ENVIRONMENTAL AND GENETIC FACTORS INFLUENCING TRAIT VARIATION IN WHITE-TAILED DEER

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ABSTRACT

Environmental and Genetic Factors Influencing Trait Variation in White-tailed Deer

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Trait variation in wild populations is shaped by the interaction of genetics and the environment. Given these interactions, this thesis explored trait variation in white-tailed deer from two angles: one focused on broad-scale environmental factors, the other on fine-scale genetic mechanisms. The first chapter investigated how climate and habitat variation influence antler size, morphology, and the distribution of record-scoring deer across Ontario, Canada. Our results showed that warmer temperatures and higher percentages of rangeland and forest landcover were linked to larger antlers, while harsher winters with more precipitation had negative effects. The second chapter described the development of novel SNP assays designed to target genetic markers associated with leucism and malocclusions in an isolated island population of white-tailed deer. Together, these results highlight the importance of considering both environmental and genetic factors to understand trait variation in white-tailed deer.

KEYWORDS: white-tailed deer, *Odocoileus virginianus,* phenotypic variation, antlers, climate effects, land cover, Runs of homozygosity, leucism, malocclusion, SNP assay

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TABLE OF CONTENTS

LIST OF TABLES

CHAPTER 2

CHAPTER 3

LIST OF FIGURES

CHAPTER 1

CHAPTER 2

CHAPTER 3

Figure 1: Genotype clustering of a candidate SNP for leucism in white-tailed deer (position 1,514,222 within an ROH on scaffold ref0002511: 1,368,616–1,525,114). Each point represents one individual, with clusters corresponding to homozygous reference (red), heterozygous (green), and homozygous alternate (blue) genotypes. All four leucistic individuals were homozygous for the alternate allele. Among controls, mainland deer (n = 23) included 21 homozygous reference, 1 heterozygous individual and 1 undetermined individual, while Saint Pierre and Miquelon deer (n = 29) included 17 homozygous reference, 8 heterozygous individuals, and 4 undetermined individuals. No controls were homozygous alternate.

CHAPTER 1

GENERAL INTRODUCTION

1.1 GENERAL INTRODUCTION

Variation is the foundation of biodiversity and refers to the measurable differences among two or more samples (Darwin, 1859; Hallgrímsson and Hall, 2011). These differences can be either quantitative or qualitative and can manifest at various biological levels (Gregorius and Gillet, 2015). Biodiversity reflects the variation in traits and functions that allows organisms to adapt to changing environments and ecological pressures like disease, climate change, or habitat loss (Keesing *et al.*, 2010; Gizachew, 2022; Hong *et al.*, 2022). Therefore, variation is vital for maintaining the long-term stability of ecosystems.

1.2 WHAT INFLUENCES TRAIT VARIATION?

Many traits are determined by allelic variation influencing the expression of genes, where the combination of alleles inherited from both parents ultimately dictates how these traits manifest (Cooper, 2000). A dominant allele is one that expresses its phenotype when only one copy is present, while a recessive allele expresses its phenotype only when two copies of the allele (one from each parent) are present since the dominant allele will mask the effect of the recessive one (Cooper, 2000; Alliance and Screening Services, 2009). However, inheritance is not always that simple; most traits are considered complex, meaning they involve interactions between multiple alleles and environmental factors.

Mechanisms underlying genetic variation (or genetic diversity) impact allele combinations and trait expression, thereby affecting the likelihood that these traits will be inherited (Reed, 2007; Bijma, 2011; Almeida *et al.*, 2019). Natural selection, for example, allows populations to respond to selective pressures and can make a species more resilient when facing environmental change (Bell and Gonzalez, 2009; Gregory, 2009). An example of this can be seen in populations of *Arabidopsis thaliana* where differences in flowering times are due to differing temperatures across regions that controls gene expression (Brightbill and Sung, 2022). In warmer regions, the earlier-flowering genotypes have higher fitness, while in cooler climates, the later-flowering genotypes have higher fitness (Brightbill and Sung, 2022).

Genetic drift is another evolutionary process underlying genetic diversity, but instead of being based on differential survival and reproductive success like natural selection, genetic drift occurs by chance through random changes in allele frequencies (Wright, 1931). For instance, in a small population of individuals, a catastrophic event like a severe storm or flood could reduce the number of individuals in the population, leading to the loss of alleles purely by chance. Over time, these random losses result in a population with reduced genetic diversity (Gallardo *et al.*, 1995; Pujolar *et al.*, 2011).

Geographically isolated populations often face reduced gene flow and increased genetic drift, and the isolation can increase chances of mating with a related individual which increases the occurrence of runs of homozygosity (ROHs) (Wright, 1931; Villanova *et al.*, 2017). These ROHs are long stretches of homozygous genotypes that arise from inbreeding, meaning the transmission of identical haplotypes from both parents to offspring (Gibson *et al.*, 2006; Kirin *et al.*, 2010). These regions are distributed in tracks on the chromosome instead of being evenly scattered throughout the genome which can cause an increase in the expression of deleterious traits (McQuillan *et al.*, 2008; Kirin *et al.*, 2010). Understanding these interactions is key to understanding how the drivers of variation influence the inheritance and expression of traits over time.

The environment in which individuals live surrounded also affects phenotypic traits. Access to food, water, and shelter will support an individual's development, while environmental stressors such as malnutrition or exposure to disease can impair it. Studies on wild populations have shown that poor early-life conditions such as limited food availability can result in smaller adult body size and reduced reproductive success in adulthood (Holden *et al.*, 2019; Petrullo *et al.*, 2021; Levy *et al.*, 2023). Human population growth and subsequent development can also disrupt natural habitat use, forcing wildlife to adapt to fragmented and altered landscapes, often leading to dominance by a few adaptable species, loss of biodiversity and a reduction in resource availability (Beissinger and Osborne, 1982; Andren, 1994; Patterson and Power, 2002). At the same time, the human-driven effects of climate change such as rising temperatures, increasing sea levels, and more frequent extreme weather events are causing disturbances to ecosystems around the globe (Pujolar *et al.*, 2011; Hatfield and Prueger, 2015; Dawe and Boutin, 2016; Cockerill *et al.*, 2022). All of these environmental changes can have major consequences on food availability, shelter, migration patterns and subsequently phenotypic variation of individuals (Hautier *et al.*, 2015).

