (Stone 2003). Populations of deer were reintroduced through planned releases as well as escapes from captive herds in the early 1900's, expanding across the state until hunting seasons were opened in 1953 (Stone 2003). Antlered deer harvest regulations in Iowa have undergone few major changes since the 1990s. Specifically, some hunting seasons in the northwest part of the state remain only open to antlered deer with the difference before 1990 being that the antlered-only seasons were more common across Iowa as the Iowa Conservation Commission, the state natural resources agency preceding the Iowa DNR, was attempting to grow and expand deer populations in Iowa (Stone 2003). Since implementation of a hunting season in 1953, Iowa has not had any selective harvest criteria (i.e., antler point restrictions) for antlered deer.

Monteith et al. (2013) did not evaluate spatial trends in antler size in the Boone and Crockett Club's record book. Spatial trends in antler size might be expected depending on the amount of habitat heterogeneity across the region of interest. The state of Iowa is comprised of a more homogenous landscape than North America, as a whole, is (Ricketts et al. 1999). White-tailed deer in North America range over more than half of the 116 ecoregions in Canada and the United States set forth by Ricketts et al. (1999), encapsulating many different habitats and varying soil quality (Heffelfinger 2011). According to the U.S. Department of Agriculture (USDA; USDA 2015a), only 7% of Iowa's land is forested while 72% is covered in cultivated crops and, in 2016, planted corn and soybeans accounted for 88% of that cropland (Iowa State

University Extension and Outreach 2017). Highly-fertile Mollisol soils compose much of Iowa's soils (Griffith et al. 1994), which partly explains the high density of agricultural land. It remains to be seen if spatial differences in a phenotype, such as antler score, can be detected on the statewide scale using data in a record book.

The objective of this study was to examine temporal and spatial trends in entry rates and antler score in the Iowa DNR's Iowa Trophy Deer record book. I hypothesized that there would not be statistically significant temporal or spatial trends in antler score detected within the record book. These hypotheses were due to (1) minimal records within the Iowa Trophy Deer record book before the mid-1990s when many annual entries became regular, which I thought would lead to a shortened timescale applicable to analyses, and (2) the stable management of the harvest of antlered deer in Iowa over that same timespan, as well as the homogeneity of Iowa's landscape.

Methods

Records of Trophy Deer in Iowa

I received a digital version of the Iowa Trophy Deer record book from the Iowa DNR. A pdf scan of an earlier version of the Iowa Trophy Deer record book was discovered online after analysis was completed that included entries not in the version I received, but I did not have the time or resources to add these additional entries to my data. Entries included in my analysis spanned from 1939-2017, with entries every year after 1994, but entries appearing less consistently and less frequently in years preceding that. Entry into the record book was free of cost, differing from national record books that are popular among hunters where there is a cost associated with entry (i.e., Boone and Crockett Club, Pope and Young Club). Entries are from white-tailed deer harvested by hunters and were evaluated based on the B&C scoring system. All scores are net scores, which is the summation of four types of measurements from the antlers

(gross score) minus the measurements of asymmetry from opposite antlers (Wright and Nesbitt 2003). Entries in Monteith et al.'s (2013) analysis were gross scores, which have been shown to be correlated with antler mass (Strickland et al. 2013). It is probable that net scores are slightly less correlated to antler mass because of the deductions in score for asymmetry, although I do not believe this impacted my results. Therefore, antler score was considered representative of overall antler size. Entries were divided into two categories, typical (n=1,452) and non-typical (n=591). The non-typical category recognizes specimens that would otherwise be severely penalized for possessing abnormal tines by awarding those measurements to the net score. Minimum entry scores for each category were parallel to those minimums defined by the Boone and Crockett Club's *Records of North American Big Game* (Typical: 160 inches [406.4 cm]; Non-Typical: 185 inches [469.9 cm]) (Wright and Nesbitt 2003). The spatial resolution for entries was the county of harvest.

Temporal Trends

I used Pearson correlation tests ($\alpha = 0.05$) to test for significant correlations between the number of entries per year and mean annual antler score for the typical and non-typical categories. I used linear regression to investigate temporal trends in antler score of deer for both the typical and non-typical categories of the Iowa Trophy Deer record book following the approach used by Monteith et al. (2013) described below. Prior to 1995, there were not entries for every year, with the typical and non-typical categories having an average of 2.3 and 0.4 entries per year, respectively. Annual number of entries averaged 61.5 and 26.0 for the typical and non-typical categories, respectively, thereafter. Because these data were sparse prior to 1995, I binned data to meet the assumption of homogenous variances. Based on the variance of the data, the minimum number of samples per bin to yield a 95% confidence interval that was no larger than $\pm 5\%$ relative to the mean was calculated to be ≥ 10 samples (Krebs 1999). I created

bins by beginning with the earliest year of record (1953-typical; 1939-non-typical) and adding subsequent years until ≥ 10 samples were reached, never splitting data from a single year into separate bins. The bin means and their associated variances were used in a weighted regression with mean antler score and mean entry year as the dependent and independent variables, respectively (Kutner et al. 2005, Monteith et al. 2013). The regression was weighted by the inverse of the bin variance in antler score to avoid more variable bins being unduly weighted when fitting the regression (Kutner et al. 2005). Bins with a smaller variance contain a more precise estimate of the mean compared to bins containing large variances and less precise estimates of the mean; therefore bins with a small variance should receive more weight in the regression (Kutner et al. 2005).

Just as Monteith et al. (2013) did to investigate whether there was a “sociological effect” on antler size, I further utilized the variance-weighted linear regression technique to investigate any trends that may have occurred in the largest and smallest third of entries (based on score) within the typical and non-typical categories. The dataset required re-binning for this analysis, because by utilizing the largest and smallest third of entries from each bin from the previous analysis, our new bins would not meet our conditions of sample size. Variance was lower in the smallest and largest thirds of the full dataset, so I recalculated the minimum sample size per bin, following the conditions of the 95% confidence intervals, to be ≥ 8 samples (Krebs 1999). To create new temporal bins for the largest and smallest third of entries, I binned data for each category from the full dataset to include ≥ 24 samples per bin, again never splitting data from a single year, and extracted the ≥ 8 largest and ≥ 8 smallest samples from each bin of ≥ 24 to analyze (Monteith et al. 2013). This provided parallel bins, in terms of sample sizes, between the largest and smallest entries, but not between the typical and non-typical categories.

Spatial Trends

I used a trend surface analysis to examine overall spatial trends in antler score (Gittins, 1968). I assigned the coordinates, in units of decimal degrees, of the center of the county of harvest to spatially orient each entry in the record book. For each category, I explored a candidate set of models that ranged from a null (intercept only) model to a model that included both linear and quadratic effects of latitude and longitude, as well as their interaction, on antler score through linear regression. I chose the most parsimonious model to describe the data based on Akaike Information Criterion corrected for small sample size (AIC_c ; Burnham and Anderson 2002). Models within 2 AIC_c of the highest-ranking model were considered to have equivalent support (Burnham and Anderson 2002). If the most parsimonious model for the given data was not the null model, I explored the model for statistically significant parameters. I also conducted this analysis on the largest third of both the typical and non-typical entries.