1.3 WHITE-TAILED DEER

Odocoileus virginianus, more commonly known as the white-tailed deer, is one of the most widely distributed mammal species in North America (Hewitt, 2011). Ranging from the northern forests of Canada to the tropical regions of Central and South America, white-tailed deer inhabit a broad spectrum of environments (Hewitt, 2011). This ability to thrive in such a variety of regions is why they are often referred to as habitat generalists (Anstedt, 2016; Staudenmaier *et al.*, 2021). Just as deer adapt to diverse landscapes, they also adjust their diet to suit local food availability. In northern environments, white-tailed deer consume woody browse such as twigs and bark during harsh winters, while in southern environments, they feed on a variety of vegetation year-round including fruits, forbs, and crops (Hewitt, 2011). This flexibility enables not only broad distribution but also the expression of trait differences shaped by the unique environmental conditions white-tailed deer face across their range.

One of the most prominent traits of the white-tailed deer are their antlers. Antlers are large, branched structures composed primarily of bone that are grown from the skulls of male white-tailed deer (Rue, 1989; Hewitt, 2011). Unlike horns, which are permanent, antlers are shed and regrown each year and originate from bony outgrowths called pedicles, which serve as the base for regrowth (Goss, 1983). Antler development is triggered in the spring from increasing day length and rising testosterone levels (Goss, 1983). During this period, antlers grow rapidly beneath a soft layer of highly vascularized skin, known as velvet, which supplies nutrients to the developing tissue. As summer progresses and testosterone levels continue to rise, the antlers finish mineralizing and the velvet begins to dry and is shed, revealing the hardened bone commonly recognized as the antler (Goss, 1983). These mature antlers are used during the autumn breeding season (rut) for dominance displays and combat between males (Clutton-Brock, 1982). In late winter, testosterone levels drop sharply, triggering bone resorption at the base of the antler. This weakens the connection to the pedicle, ultimately leading to antler shedding. The cycle then begins again with the return of spring (Goss, 1983). Because antlers are shed and regrown every year, they often reflect the external conditions of that particular year (Goss, 1983). This characteristic makes them useful for examining the factors that influence trait expression across populations over time.

Antler characteristics, such as size and morphology, are heritable in white-tailed deer with the length of the main beam having an estimated heritability of ~45% and the number of antler tines having an estimated heritability of ~32% (Jamieson *et al.*, 2020). However, the expression of heritable traits can vary depending on environmental factors, especially in traits like antlers which develop annually and over a short time. For example, antler characteristics like number of tines has been found to be highly variable in areas with inconsistent rainfall (Baccus et al., 2017), and antler size has been linked to landscape composition, such as the proportion of agricultural land or pine forest, due to differences in forage quality (Strickland and Demarais, 2008a).

In Ontario, Canada, white-tailed deer are at the northern edge of their eastern North America range (Figure 1; Kennedy-Slaney *et al.*, 2018). Historically, their distribution was concentrated in southern Ontario, where a combination of relatively mild winters, longer growing seasons, and abundant forage in agricultural and deciduous forest landscapes provided adequate habitat and food availability (Ecological Stratification Working Group, 1995; Kennedy-Slaney *et al.*, 2018; Government of Ontario, 2021). As the deer move northward to the boreal forest region, they encounter primarily coniferous and mixed-wood forests, greater snow accumulation, and longer, colder winters (Ecological Stratification Working Group, 1995; Kennedy-Slaney *et al.*, 2018; Government of Ontario, 2021). These harsher conditions had previously limited the white-tailed deer's northern range as greater winter severity reduced forage availability and made movement through deep snow more difficult (Garroway and Broders, 2005;

Kennedy-Slaney *et al.*, 2018). However, since the mid-20th century, average winter temperatures have been on the rise, average snow depths have been decreasing, and spring snow melt has been earlier, all of which have supported a continued northward range expansion (Dyer and Mote, 2006; Kunkel *et al.*, 2016; Kennedy-Slaney *et al.*, 2018). This expansion was further supported in the 1970s and 1980s by intensive management strategies, including regulated hunting via the selective harvest system and winter feeding of white-tailed deer during severe winters (Ontario Ministry of Natural Resources and Forestry, 1997, 2019). The climatic and ecological diversity of Ontario, combined with the continued northward expansion of white-tailed deer, provides a unique framework to study how ecological variation affects trait development. In Chapter 2, we focus on how environmental variables like climate and landcover impact antler size and morphology in white-tailed deer across Ontario, providing a clearer understanding of how environmental conditions can shape antler trait characteristics in the white-tailed deer's more northern range.

While white-tailed deer are widespread across mainland North America, they also inhabit a number of notable islands, including Anticosti Island (Quebec), the Florida Keys (USA), and the French territory of Saint Pierre and Miquelon (France, near the coast of Newfoundland) facilitated by climatic events and deliberate translocation by humans (Lazell, 1989; ONCFS, 2016; Villanova *et al.*, 2017; Fuller *et al.*, 2019). These insular populations present unique ecological conditions such as isolation, limited resources, and reduced gene flow that could influence both the expression of traits and the genetic structure of deer in different ways from their mainland counterparts (Villanova *et al.*, 2017). Saint Pierre and Miquelon (SPM) is a small French territorial archipelago located about 10 km off the southern coast of Newfoundland. The islands offer a unique environment for white-tailed deer with a landscape characterized by rocky, sparsely forested, and shaped by a cold, foggy maritime climate (ONCFS, 2016; Etcheberry, 2022). In 1953, 14 white-tailed deer were introduced to Miquelon-Langlade, the largest island, likely for hunting purposes (origine archives SCM, 1953). Since then, deer harvest regulations have been implemented and the population has become established (origine archives SCM, 1953; ONCFS, 2016).

The white-tailed deer on SPM exhibit a relatively high frequency of two uncommon traits, leucism and malocclusions. Leucism is a partial to complete lack of pigmentation that can result in an unusually pale or white coat in white-tailed deer, which are typically reddish-brown with white fur found on the abdomen, chest, inner legs, chin, ears, around the eyes, and underside of the tail (Hewitt, 2011; Arriaga-Flores *et al.*, 2016). Malocclusions involve the incorrect alignment of the maxillary and the mandible bone whether that be an overbite (maxillary prognathism) or an underbite (mandibular brachygnathism) (Robinette and Aldous, 1955; Signer-Hasler *et al.*, 2014). Leucism is recognized as a recessive trait (Pereira *et al.*, 2023), but inheritance patterns of malocclusions are not as clear (Cakan *et al.*, 2012). These abnormalities are rarely observed elsewhere in the species and could be more common on SPM due to the island's small founding population and prolonged isolation (Cars *et al.*, 2024), which can increase the expression of recessive alleles (McQuillan *et al.*, 2008).

Cars et al. (2024) investigated the effects of isolation and genetic drift on this island population of white-tailed deer in SPM and highlighted how small, isolated populations lead to reduced genetic diversity and an increased frequency of recessive traits, such as leucism and malocclusion. By employing a pseudo case-control design, Cars et al. (2024) were able to pinpoint several ROHs that contained candidate genes possibly linked to these traits, including *LAMTOR2*, associated with pigmentation changes, and *NPVF*, linked to craniofacial abnormalities. This previous work provided a foundation for Chapter 3, where we explored the specific genetic variants within the previously found ROHs that could be associated with leucism and malocclusion. By identifying single nucleotide polymorphisms (SNPs) unique to these ROH when compared to wildtype animals, we aim to uncover diagnostic mutations behind these recessive abnormalities and provide further evidence of these ROHs being biologically meaningful.

Chapters 2 and 3 highlight the complex mechanisms driving trait variation in white-tailed deer. The forces of genetic drift, isolation, and environmental factors each offer deeper insight into how traits evolve across different contexts. Together, these findings contribute to our broader understanding of the forces shaping genetic diversity and trait expression in wildlife populations.

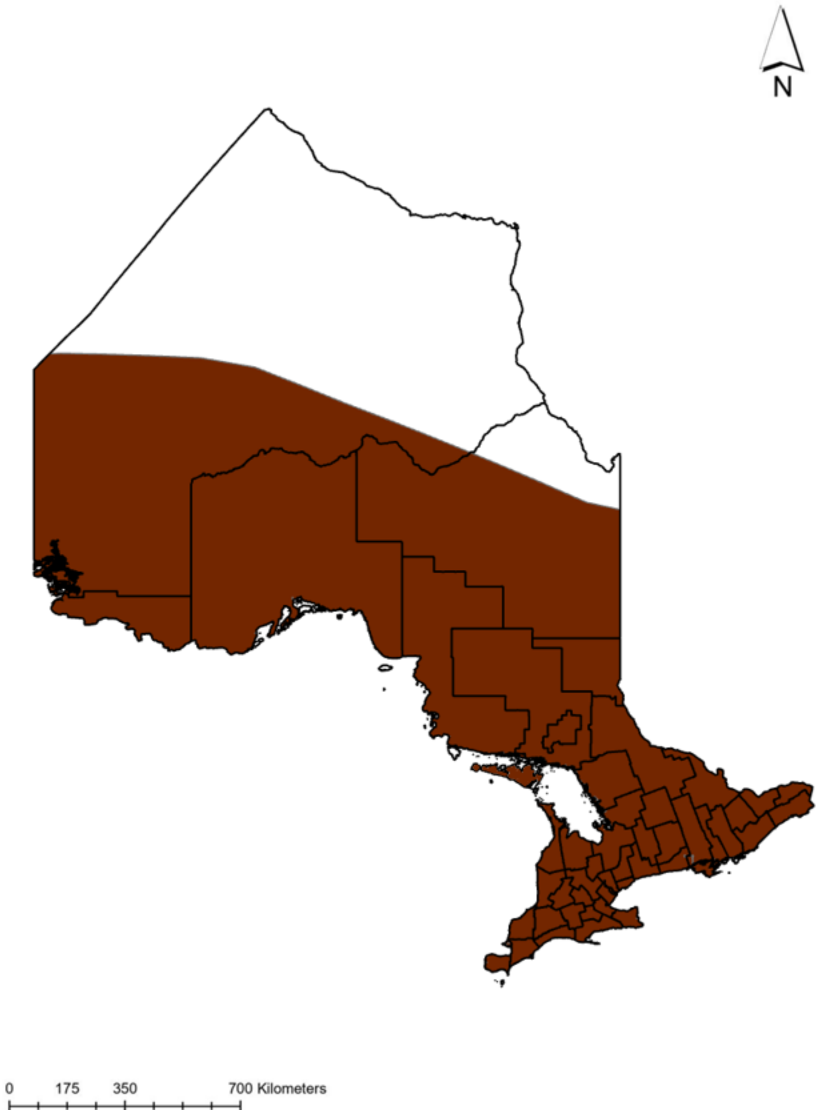

Figure 1. Coarse white-tailed deer range in Ontario, Canada (Gallina, 2015).

CHAPTER 2

ENVIRONMENTAL FACTORS AND TEMPORAL TRENDS INFLUENCING ANTLER CHARACTERISTICS OF TROPHY WHITE-TAILED DEER IN ONTARIO, CANADA

2.1 ABSTRACT

White-tailed deer (*Odocoileus virginianus*) are an ecologically and economically important species in North America. Their antlers, one of their most recognizable features, are used for dominance displays, mate attraction, and defense, with size and morphology being key determinants of success. Antler characteristics are influenced by a combination of genetic and environmental factors, including habitat quality and resource availability. In this study, we explored how diverse environmental factors, including climate and land cover composition, impact antler size, morphology, and the distribution of record-scoring white-tailed deer across Ontario, Canada, using hunter-submitted data from long-term antler scoring records (1997-2022). We used conditional autoregressive (CAR) models to examine these relationships and found that warmer temperatures during the year of harvest were positively associated with larger antlers and more record deer in a given county, while winter precipitation during the year of harvest was negatively associated with these characteristics, likely due to reduced forage availability or increased energy expenditure during more severe winters. Rangeland and forest land cover types were positively associated with increased antler size and tine number. We observed no temporal changes in antler size in Ontario, contrasting with broader trends observed in North America. These results show how local environmental conditions and land cover composition influence antler traits and the distribution of record white-tailed deer, highlighting the complexity of environmental influences on trait variation.