I examined spatial patterns in the Iowa Trophy Deer record book (e.g. sample size, mean antler score, standard deviation of antler score, and maximum antler score) at four scales, some of which may be related to deer by differing ecologically and some that are of interest based on the structure of deer management within the Iowa DNR. The first scale I examined was the Wildlife Management District (WMD). The Iowa DNR divides the state of Iowa into five WMDs, which oversee public lands management across the state and roughly divide the state into northeast, southeast, southwest, northwest and central zones. WMDs are further divided into three or four Wildlife Management Units (WMU) within those WMDs, which was my second spatial scale of interest (Iowa DNR 2018) (Fig. 1). The WMUs are delineated along county line boundaries for deer management purposes (e.g., harvest quotas, allotment of antlerless tags, etc.). WMUs also resemble the former deer management zones that were phased out in favor of county deer management in 1992 (Stone 2003). My third spatial scale of interest was based on the

National Oceanic and Atmospheric Administration (NOAA) Climate Divisions, nine of which occur in Iowa and are used to collect temperature and precipitation values (NOAA 2005) (Fig. 2). My final scale represented eight physiographic regions of Iowa demarcated based on appearance and the geologic makeup of the landscape and referred to as landform regions (hereafter, landforms; Prior 1991, Fig. 3). Since the record book entries are recorded at the county level and the landforms do not follow the political boundaries of the county, I assigned the landform with the most area within the county as the landform associated with that county. Because of this method, the Mississippi River Alluvial Plain landform was not assigned to any county, thus not represented in these data.

I used an unbalanced analysis of variance (ANOVA) to test for differences in antler score at the four different spatial scales for the typical and non-typical categories. To examine any spatial trends in the largest entries of both the typical and non-typical categories, I also applied the same ANOVAs to the largest third of each category. I identified the largest third of each category by sorting by antler score and extracting the largest third of entries within each category.

To further investigate spatial variation in antler score, I examined the relationship between antler score and soil productivity using the Corn Suitability Rating 2 (CSR2), which was developed to rate soils in Iowa based on corn productivity and is the most detailed soil productivity metric available in Iowa (Burras et al. 2015, Fenton et al. 1971). CSR2 values are assigned to soil mapping units, areas classified by soil components and location on the landscape (Soil Science Division Staff 2017). The weighted-average of CSR2 values within each county were assigned to the trophy book entries' corresponding county of harvest. I used linear

regression to examine if CSR2 was significantly ($\alpha = 0.05$) related to antler score of the entries in both typical and non-typical categories and the largest thirds of both categories.

Results

More than 2,000 entries from the Iowa Trophy Deer record book were included in these analyses. Entry rates increased markedly after the mid-1990s and appeared to peak approximately 10 years thereafter (Fig. 4). Spatial examination indicated fewer entries to the Iowa Trophy Deer record book from the northcentral and northwestern areas of Iowa when compared to other areas of Iowa in both the non-typical (Tables 1-3) and typical (Tables 3-6) categories. The number of entries per year was not significantly correlated to mean annual antler score for the non-typical ($r = -0.10$, $P = 0.57$) or typical ($r = 0.19$, $P = 0.19$) categories.

There were no statistically significant temporal trends in antler score for either the non-typical or typical categories (Fig. 5; Table 7). I also did not find not find any significant temporal trends when examining the largest and smallest submissions of each category (Fig. 6, Table 8).

The trend surface analysis of the non-typical category resulted in three models being supported: the null model, the model containing the linear longitude parameter, and the model containing the linear latitude parameter (Table 9). Both models containing a singular, linear spatial parameter, however, had an adjusted $R^2 < 0$ and neither contained significant parameters. The competitive models for the typical category were the linear latitude model (adj. $R^2 < 0.01$), the model containing both the linear latitude and longitude parameters (adj. $R^2 < 0.01$), and the model containing the linear and quadratic latitude parameters (adj. $R^2 < 0.01$; Table 10). The linear latitude parameter was a statistically significantly negative parameter in both the model containing only that parameter ($\beta = -1.14$, $P = 0.04$) and the model also containing the linear longitude parameter ($\beta = -1.32$, $P = 0.02$) for the typical category. The null model and the model containing the linear latitude parameter (adj. $R^2 < 0$) were models supported when examining the

largest third of entries of the non-typical category (Table 11), but the latitude parameter was not statistically significant. The competitive models for the largest third of entries in the typical category were the linear latitude model (adj. $R^2 < 0.01$), the model containing the linear and quadratic latitude parameters (adj. $R^2 < 0.01$), and the model containing both the linear latitude and longitude parameters (adj. $R^2 < 0.01$; Table 12). The linear latitude parameter was a statistically significantly negative parameter in both the model containing only that parameter ($\beta = -1.72$, $P = 0.03$) and the model also containing the linear longitude parameter ($\beta = -1.63$, $P = 0.04$) for the largest third of entries in the typical category.

There were no statistically significant relationships between antler score and WMD, WMU, Climate Division, or landform for typical or non-typical entries or when examining only the largest third of entries of either category (Tables 13 and 14). Evaluation of the influence of CSR2 on antler score was not significant for either the typical or non-typical categories (Table 15). CSR2 was not significantly related to antler score in the largest entries of the typical or non-typical categories (Table 16).

Discussion

Analysis of entries in the Iowa DNR's Iowa Trophy Deer record book failed to reveal significant temporal or spatial patterns in antler score with the exception of a weak negative correlation with latitude for entries within the typical category. Unlike Monteith et al.'s (2013) examination of the Bonne and Crockett Club's record book, where researchers documented significant negative trends in antler score of white-tailed deer over time, I failed to find any evidence for a temporal trend in antler score. The quality of the Iowa Trophy Deer record book, in relation to annual entry rates, could have been a confounding factor that inhibited the possible observation of temporal trends. The temporal pattern of entry rates of deer into the Iowa Trophy Record Book differed from that documented by Monteith et al. (2013) in the Boone and Crockett

Club's record book. Whereas annual entries to the Boone and Crockett Club's record book have steadily increased since the 1970s ($\geq 300\%$ increase in annual entries from 1970-2010, Monteith et al. 2013), the Iowa Trophy Deer record book had sporadic submissions before 1995, but then experienced a sharp 10-year increase (1995-2005) in annual entries, which was followed by a similar decline in annual entry rates over the next decade. I would not expect a decline in deer eligible to be submitted to the Iowa Trophy Deer record book, specifically because I observed no negative trends in antler score. A negative trend in antler score would suggest the possibility that if antler size was decreasing within a population, the number of eligible specimens would decrease as well, which is the opposite of what Monteith et al. (2013) observed. Also, while the Iowa deer population has decreased by an estimated 13% since 2007 (Harms 2018), entries to the Iowa Trophy Deer record book decreased by more than 62% from 2005-2017 in both the typical and non-typical categories (Fig. 4), suggesting that another factor could be cause for the decline in entries. Perhaps a decline in popularity or a perceived lack of recognition by submitting to the Iowa Trophy Deer record book may explain the decrease in annual entries.

Like Monteith et al. (2013), Rivrud et al. (2013) also observed temporal trends in antler metrics, specifically in red deer (*Cervus elaphus*) records from trophy shows spanning over a century (1881-2008) in Hungary, which is smaller than the state of Iowa (Iowa: 145,750 km²; Hungary: 93,030 km²), but the trends they observed were not consistent throughout the time of records. The 127-year timeframe of submissions was noticeably segmented into three unique trends: a 76-year slight decline in size of antler metrics, followed by a 16-year large increase in sizes of antler metrics that reached levels similar to initial sizes of antler metrics at beginning of the records, with a mostly stable trend observed in the last 35 years of the records (Rivrud et al. 2013). The management regulations of red deer in Hungary were mostly unchanged during the

period of records, but enforcement of these regulations and turnover of national political regimes caused harvest of red deer within Hungary to vary (Rivrud et al. 2013). Rivrud et al. (2013) attributed the changing trends over time in recorded antler metrics to hunting pressure: that heavy harvest of males created a younger age-structure and when harvest was reduced, the age-structure returned to a composition similar to the beginning of the records, as did size of antler metrics. However, conditions for qualification for the trophy shows were not reported so trophy show records may not be directly comparable to formal record books (i.e., Iowa Trophy Deer record book) that contain a minimum criterion for submission because of possible selection biases associated with both (Festa-Bianchet et al. 2015).

The lack of differences in antler score across the four selected spatial scales of Iowa was expected due to the homogeneity of the Iowa landscape; a landscape that predominantly contains cultivated crops with small wooded and grassland areas interspersed throughout (Iowa DNR 2017). Strickland and Demarais (2000) identified regional differences in an antler size index within age classes of harvested white-tailed deer in Mississippi, but their study site and data differed from mine. Mississippi's land composition differs from Iowa's as Mississippi contains 16% and 57% cropland and forested area (USDA 2015b), respectively, but forest types (e.g., hardwood stands, pine plantations, mixed, etc.) and the distribution of these agricultural and forested habitats varies and is related to regional differences, creating a heterogeneous landscape (Strickland and Demarais 2008). Strickland and Demarais' (2000) data were from harvested deer rather than from a record book so they, theoretically, had a more representative sample of the population than I did. Their differences in antler size index were also discerned within regions that were much more contrasting to each other (e.g., rich, alluvial and loess soils vs. leached, sandy soils; agriculture-dominated areas vs. pine plantation-dominated areas; Strickland and

Demarais 2000) than regions within Iowa, which typically only vary in the degree to which cultivated crops dominate the landscape.

While I did not observe significant temporal trends, I did observe a significant relationship between antler score and latitude within entries in the typical category. Using my top-ranking model (Table 10) to make predictions, the difference between the predicted antler score of the southernmost (426.8 cm) and northernmost (424.6 cm) points of Iowa was less than three centimeters, which is less than a one percent difference. Similar patterns were observed within the largest third of entries of the typical category using the top-ranking model to produce predictions (1.4% difference; Table 12), which also had a negative relationship with latitude. Established mean antler scores of mature white-tailed deer across North America do not exist, but Hewitt et al. (2014) reported deer in South Texas aged as ≥ 5.5 years old had an average antler score of approximately 325 cm. Additionally, data from captive deer in Mississippi reported a mean antler score of 361 cm at 5.5 years old (Jacobson 1995). A deer meeting the minimum antler score required to be entered into the Iowa Trophy Deer record book's typical category (406.4 cm) is already a large-antlered deer, so it is unclear whether the differences I observed have any biological consequences or relevance. While I observed differences in antler score of one percent, Strickland and Demarais (2000), in contrast, observed statistically significant regional disparities in an antler size index that ranged from 8-24% differences in mature deer in Mississippi.

By examining the landforms, it is apparent that the Southern Iowa Drift Plain landform (SIDP) spans much of the southern half of Iowa and ecological differences between that landform and other landforms may be associated with the latitudinal trend. I performed a post-hoc two-sample *t*-test to compare antler scores between entries from the SIDP to entries from all

other landforms combined, from the typical category, to identify if the mean antler score within the SIDP was significantly different from the mean antler score of all other landforms combined. Entries from the SIDP had significantly larger antler scores than entries from other landforms (Table 17). When examining the largest third of entries from the typical category, the trend was the same though the difference was not statistically significant (Table 18). The SIDP contains a landscape of rolling terrain comprised of a matrix of cultivated crops, grasslands, and wooded areas (Iowa DNR 2017, Prior 1991). The landscape composition of the SIDP differs from the agriculture-dominated landscapes of the northcentral and northwestern areas of Iowa, where row-crops near 80-90% of the landscape, or the heavily-forested Paleozoic Plateau landform in the extreme northeast (Iowa DNR 2017, Prior 1991). It is possible that the observed differences between the SIDP and all the other landforms combined may be related to landscape composition or spatial differences in male deer age-structure between the areas (Monteith et al. 2013, Rivrud et al. 2013). To corroborate my observed findings and further explore population-level differences among landforms, I suggest further examination of antler size of deer among landforms and landscape composition within those landforms that includes specimens ranging the distribution of possible antler size, rather than just the specimens with the largest antlers, while considering age information of the specimens.

There are several limitations to record books that may limit the inferences that can be made about population-level changes or differences in phenotype from the data they contain: a) they only contain the largest specimens of the population due to the minimum size requirements, which are not representative of the entire population, b) they are based on self-reporting by the hunter, so they are unlikely to be complete representations of harvested deer with the largest antlers, especially in early years of record-keeping as full compliance of submission to the record

book cannot be expected immediately after creation, and c) most importantly, most record books do not contain the age of the animal. The lack of age information may be the largest limitation to record books because antler score is heavily influenced by age (Hewitt et al. 2014, Jacobson 1995), and not being able to discern the age of specimens in relation to antler score could cause misinterpretation of data and results of analyses. Festa-Bianchet et al. (2015) demonstrated the limitations of using record books for attempting to monitor population trends through time. Using horn length of bighorn sheep (*Ovis canadensis*) in a simulated record book, they failed to identify simulated population-level phenotypic temporal trends known to be present in the data (Festa-Bianchet et al. 2015).

While record books may be difficult to utilize for making inferences about populations because of the potential biases mentioned previously, they still offer hunters an opportunity to share their harvest statistics with others. Monitoring a more representative sample of the population, such as a segment of the harvested population that includes antler sizes across the normal distribution as well as age information of the specimen, as opposed to the truncated segment available in record books, may be a more effective option for monitoring population-level antler size trends among cervids, but any biases associated with harvest (i.e., selective harvest criteria applied by hunters or management agencies) must be accounted for (Demarais and Strickland 2011).

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Tables and Figures

Table 1. Number of entries, mean antler score, margin of error of mean antler score, and maximum antler score of entries of the non-typical category in the Iowa Trophy Deer record book within the Iowa Department of Natural Resources' Wildlife Management District and Units. Wildlife Management Units are nested within Wildlife Management Districts.

Wildlife Management District	<i>n</i>	Mean	Margin of Error	Max	Wildlife Management Unit	<i>n</i>	Mean	Margin of Error	Max
Central	139	506.2	6.5	745.2	Iowa River	40	508.7	10.3	588.6
					Red Rock	67	500.1	7.7	610.2
					Saylorville	32	515.7	20.0	745.2
Northeast	126	506.8	7.2	716.9	Cedar-Wapsi	16	512.6	27.0	642.9
					Maquoketa	47	508.9	11.1	700.1
					Upper Iowa	63	503.8	10.3	716.9
Northwest	19	504.3	15.1	578.5	Blackhawk	5	494.0	35.4	543.2
					Clear Lake	1	491.2	NA	491.2
					Great Lakes	6	517.4	44.9	578.5
					Prairie Lakes	7	502.2	22.6	547.1
Southeast	178	508.9	5.3	644.5	Odessa	38	515.8	12.5	608.6
					Rathbun	69	508.3	9.4	639.8
					Sugema	71	505.7	7.6	644.5
Southwest	127	505.8	5.6	618.5	Grand River	68	508.1	7.8	584.8
					Missouri River	28	505.5	14.6	618.5
					Nishnabotna	31	501.0	9.3	566.7

Table 2. *Number of entries, mean antler score, margin of error of mean antler score, and maximum antler score of entries of the non-typical category in the Iowa Trophy Deer record book within the National Oceanic and Atmospheric Administration's Climate Divisions.*

Climate Division	n	Mean	Margin of Error	Max
Central	57	506.1	11.9	745.2
Central-East	73	508.0	8.3	700.1
Central-West	36	502.7	12.2	618.5
Northcentral	11	494.0	8.7	513.7
Northeast	90	507.3	8.8	716.9
Northwest	14	517.8	21.4	578.5
Southcentral	161	506.4	5.6	639.8
Southeast	100	510.5	7.0	644.5
Southwest	47	503.1	7.5	566.7

Table 3. *Number of entries, mean antler score, margin of error of mean antler score, and maximum antler score of entries of the non-typical category in the Iowa Trophy Deer record book within Prior's (1991) Landform Regions.*

Landform Region	n	Mean	Margin of Error	Max
Des Moines Lobe	58	507.2	11.8	745.2
Iowan Surface	60	508.7	11.8	716.9
Loess Hills	1	483.2	NA	483.2
Missouri River Alluvial Plain	7	512.5	33.2	569.3
Northwest Iowa Plains	10	524.7	27.5	578.5
Paleozoic Plateau	58	504.0	8.4	610.9
Southern Iowa Drift Plain	395	506.6	3.4	700.1

Table 4. *Number of entries, mean antler score, margin of error of mean antler score, and maximum antler score of entries of the*

typical category in the Iowa Trophy Deer record book within the Iowa Department of Natural Resources' Wildlife Management District and Units. Wildlife Management Units are nested within Wildlife Management Districts.