2.2 INTRODUCTION

The Cervidae (deer) family emerged during the late Miocene where they developed the secondary sex characteristics that we associate with modern deer (Gilbert *et al.*, 2006). One such secondary sex characteristic, antlers, are bony extensions of the skull that generally shed every year, and apart from caribou (*Rangifer tarandus*) are found only on males (Rue, 1989; Hewitt, 2011). Antlers have multiple purposes including dominance displays and interactions, use as weapons against predators and conspecific males, and as indicators to females that they are of good genetic quality (Clutton-Brock, 1982; Goss, 1983). In white-tailed deer (*Odocoileus virginianus*), males are the dominant sex where social dominance is largely dictated by age and body mass, both of which are closely tied to antler size (Townsend and Bailey, 1981). Fully matured males tend to have larger antlers due to the lower energy demands for body growth and thus their ability to allocate resources to antlers (Goss, 1983). Likewise, in red deer, larger antlers are associated with increased reproductive success (Kruuk *et al.*, 2002). That being said, younger or smaller-antlered males can achieve mating success if they are more dominant and in good overall health, particularly in populations with a female-skewed sex ratio or a younger male age structure, or by avoiding direct competition with larger males and engaging in opportunistic mating (Townsend and Bailey, 1981; Turner *et al.*, 2016; Partridge, 2017).

Antler characteristics are influenced by both genetic and environmental factors. Jamieson et al. (2020) found that in white-tailed deer >1.5 years old the number of antler tines were approximately 33% heritable, while Michel et al. (2016) found that in captive white-tailed deer 2.5–5.5 years old antler score and main beam length were 56% and 45% heritable, respectively. Accordingly, Anderson et al. (2022) found a suite of genes, with some related to animal health, underlying large antlers. Cain et al. (2019) showed that larger-antlered deer in the Midwest

United States were associated with areas that had an intermixed landscape with more fragmented patches of land cover, suggesting that habitat composition and variety can shape antler growth through changes in resource availability. In the southern United States, Strickland and Demarais (2008) observed a positive association between mean antler size and landcover types that favour early-stage herbaceous vegetation such as agriculture. Intergenerational maternal effects have also been seen to influence antler and other physical traits (Freeman *et al.*, 2013), with for example maternal nutrition influencing offspring body mass and antler size in white-tailed deer (Monteith *et al.*, 2009). Similarly, Peterson et al. (2019) found that years with extreme droughts had lasting effects on antler development in white-tailed deer and that deer born during these years had smaller antlers in later years, suggesting that environmental stress affecting maternal investment and the early-life of deer can have persistent effects on antler growth. Collectively, these studies highlight the need to consider multi-year and spatial environment covariates when modelling trait variation.

In addition to understanding the genetic and environmental factors affecting antler development, white-tailed deer management can have an effect on antler distribution. Across North America, management strategies vary widely, ranging from highly regulated systems with antler-point restrictions and controlled harvests (Strickland and Demarais, 2007) to more liberal frameworks with longer seasons and fewer restrictions on age or sex class (Florida Fish And Wildlife Conservation Commission, 2025). In Ontario (Canada) hunters can purchase a white-tailed deer licence and an antlered deer (i.e. Buck) tag valid for any open deer season, while antlerless deer (female/fawn buck) tags are awarded via random draw for a specific Wildlife Management Unit (WMU) (Ontario Ministry of Natural Resources and Forestry, 2019). This system allows wildlife managers to regulate the population through antlerless tag quotas as females are critical for population growth. Hunters that target male white-tailed deer are often seeking trophy bucks with higher scoring antlers, which are evaluated based on characteristics such as tine length and number, beam length and circumference, and antler spread (D'Angelo and Grund, 2015; Boone and Crockett Club, 2025). As a result of high-scoring bucks often experiencing heavier harvests, there has been a broad, negative trend in the mean antler size of trophy white-tailed deer across North America over the last century (Monteith *et al.*, 2013). This decline is not only important for hunters who might experience reduced opportunities for harvesting large trophy bucks, but the removal of larger males could also disrupt mating structure, potentially resulting in smaller less dominant males having more success (Langvatn and Loison, 1999; Pigeon *et al.*, 2016). This shift could in theory reduce antler size, which would weaken sexual selection and could, in extreme cases, lead to reduced reproductive success and fitness. Evidence of this comes from Malo et al. (2005) who found that in red deer, antler size and complexity were positively associated with sperm quality and quantity. Similarly, Ditchkoff et al. (2001) found that in white-tailed deer, antler development was linked to elevated testosterone during the breeding season and pathogen resistance.

This study aims to determine which environmental factors influence antler size and morphology in white-tailed deer across Ontario, Canada. Long-term antler scoring records provided us with a notable opportunity to examine white-tailed deer antler characteristics and temporal patterns over time and space in the province. We examined the influence of environmental factors on the spatial distribution, tine number, antler symmetry, and overall antler score of record white-tailed deer across Ontario. We hypothesized that antler size in white-tailed deer is positively associated with environmental factors that promote forage availability and minimize energy expenditure. Specifically, we predicted larger antlers in counties with higher proportions of agricultural, rangeland, and forest cover, which provide accessible food and shelter. We also hypothesized that warmer temperatures during growing seasons would be associated with increased antler size, while higher winter precipitation would have a negative effect due to increased energetic demands. Finally, we hypothesized that decades of selective harvest of large-antlered individuals has led to a decline in antler size across Ontario.