Wildlife Management District	<i>n</i>	Mean	Margin of Error	Max	Wildlife Management Unit	<i>n</i>	Mean	Margin of Error	Max
Central	346	425.7	1.7	486.1	Iowa River	98	425.0	3.3	478.2
					Red Rock	160	426.4	2.6	482.9
					Saylorville	88	425.1	3.6	486.1
Northeast	327	425.9	1.7	488.6	Cedar-Wapsi	43	426.1	6.4	488.6
					Maquoketa	112	426.3	3.0	480.4
					Upper Iowa	172	425.6	2.2	473.4
Northwest	50	423.4	4.2	464.2	Blackhawk	16	421.6	8.0	464.2
					Clear Lake	9	426.8	13.4	454.0
					Great Lakes	8	428.5	11.8	445.1
					Prairie Lakes	17	420.9	7.2	450.2
Southeast	433	427.1	1.7	493.1	Odessa	101	427.8	3.4	483.2
					Rathbun	167	427.1	2.7	493.1
					Sugema	165	426.7	2.7	489.9
Southwest	283	426.3	2.1	500.7	Grand River	144	426.4	2.9	500.7
					Missouri River	63	425.2	4.5	482.9
					Nishnabotna	76	427.0	4.1	493.7

Table 5. Number of entries, mean antler score, margin of error of mean antler score, and maximum antler score of entries of the typical category in the Iowa Trophy Deer record book within the National Oceanic and Atmospheric Administration's Climate Divisions.

Climate Division	<i>n</i>	Mean	Margin of Error	Max
Central	131	424.6	2.8	486.1
Central-East	184	427.0	2.4	480.4
Central-West	95	425.1	3.3	482.9
Northcentral	31	423.8	6.6	484.5
Northeast	232	425.6	2.0	488.6
Northwest	38	422.8	5.1	464.2
Southcentral	376	427.0	1.8	500.7
Southeast	236	426.7	2.3	489.9
Southwest	116	427.0	3.3	493.7

Table 6. Number of entries, mean antler score, margin of error of mean antler score, and maximum antler score of entries of the typical category in the Iowa Trophy Deer record book within Prior's (1991) Landform Regions.

Landform Region	<i>n</i>	Mean	Margin of Error	Max
Des Moines Lobe	108	423.0	2.9	486.1
Iowan Surface	151	425.8	2.7	488.6
Loess Hills	13	425.5	10.6	466.7
Missouri River Alluvial Plain	18	424.4	9.2	473.7
Northwest Iowa Plains	38	423.3	5.0	464.2
Paleozoic Plateau	169	425.7	2.3	473.4
Southern Iowa Drift Plain	942	426.9	1.1	500.7

Table 7. Results of linear regression analysis used to evaluate temporal trends in antler score in the Iowa Trophy Deer record book. Sample size represents the number of bins for each category.

Trophy category	<i>n</i>	β	<i>P</i>-value
Non-typical	24	-0.03	0.89
Typical	30	-0.05	0.30

Table 8. Results of linear regression analysis used to evaluate temporal trends in antler score of largest and smallest third of entries recorded in the Iowa Trophy Deer record book. Sample size represents the number of bins for each category.

Trophy Category	Largest third of specimens			Smallest third of specimens		
	<i>n</i>	β	<i>P</i>-value	<i>n</i>	β	<i>P</i>-value
Non-typical	15	1.31	0.09	15	0.00	0.97
Typical	24	-0.09	0.11	24	0.02	0.46

Table 9. Summary of eight models of trend surface analysis of the non-typical category within the Iowa Trophy Deer record book. Models are ordered by ΔAIC_c .

Model^a	AIC_c	ΔAIC_c
Score ~ 1	5919.52	0.00
Score ~ x	5921.30	1.78
Score ~ y	5921.38	1.87
Score ~ x + x ²	5922.79	3.27
Score ~ x + y	5923.05	3.53
Score ~ y + y ²	5923.25	3.73
Score ~ x + y + x ² + y ²	5926.15	6.63
Score ~ x + y + x ² + y ² + x*y	5926.63	7.11

^aVariables were latitude (*y*) and longitude (*x*).

Table 10. Summary of eight models of trend surface analysis of the typical category within the Iowa Trophy Deer record book. Models are ordered by ΔAIC_c .

Model ^a	AIC _c	ΔAIC_c
Score ~ y	12213.36	0.00
Score ~ x + y	12213.50	0.14
Score ~ y + y ²	12214.96	1.60
Score ~ 1	12215.60	2.24
Score ~ x + y + x ² + y ²	12216.10	2.74
Score ~ x	12216.87	3.51
Score ~ x + y + x ² + y ² + x*y	12217.74	4.38
Score ~ x + x ²	12218.87	5.51

^aVariables were latitude (y) and longitude (x).

Table 11. Summary of eight models of trend surface analysis of the largest third of entries in the non-typical category of the Iowa Trophy Deer record book. Models are ordered by ΔAIC_c .

Model ^a	AIC _c	ΔAIC_c
Score ~ 1	1992.17	0.00
Score ~ y	1994.01	1.84
Score ~ x	1994.21	2.04
Score ~ y + y ²	1996.03	3.86
Score ~ x + y	1996.09	3.92
Score ~ x + x ²	1996.13	3.96
Score ~ x + y + x ² + y ²	1999.89	7.71
Score ~ x + y + x ² + y ² + x*y	2002.01	9.84

^aVariables were latitude (y) and longitude (x).

Table 12. Summary of eight models of trend surface analysis of the largest third of entries in the typical category of the Iowa Trophy Deer record book. Models are ordered by ΔAIC_c .

Model ^a	AIC _c	ΔAIC_c
Score ~ y	3872.81	0.00
Score ~ y + y ²	3874.23	1.41
Score ~ x + y	3874.69	1.87
Score ~ 1	3875.86	3.04
Score ~ x	3876.83	4.02
Score ~ x + y + x ² + y ²	3878.12	5.31
Score ~ x + y + x ² + y ² + x*y	3878.22	5.40
Score ~ x + x ²	3878.26	5.45

^aVariables were latitude (y) and longitude (x).

Table 13. Results of analysis of variance used to evaluate spatial trends in antler score in Iowa Trophy Deer record book at four different spatial scales.