2.3 STUDY AREA

White-tailed deer in Ontario, Canada, occupy a diverse landscape with varying anthropogenic influences. Historically, white-tailed deer populations have been concentrated in southern Ontario, where winters are milder and growing seasons are longer compared to more northern parts of the province (Kennedy-Slaney *et al.*, 2018). Southern Ontario is dominated by agricultural and deciduous forests, which provide high-quality forage such as grasses, forbs, and crops during spring and summer (Ecological Stratification Working Group, 1995; Government of Ontario, 2021). The white-tailed deer that live in more central and northern Ontario, including the boreal forest region, experience harsher winters, but inhabit coniferous and mixedwood forests, which offer shelter from snowfall and winter browse (Hewitt, 2011). While browse is lower in nutritional quality, it is abundant during Ontario's colder seasons, making up 74-91% of the white-tailed deer's diet when other vegetation is scarce (Mautz *et al.*, 1976; Hewitt, 2011). Wolves (*Canis lupus*) are the primary predators of white-tailed deer in Ontario, while coyotes (*Canis latrans*) are known to target fawns or individuals in poor condition (Kolenosky, 1972; Cherry *et al.*, 2016). In addition to climate variation, Ontario's expanding infrastructure and growing human population, which has tripled in the last 50 years, has led to an increase in white-tailed deer density and a decline in the availability of their habitat and food (Armstrong *et al.*, 1983; Government of Canada, 2016, 2022). However, the proliferation of agricultural landscapes might increase food availability in some regions further north (Hewitt, 2011).

2.4 METHODS

2.4.1 Data collection

We obtained Ontario antler data from The Foundation for the Recognition of Ontario Wildlife (FROW) for the years 1941 to 2022. FROW is a non-profit organization that manages the records of big game animals in Ontario. Antler measurements for white-tailed deer were submitted by hunters to FROW from every county in Ontario, except Temiskaming. The antler dataset included date of kill (DOK), antler type (typical or atypical), tine numbers and multiple scores following FROW's scoring system, which assigns scores based on additive measurements of the antler including tine length, beam circumference, and spread. FROW has a minimum requirement that must be met in order for a white-tailed deer to be entered into the record book (Atypical score 130 and Typical score 120; Foundation for the Recognition of Ontario Wildlife, 2015), so we refer to these deer as "record deer" hereafter. Because we were interested in assessing the influence of spatial and temporal variables on records, we removed entries that did not contain a county or DOK. Lack of landcover data before 1999 resulted in all record deer entries prior to 1997 being removed in the spatial models. We then assessed the influence of a series of environmental and temporal variables on tine number, gross score, net score, symmetry and the number of record deer per county (All response and predictor variable descriptions can be found in Table S1, available in Supporting Information).

Predictor variables in our model included temperature (^{o}C), precipitation (mm), and number of growing degree days for each county corresponding to the year a record deer was harvested (Table S2, available in Supporting Information). These variables were obtained from Natural Resources Canada (Hutchinson et al., 2009; Hopkinson et al., 2011; McKenney et al., 2011). We extracted temperature and precipitation data from the months March to August as these are the months when antler growth occurs (Hewitt, 2011). For precipitation we also extracted the months January to March to gauge winter severity through snow fall. Precipitation data were averaged per year and county. For temperature, we followed Siegert *et al.* (2013) and calculated the yearly temperature difference by subtracting each county's average temperature over the time series from the temperature for each individual year. The temperature and precipitation data for one year prior to the DOK and two years prior to the DOK were also extracted.

ArcGIS pro (version 3.1.3; Johnston and Environmental Systems Research Institute, 2004), was used to extract landcover data. We used two land cover layers: the Ontario Land Cover Compilation v.2.0 (Land Information Ontario, 2023a) which captured the years 1999 to 2011 and Ontario Land Cover Version 1.0 (‘Ontario Land Cover Version 1.0 - Overview’) which captured the years 2015 to 2020. Both land cover layers are raster datasets with a 15-metre spatial resolution and a minimum mapping unit of 0.5 hectares. Depending on their DOK the record deer were assigned to a landcover dataset (Table S2). For the years not captured by the landcover databases (2012-2014), whichever layer encompassed the year closer to the DOK was used. Reclassification of the land cover categories within these databases was completed to ensure consistency between land cover types: reclassified categories were: agriculture, infrastructure, deciduous forest, coniferous forest, mixed forest, other forest, rangeland, water, wetlands, and other landcover types (Fig. 1, Table S3). The proportion of each landcover type per county was calculated (Table S4), and “other landcover” was dropped in order to interpret the relationship between the response variable and the proportion covariates (Valle *et al.*, 2024).

The final three predictor variables used were average county elevation (meters;

TessaDEM v1.2 2024), county size (km^2) and deer abundance (Table S2). Average county elevation and county size were fixed variables, with the values used per county staying constant over the study period. A relative index of white-tailed deer abundance per county was generated using data from provincial hunter surveys (Government of Ontario, 2025b). Each year, the Ontario Ministry of Natural Resources has collected information through hunter surveys on hunting activities. As part of this survey, hunters are asked to report the number of deer they saw during their hunt and the total number of days they hunted, providing a metric of the deer seen per day. These values were averaged across all available years (2008-2023) in each county to provide a single estimate per county.

2.4.2 Statistical analysis

The following predictor variables were standardized (centered to a mean of zero and scaled to a standard deviation of one) prior to analysis: average county elevation, precipitation (winter and antler growing season), estimated deer abundance, and growing degree days. Temperature predictors were not standardized because they were already transformed to reflect deviations from long-term county-level averages. We assessed pairwise correlations among the variables, removing those with a correlation greater than 0.70 or less than -0.70 (i.e. Dormann et al. 2013). Landcover variables were excluded from the correlation assessment since they are proportion data, therefore, changes in one necessarily correspond to changes in others, making high correlations expected and not indicative of problematic collinearity (Valle *et al.*, 2024). We then fit a series of models to each response variable. All spatial models were fitted using the S.CARmultilevel function from the CARBayes package in R (v.6.1.1Lee, 2013, R Core Team 2023). These models capture spatial autocorrelation by incorporating spatial random effects modeled with a Leroux conditional autoregressive prior, where neighboring counties are defined by shared borders. Model fitting occurred within a Bayesian framework using Markov chain Monte Carlo (MCMC) simulation with default priors applied to all model parameters. All model specifications, including response variables and full lists of predictors, can be found in Table S5, available in supporting information.

To assess the number of record deer harvested in each county, we used a Poisson regression with a county area offset to ensure that the number of record deer was not an artifact of county size. We summed the total number of record deer harvested per county across all years so DOK was not considered when assigning temperature and precipitation in this model. Instead, average values for the temperature and precipitation of each county over the specified time span were used. The averaging of these environmental variables allowed us to observe relationships between the environment and the spatial distribution of record deer harvests across Ontario counties over the entire study period.

To evaluate antler characteristics, we used DOK when assigning temperature, precipitation and landcover values which allowed us to observe spatial-temporal relationships at the individual level. Each model used one of three distributions and their standard link functions: Poisson regression model with a log link to assess the number of antler tines, a binomial regression model with a logistic link (logit) to assess antler symmetry (symmetrical = 0, asymmetrical = 1) and gaussian regression models with identity links to assess antler score (Net and Gross). Antler score was also log-transformed to normalize its distribution and improve model fit.

We evaluated parameter significance based on the probability of direction (pd) which provided the probability each covariate either positively or negatively influenced antler characteristics (Makowski *et al.*, 2019). Parameters with a probability ≥ 97.5% were considered to have a high probability of affecting the antler trait. Parameters with a probability of 95 – 97.5% were considered to have a moderate probability of affecting the antler trait. And parameters with a probability of 90 – 95% were considered to have a weak, but present, probability of affecting the antler trait. All probabilities below 90% were considered to have no effect (Lohr *et al.*, 2020; Dias *et al.*, 2025). Spatial autocorrelation (ρ) was interpreted such that values near 0 indicated spatial independence and values near 1 indicated strong spatial dependence, so, ρ was considered high if > 0.7, moderate if 0.3–0.7, and low if < 0.3. Spatial variance (τ^2) and residual variance (σ^2) were considered high if values approached or exceeded 1 and low if around or below 0.01, based on the Inverse-Gamma (1, 0.01) priors, which assume most variation is near zero unless the data strongly indicates otherwise (Lee, 2013).

Finally, standard generalized linear models (GLMs) from the base r package (R Core Team, 2023) were used to assess temporal trends in antler score and tine number, with year as the predictor variable. Harvest data were sparse before 1980 and so we used only entries from 1980 onward for these GLMs. Additionally, minimum scoring requirements increased in 2006, so all records from 1980 to 2006 below this adjusted score were excluded (i.e. Atypical score 130 and Typical score 120; Foundation for the Recognition of Ontario Wildlife, 2015).

No additional offsets or weights were applied to the models. Model assumptions were assessed using standard analyses, including residual normality and homoscedasticity for the Gaussian models, and overdispersion for Poisson and Binomial models. It should also be noted that this data was hunter-submitted and therefore is likely to be non-random and influenced by variation in hunting effort or harvest efficiency, which are not explicitly captured in our models.

2.5 RESULTS

The final dataset after cleaning consisted of 2,413 entries between 1997 and 2022, and

3,072 entries between 1980 and 2022. Number of growing days was removed due to its high correlation with temperature (Fig S1). Temperature was kept as it directly reflects seasonal climate variation and is easier to interpret. Deer abundance was also removed due to its high correlation with agriculture (Fig S1). Residuals from gaussian models were normal, and no overdispersion was detected in binomial or Poisson models.

Average temperature had a strong probability of having a positive effect on the number of record deer per county (Fig. 2; $\beta = 1.24$, pd = 99.9%). Elevation then showed a weak probability of having a positive effect (Fig. 2; $\beta = 0.31$, pd = 94.3%). This model had a strong τ^2 (0.98) and moderate ρ (0.46). For tine number, the temperature 1 year prior to the year of harvest had a strong probability of having a positive effect (Fig 2; $\beta = 0.02$, pd = 99.1%). The temperature of the year of harvest and the percentage of Rangeland per county then had a weak probability of having positive effects (Fig 2 & 3; $\beta = 0.01$, pd = 91.1% and $\beta = 0.94$, pd = 92.2%, respectively). This model had a low τ^2 (0.003) and moderate ρ (0.63). For antler symmetry, precipitation during antler growth 2 years prior to the year of harvest had a strong probability of having a negative effect (Fig 2; $\beta = -0.12$, pd = 98.6%), while the temperature of the year of harvest had a moderate probability of having a positive effect (Fig 2; $\beta = 0.10$, pd = 95.6%). This model had a low τ^2 (0.03) and moderate ρ (0.38).

For Gross Score, we found the temperature the year of harvest had a strong probability of having a positive effect (Fig 2; $\beta = 0.01$, pd = 100%), while precipitation during the winter the year of harvest had a strong probability of having a negative effect (Fig 2; $\beta = -0.01$, pd = 97.8%). Precipitation during antler growth during the year of harvest and precipitation during the winter 1 year prior to the year of harvest both had moderate probabilities of having positive effects (Fig 2; $\beta = 0.01$, pd = 96.8% and $\beta = 0.01$, 96.5%, respectively), and temperature 2 years prior to harvest and the percentage of Deciduous Forest per county had weak probabilities of positive effects (Fig 2 & 3; β = 0.003, pd = 91.4% and β = 0.22, 93.4%, respectively). This model had τ^2 and v^2, which were relatively low (0.001 and 0.01 respectively), and a moderate ρ (0.70).

For Net Score, temperature the year of harvest, temperature 2 years prior to the year of harvest and the percentage of Rangeland per county had strong probabilities of having a positive effect (Fig 2 & 3; β = 0.01, pd = 100%, β = 0.01, pd = 99.2% and β = 0.58, 98.9%, respectively). The percentage of Deciduous Forest per county had a moderate probability of having a positive effect (Fig 3, β = 0.27, pd = 96.0%). The precipitation during antler growth the year of harvest and the percentage of Coniferous Forest per county both had weak probabilities of positive effects (Fig 2 & 3; β = 0.004, pd = 92.8% and β = 0.28, pd = 94.8%, respectively), while the precipitation during the winter the year of harvest had a probability of having a weak but negative effect (Fig 2 & 3; β = -0.004, pd = 91.1%). τ^2 and v^2 were relatively low (0.002 and 0.01 respectively), and ρ was moderately high (β =0.74). Finally, there was no temporal trend in size and tine number over time (Table S6, available in Supporting Information).