Trophy Category	Wildlife Management District		Wildlife Management Unit		Climate Division		Landform Region	
	ANOVA	P-value	ANOVA	P-value	ANOVA	P-value	ANOVA	P-value
Non-typical	F _{4,584} = 0.19	0.94	F _{15,573} = 0.66	0.83	F _{8,580} = 0.58	0.80	F _{6,582} = 0.58	0.75
Typical	F _{4,1434} = 0.76	0.55	F _{15,1423} = 0.40	0.98	F _{8,1430} = 0.72	0.68	F _{6,1432} = 1.18	0.31

Table 14. Results of analysis of variance used to evaluate spatial trends in antler score of largest third of entries recorded in Iowa Trophy Deer record book at four different spatial scales.

Trophy Category	Wildlife Management District		Wildlife Management Unit		Climate Division		Landform Region	
	ANOVA	P-value	ANOVA	P-value	ANOVA	P-value	ANOVA	P-value
Non-typical	F _{4,191} = 0.30	0.88	F _{14,181} = 0.71	0.76	F _{8,187} = 0.68	0.71	F _{5,190} = 0.52	0.76
Typical	F _{4,475} = 1.48	0.21	F _{15,464} = 0.96	0.50	F _{8,471} = 1.09	0.37	F _{6,473} = 1.44	0.20

Table 15. Results of linear regression analysis used to evaluate the influence of county weighted average of Corn Suitability Rating 2 (CSR2) on antler score in Iowa Trophy Deer record book.

Trophy category	n	β	P-value
Non-typical	589	0.01	0.92
Typical	1439	-0.06	0.10

Table 16. Results of linear regression analysis used to evaluate the influence of county weighted average of Corn Suitability Rating 2 (CSR2) on antler score of largest third of entries recorded in Iowa Trophy Deer record book.

Trophy category	n	β	P-value
Non-typical	196	0.07	0.77
Typical	480	0.05	0.33

Table 17. Results of post-hoc two-sample t-test comparing antler scores of the typical category in the Iowa Trophy Deer record book between the Southern Iowa Drift Plain (SIDP) Landform Region and all other Landform Regions combined.

Landform Region	<i>n</i>	Mean	Margin of Error	<i>t</i>	df	<i>P</i>-value
SIDP	942	426.9	1.1	-2.13	1437	0.03
Not SIDP	497	424.9	1.4			

Table 18. Results of post-hoc two-sample t-test comparing antler scores of the largest third of entries in the typical category of the Iowa Trophy Deer record book between the Southern Iowa Drift Plain (SIDP) Landform Region and all other Landform Regions combined.

Landform Region	<i>n</i>	Mean	Margin of Error	<i>t</i>	df	<i>P</i>-value
SIDP	322	446.5	1.6	-1.68	478	0.09
Not SIDP	158	444.3	1.9			

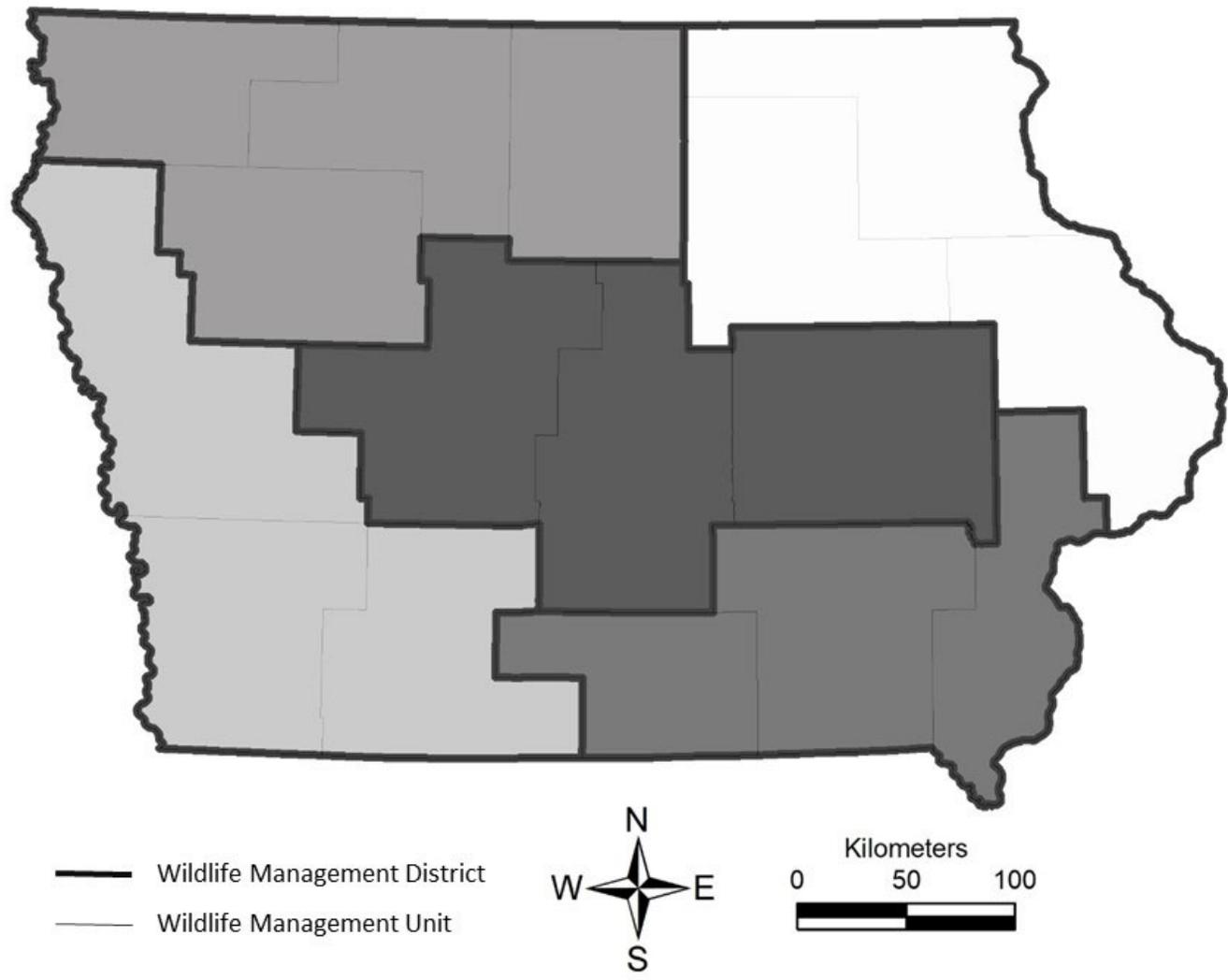


Figure 1. Iowa Department of Natural Resources' Wildlife Management Districts (WMDs). WMDs are further subdivided into Wildlife Management Units.

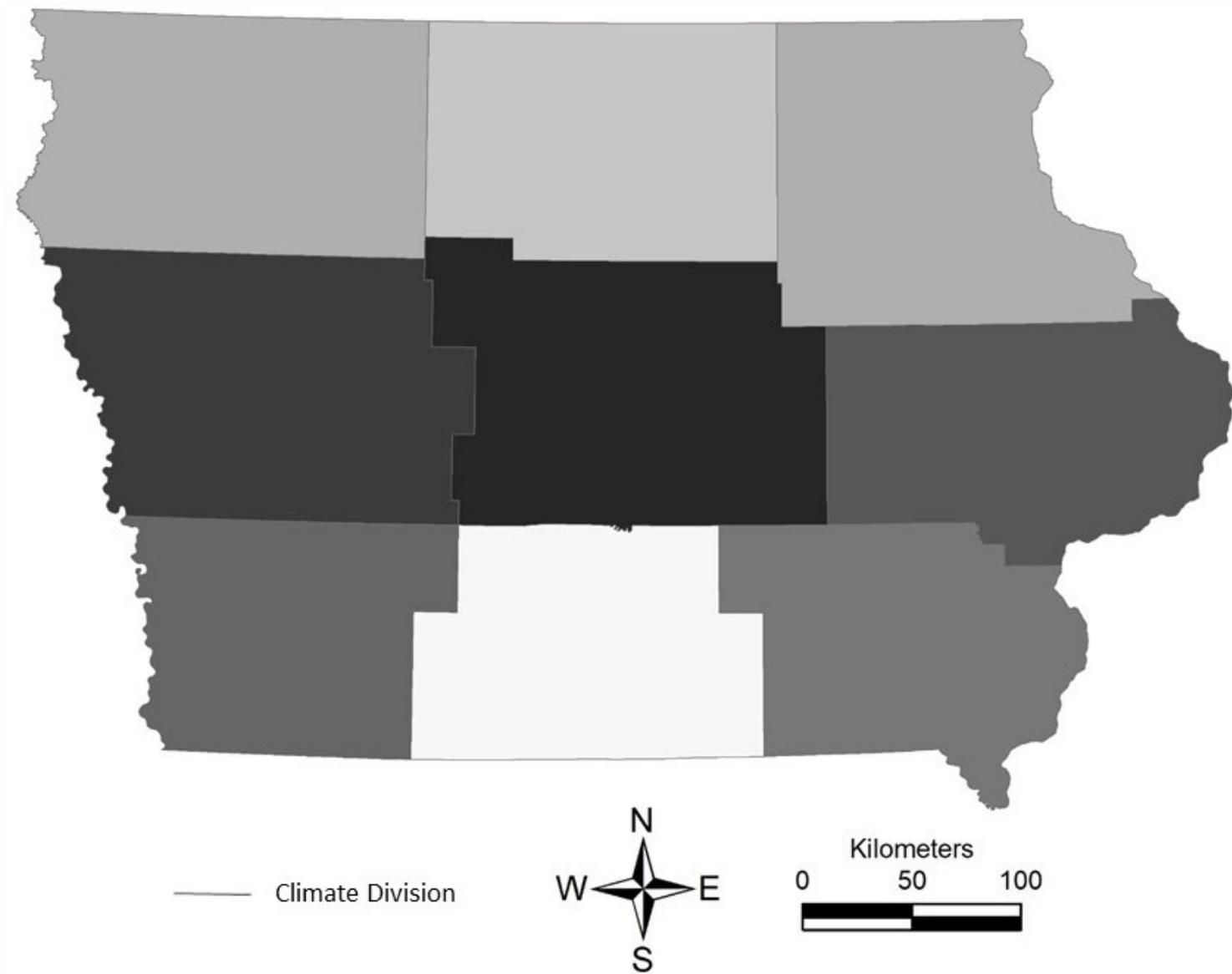


Figure 2. *National Oceanic and Atmospheric Administration's Climate Divisions of Iowa.*

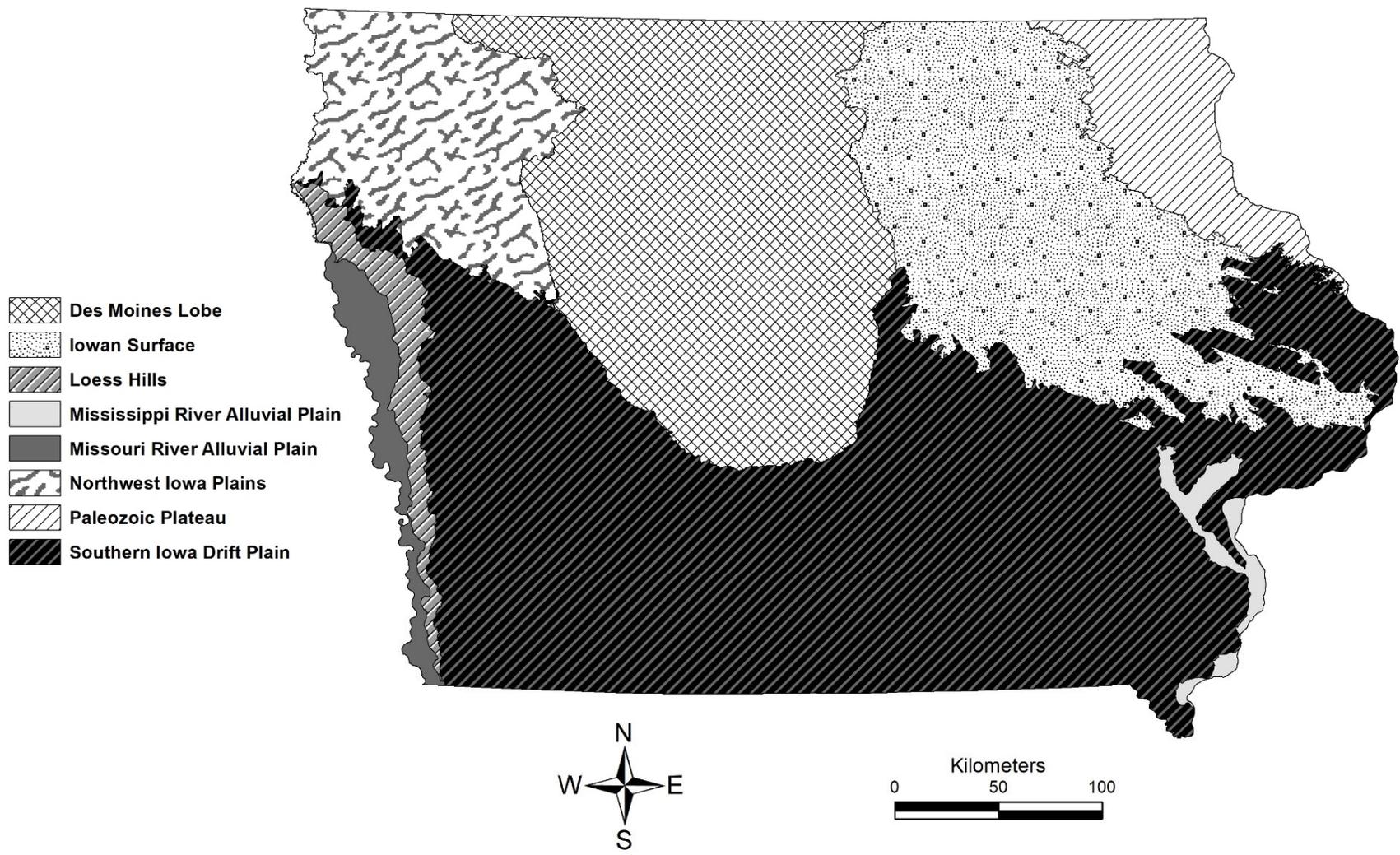


Figure 3. Landform regions of Iowa (Prior 1991).