2.6 DISCUSSION

The recreational hunting of white-tailed deer brings in millions of dollars to the Canadian economy annually (Fish and Wildlife Ontario, 2016). To the Indigenous peoples of North America, white-tailed deer are a food source whose antlers and hides provide material for clothing, tools, and shelter, while also playing an important role in spiritual ceremonies (Brown, 2011). Despite their economic and cultural importance, the size of trophy antlers appears to be declining across North America (Monteith *et al.*, 2013). This decline showcases the need to better understand the factors influencing antler growth on a regional level, with some studies suggesting that landscapes featuring a mixture of forest, grassland, and agriculture that create an abundance of edge habitats could increase the abundance of harvested record deer (Cain *et al.*, 2019). Accordingly, we investigated spatial drivers and temporal patterns of harvested record deer in Ontario, Canada. We observed that increases in temperature during the month's antler growth is occurring (March-August), positively influenced all antler characteristics (Fig 2), and that rangeland and forest makeup are key landscape components correlated to overall increase in antler size. Further, the temporal trend model found no change in antler size from 190 to 2022 in Ontario (Fig. 4), likely due to relatively lower deer densities and harsher winters compared to southern regions of North America where longer growing seasons aid in antler growth (Garroway and Broders, 2005; Conner, 2021; Sontheimer *et al.*, 2024). This data set is representative of adult antlered white-tailed deer in Ontario and although not a random sample, the data captures a large range of variation in antler size across the population (Fig S2, available in Supporting Information) and temporal, spatial and environmental influences will be reflected in this large sample of male white-tailed deer (see also Strickland and Demarais, 2008; Monteith *et al.*, 2013; Cain *et al.*, 2019). It should also be noted that, although some effect sizes presented are small, they nonetheless represent measurable changes that are noteworthy the interpretation of this study.

To account for spatial dependence in our data and better understand regional patterns, we used CAR models, which revealed moderate to high spatial autocorrelation (ρ) in all models, revealing that nearby counties tend to have similar conditions (i.e., temperature). However, these values also indicate that some unaccounted-for spatial covariates are still present but not explicitly modeled. Possible missing covariates worth further exploration include land productivity, which affects forage availability, landcover structure that shapes shelter and feeding opportunities, and the distribution of minerals like phosphorus and calcium, which are involved in bone and antler development (Grasman and Hellgren, 1993; Cain *et al.*, 2019), though the appropriate GIS layers currently do not exist for Ontario. We also observed low τ^2 in models assessing antler characteristics indicating that, although the predictors often have similar conditions in neighboring counties, antler size did not exhibit strong spatial structure. However, a strong τ^2 when assessing the count of record deer per county does suggest that counties with higher numbers of record deer are more likely to have neighboring counties with similarly high counts, likely reflective of variation regional hunting interest and behaviour. Notably, hunter behaviour and success — which will vary by roads, dwellings, and accessibility and regional differences in hunter effort such as the number of hunters and frequency of hunting — might also contribute to these spatial patterns (Kilgo *et al.*, 1998; Bonnot *et al.*, 2013).

2.6.1 Environmental drivers of record antlers

Temperature was the most consistent environmental driver of antler traits: higher temperature was related to an increase in antler size metrics in all models (Fig 2). During antler growing season of the year of harvest a 1 °C increase above the county's long-term average was associated with a ~1% increase in tine number, a ~11% increase in symmetry, and a ~1% increase in score. Warmer temperatures have been linked to larger antlers and greater reproductive success in white-tailed deer and other Cervidae (Simard *et al.*, 2010; Clements *et al.*, 2010). Increased plant growth from warmer conditions means more forage availability for the deer and therefore more energy is able to be allocated to antler growth (French *et al.*, 1956; Hatfield and Prueger, 2015). Here, the unique annual regrowth of antlers makes them strongly affected by yearly temperature changes (Foley *et al.*, 2012). When looking at tine number and score, the temperature 1 year prior to harvest and 2 years prior to harvest respectively, also had positive effects on antler size and morphology (Fig. 2). Antler growth depends on the accumulation of resources stored in the animal's body, warmer environments, and in turn higher nutritional gain, in prior years can enhance fat reserves which are then used in subsequent antler cycles when that energy is needed (Hewitt, 2011).

Similar inference can be made from the influence of precipitation during antler growth the year of harvest on antler size. Wetter conditions can lead to increased plant growth which could again affect the annual regrowth of antlers (Foley *et al.*, 2012; Scharwies and Dinneny, 2019). A 1-mm increase in average precipitation was associated with a ~1% increase in net score. Conversely, we saw negative effects from precipitation during the winter the year of harvest on antler size (Fig 2). More snow in winter can make it more difficult for the deer to move around and find forage, which causes them to congregate in deer yards (Government of Ontario, 2019). Deer yards are an area made up of coniferous trees that have a large canopy which can reduce on-the-ground snow accumulation (Government of Ontario, 2019). With deer being confined to these yards the density of deer and the availability of forage for each individual animal decreases (Patterson and Power, 2002). This could then put individuals with poor body conditions at a disadvantage and minimal fat reserves when antler regrowth commences (Lesage *et al.*, 2001). Future work might corroborate this finding by incorporating direct measurements of snow depth, snow cover duration, or broader indices such as the Winter Severity Index to capture more details on the energetic challenges white-tailed deer face during the winter months.

Rangeland and Forest landcover had positive effects on antler characteristics, meaning that as the percentages of these types of landcover in each county rose so too did antler score and tine number (Fig 5). Rangeland and Forest together have been found to increase the harvest of record deer and are ideal prime edge habitats (Cain *et al.*, 2019). Forests block excessive snowfall and contain large amounts of northern deer's primary food source, browse (Hewitt, 2011). Further, rangeland allows for greater visibility of large antlered bucks from further away, potentially increasing hunter success or improving the effectiveness of dominance displays and mate attraction, while also providing food such as grasses (Gilbert *et al.*, 2006; Hewitt, 2011; Houde *et al.*, 2020). Collectively, these combined edge habitats are preferred by white-tailed deer as it allows them to have a larger variety of food sources and provides both more space for movement (rangeland) while still having adequate cover (forest) (Halls, 1984; Alverson *et al.*, 1988).