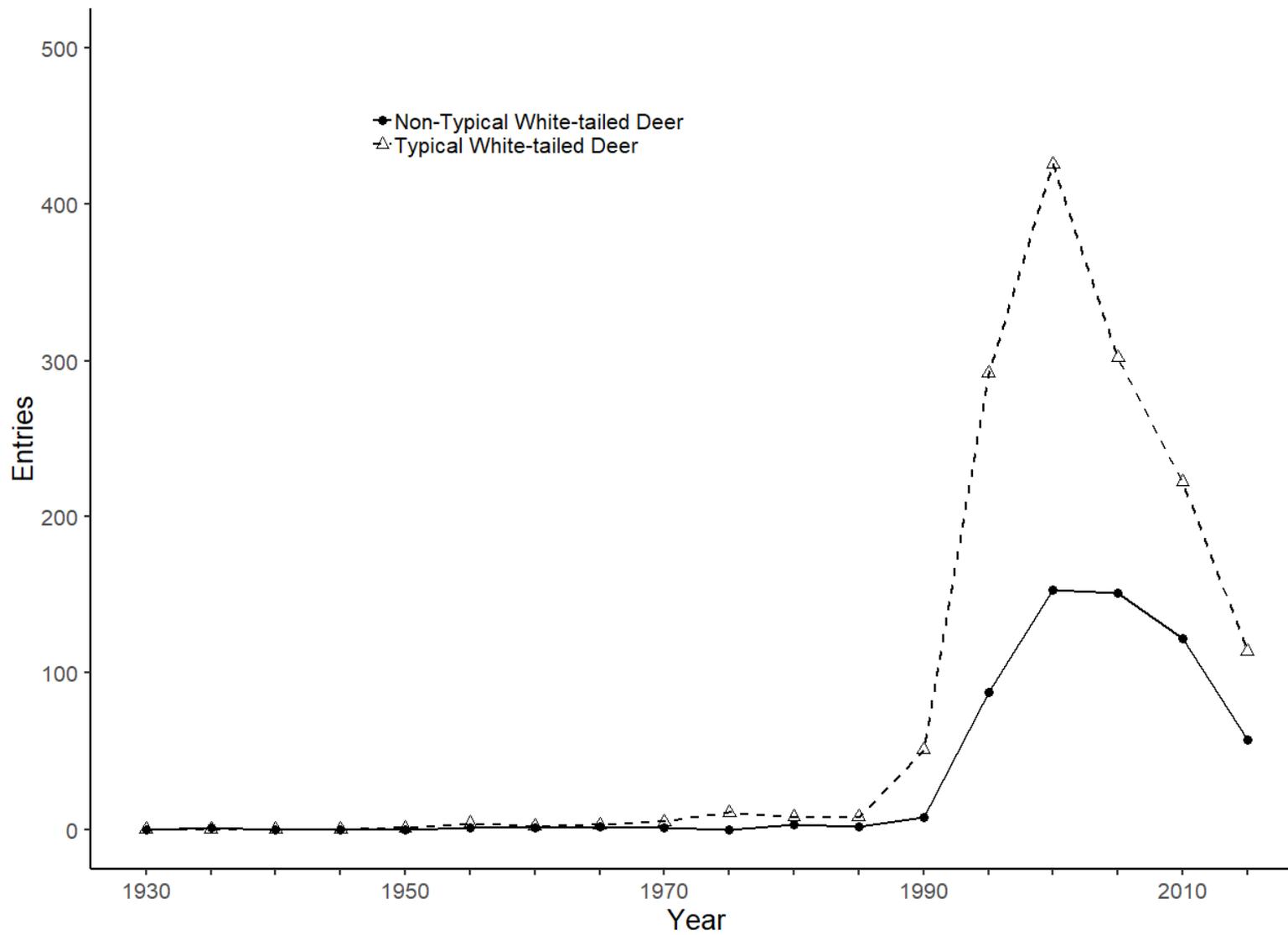


Figure 4. Half-decadal entries recorded in Iowa Trophy Deer record book. Data points represent total number of entries for each category of record book.

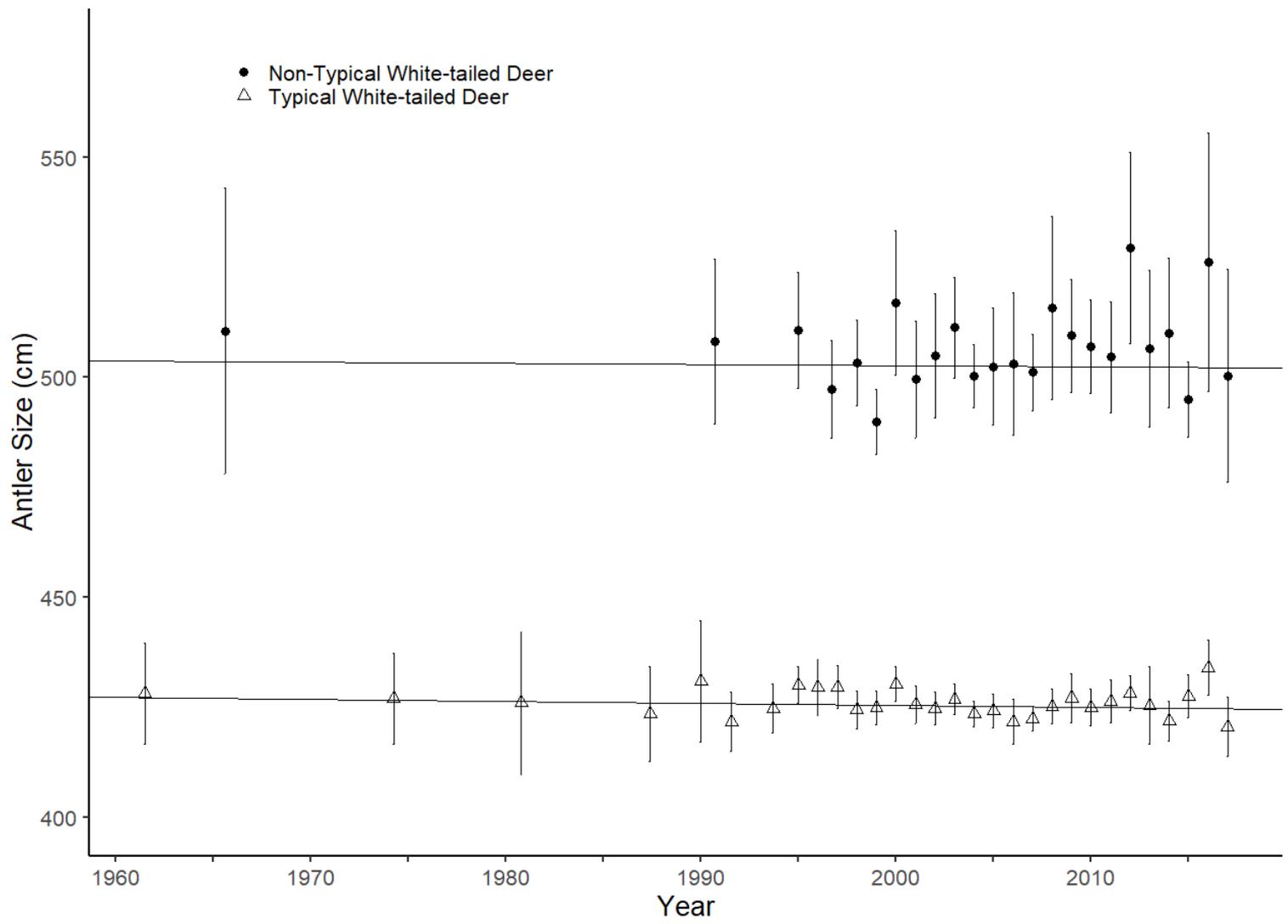


Figure 5. Temporal trends in antler score of entries recorded in Iowa Trophy Deer record book. Data points represent mean ($\pm 95\%$ CI) antler score (cm) of temporal bins containing a minimum of 10 samples; minimum bin length was 1 year. Lines represent fitted least-squares regressions weighted by the inverse of the variance associated with each bin.

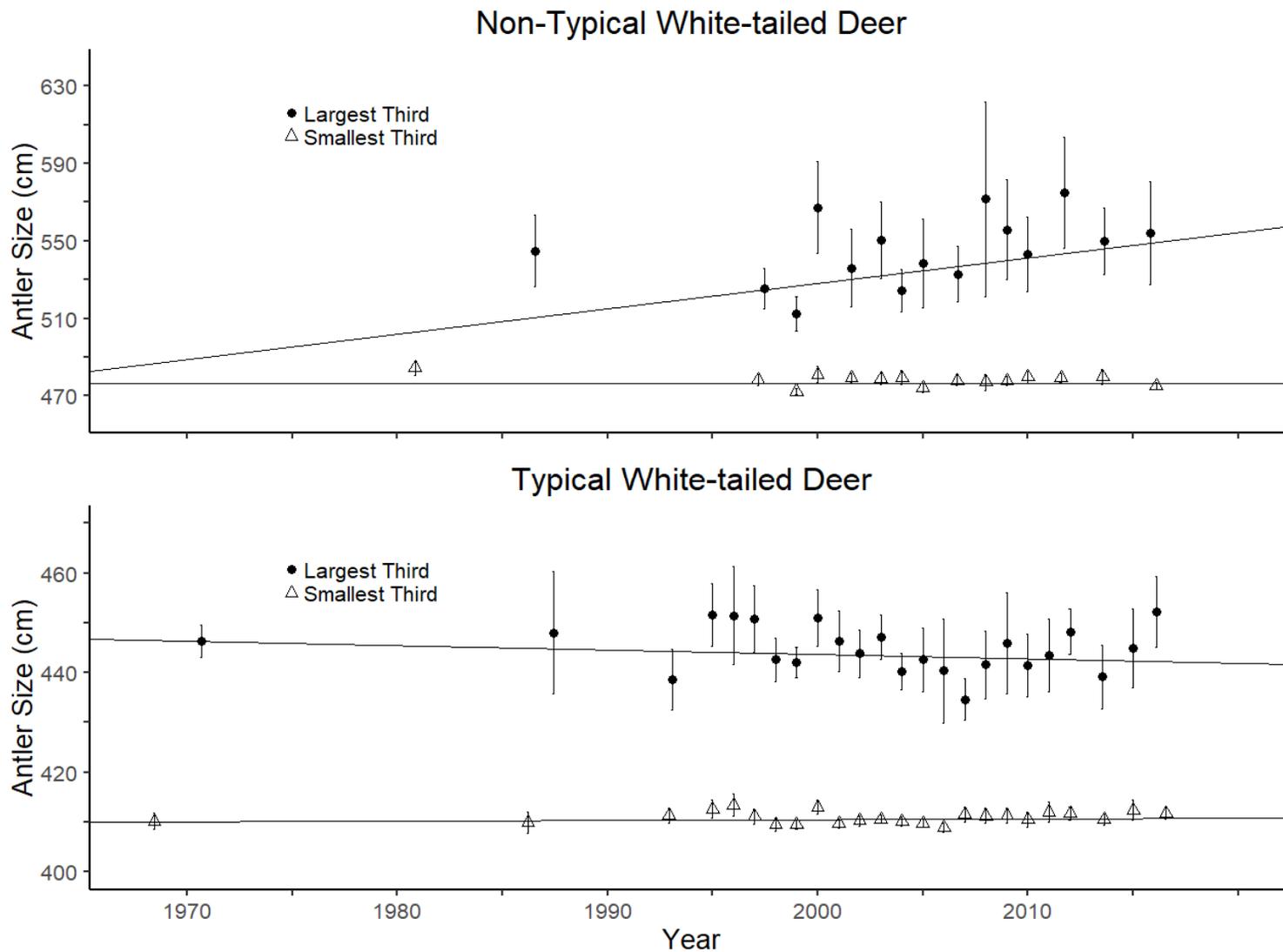


Figure 6. Temporal trends in antler score of the largest and smallest entries recorded in Iowa Trophy Deer record book. Data points represent mean ($\pm 95\%$ CI) antler score (cm) of temporal bins containing a minimum of 8 samples; minimum bin length was 1 year. Lines represent fitted least-squares regressions weighted by the inverse of the variance associated with each bin.

CHAPTER 5. GENERAL CONCLUSIONS

White-tailed deer (*Odocoileus virginianus*) are the most managed species of wildlife in the Midwest and are the economic driver to most Midwestern state wildlife agencies, so continuing to evolve management actions to maintain ecologically and socially acceptable populations is extremely important (VerCauteren and Hygnstrom 2011). My research identified factors associated with antler size of white-tailed deer in Iowa and quantified statewide variation in antler size. My results provide information to biologists and managers interested in antlers as indicators of condition and are relevant to the Midwest.

I examined the precision of cementum annuli (CA) aging and the congruence of age estimates using CA and tooth replacement-and-wear (TRW) for male white-tailed deer. Precision of CA ages from two incisors from the same deer was affected by the level of certainty assigned to the age estimate and the batch in which each of the teeth were aged in. Although a decrease in precision as certainty in the CA age estimate decreased had been documented previously (Asmus and Weckerly 2011, Storm et al. 2014), to my knowledge, this is the first documentation of a batch effect. Congruence rates between the CA and TRW aging methods were similar to another recent study in the Midwest (Storm et al. 2014). Specifically, the yearling age class had the highest congruence rates, followed by an age class comprised of multiple older ages binned into one age class (i.e., ≥ 3 years of age). The 2-year-old age class had the lowest congruence between CA and TRW methods. My findings suggest that for managers relying on TRW to age adult deer that they classify them as either yearlings or ≥ 2 -years-old. If additional age classes are required, managers should invest in CA aging as it is likely to be more, but not perfectly, accurate.

I identified environmental factors associated with variation in antler size of white-tailed deer in Iowa. While several environmental factors were statistically significantly related to antler size, their effect sizes were small compared to the influence of age. Nevertheless, it was surprising to find influence of environmental factors (e.g., land use, soil productivity, weather indices from the year of birth) on Iowa white-tailed deer antler size because deer in the Midwest are not typically considered nutritionally-limited, as they are in other parts of the U.S., due to the abundance of row-crop agriculture (Nixon et al. 1991). Because antlers are condition-dependent (Andersson 1986), these data can contribute to the monitoring of health and condition of Iowa deer populations. I also observed some regional differences in antler size where, generally, southwestern Iowa had larger antler sizes than deer from the northern regions of Iowa. These differences occurred between both Wildlife Management Districts and landform regions and among the older age classes (i.e., 2-year-old and ≥ 3 -years-old age classes) but not in the yearling age class. The regional differences could be a result of the environmental factors I documented and/or aging error. The age-specific mean antler sizes I observed in Iowa were greater than those previously documented in Mississippi and Texas (Jacobson 1995, Hewitt et al. 2014) and the magnitude of the differences of antler size among regions was smaller than previously observed in other studies in West Virginia and Mississippi examining differences in antler size metrics between physiographic regions (Gill 1956; Strickland and Demarais 2000). The ability of deer to allocate nutrients and energy to produce the size of antlers that occur in Iowa, along with only marginal influences of environmental conditions, suggests that white-tailed deer in Iowa have access to adequate forage for antler growth.

I also analyzed historical records from 1937–2017 in the Iowa Trophy Deer record book maintained by the Iowa Department of Natural Resources. I did not find any temporal trends in

antler size of this sample of large-antlered deer, but I did observe a negative latitudinal trend (i.e., antler size increased from north to south) among the typical category of the records. The spatial trends within the record book are similar to my findings from my sample of hunter-harvested deer. However, record books come with biases that may limit their usefulness for making inferences about a population (e.g., focus on the larger segment of the population, reliant on self-reporting, lack of specimen's age information; Festa-Bianchet et al. 2015).

The environmental factors I identified influenced antler size of white-tailed deer in Iowa. However, antler size, when controlling for age, did not vary as greatly across the state compared to previous studies conducted outside of the Midwest. These findings suggest the Iowa landscape offers deer adequate nutritional resources for antler growth, such that age is the primary factor explaining antler size in Iowa white-tailed deer.

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