2.6.2 Number of harvested deer and antler symmetry

We observed that increased average temperatures were associated with more record white-tailed deer being harvested in a given Ontario county, with a 1 °C increase above the county's long-term average during the year of harvest corresponding to a ~3.5-fold increase in the expected number of record-sized deer. Similar to antler size, warmer temperatures likely allow for more forage availability assuming deer densities are not overwhelming the landscape. With more food available, more energy is able to be allocated to individual deer in a county, presumably allowing more to reach record deer status. The number of record deer harvested were not significantly affected by any landcover covariates (Fig 3); so, while landcover type positively impacted antler size, the overall effect is minor such that it did not increase the net number of large animals harvested in a given year. Curiously, record deer numbers were positively affected by elevation (Fig. 2). It is tempting to suggest this being reflective of mature deer finding refuge from human activity via fewer roadways at these elevations. Less trafficked zones allow deer to move more freely and access critical resources with minimal human interference (Hamilton *et al.*, 2024) and behaviourally deer learn to avoid humans (Kilgo *et al.*, 1998; Marantz *et al.*, 2016). However, the topographic relief is small in the province (0 m – 700 m) and obfuscated when averaged across each county, as done here (66 m – 415 m), and thus finer scale analysis is warranted to better understand this effect.

The symmetry of antlers appears to be impacted by precipitation, with higher precipitation levels 2 years prior to antler growth resulting in less symmetrical antlers. Under uniform environmental conditions, white-tailed deer exhibit a genetic predisposition for antlers to grow symmetrically (Ditchkoff *et al.*, 2001). White-tailed deer can develop antler asymmetry when exposed to stressors such as environmental conditions, disease, or injury that affect energy allocation before and during antler growth (Marburger *et al.*, 1972; Goss, 1983; Wild *et al.*, 2022). However, the mechanism by which precipitation 2 years prior increases asymmetry is unclear. Nevertheless, maternal effects on antler size are documented in cervids (Freeman *et al.*, 2013), so early-in-life conditions can impact adult traits, with the impact to antlers seemingly long-lasting (Freeman *et al.*, 2013). Asymmetry has also been seen to increase as trait size increases (De Coster *et al.*, 2013), which we observed in our data set (Fig S3, available in Supporting Information); however, we saw no strong relationship between precipitation and antler size, making this explanation unlikely. It is thus conceivable that high environmental stressors might have long-term impacts on symmetry, even for antlers that are shed annually.

2.6.3 Temporal patterns of antler size

Over the last 40 years, there has been no significant change in antler size (or score) and the tine number of harvested record white-tailed deer in Ontario (Table S6). This contrasts the findings of Monteith et al. (2013) who reported a negative trend across North America in antler size in white-tailed deer from 1950 to 2008, based on trophy records of mature males submitted to the Boone and Crockett Club's *Records of North American Big Game* (Boone and Crockett Club, 2025). These negative trends were hypothesized to be a combination of harvest-induced reduction in age structure, sociological effects and density dependence (Monteith *et al.*, 2013). Our finding suggests that antler trends in white-tailed deer are region-specific and might change depending on the environment and pressures present.

In Ontario, the number of active hunters has stayed relatively consistent since 2008 while the number of records submitted to FROW has declined (Fig 6). This could be indicative of a possible shift in hunting priorities (Monteith et al. 2013), but multiple tough winters in 2007/2008 and 2010/2011, have coincided with apparent population declines (Ontario Outdoors Magazine Game Forecast, 2009, 2011) which might explain a decrease in entries. Still, the number of white-tailed deer in Ontario are relatively low especially compared to other regions of North America where population numbers are substantially higher. For example, Michigan with similar environmental conditions to Ontario and an area of 250,493 km^2 has a population of ~2 million white-tailed deer, compared to Ontario with an area of over 1 million km^2 and a white-tailed deer population of ~400 thousand (Mason, 2016; Conner, 2021). Lower density likely reduces competition for resources, allowing individual deer to achieve better body condition and maintain antler sizes (Keyser *et al.*, 2005). Additionally, Ontario's more conservative hunting regulations, such as being allotted only one antlered tag and allocating antlerless tags by lottery, help sustain a balanced age and sex structure by controlling harvest pressure, particularly on mature males and reproductive females (Government of Ontario, 2025a). In contrast, some regions in the USA with higher deer densities have more liberal harvest regulations, such as Florida that allows up to 5 deer of which 2 can be antlerless (Florida Fish And Wildlife

Conservation Commission, 2025). Together, Ontario’s lower deer density and stricter harvest regulations likely contribute to stable antler sizes by reducing overharvest of trophy bucks and preserving a healthier population structure.

In much of North America, warmer climates lead to longer growing seasons and an abundance of high-quality food, which allows white-tailed deer to reach their maximum physical size during antler growth (Mysterud *et al.*, 2005; Sontheimer *et al.*, 2024). In contrast, Ontario’s colder winters limit access to nutritious food, which could be preventing deer from achieving their full antler growth potential; this limitation could mean there is still room for growth. Our models indicate that warming temperatures in Ontario are positively influencing antler development, as milder winters and longer growing seasons improve food availability. With ongoing climate changes, we would predict a positive trend in overall antler size if environmental conditions became more favourable for deer and harvest pressures remain similar.

2.7 MANAGEMENT IMPLICATIONS

Our findings highlight how variation in habitat conditions across Ontario counties are related to differences in antler size and morphology as well as record white-tailed deer distributions. Understanding these patterns and relationships can help identify conditions more likely to produce larger antlered deer, and by communicating these findings, hunters can better manage their expectations and recognize aspects that could cause certain regions to have higher large-antlered white-tailed deer concentrations, leading to greater satisfaction (D’Angelo and Grund, 2015). An increase in hunter satisfaction should, in turn, generate revenue that supports the funding of conservation efforts, wildlife management programs, and local economies. With no significant temporal trend in antler size, the current harvest practices in Ontario are likely effective, but we note increased harvest pressure on males in other regions has led to a reduction in age structure (Langvatn and Loison, 1999; Mysterud, 2011). Density dependence also disproportionately affects large males, as they often enter the winter months with low fat reserves from energy expenditure during the mating season (Lesage *et al.*, 2001; Keyser *et al.*, 2005), which could have implications for survival and future antler growth. This reinforces the need to continue to monitor harvest practices to ensure that population dynamics and habitat limitations do not negatively impact the long-term sustainability of Ontario's white-tailed deer population. Our findings provide valuable insight into how environmental variation is shaping antler characteristics and white-tailed deer distributions, contributing to a deeper understanding of population dynamics and habitat influences.

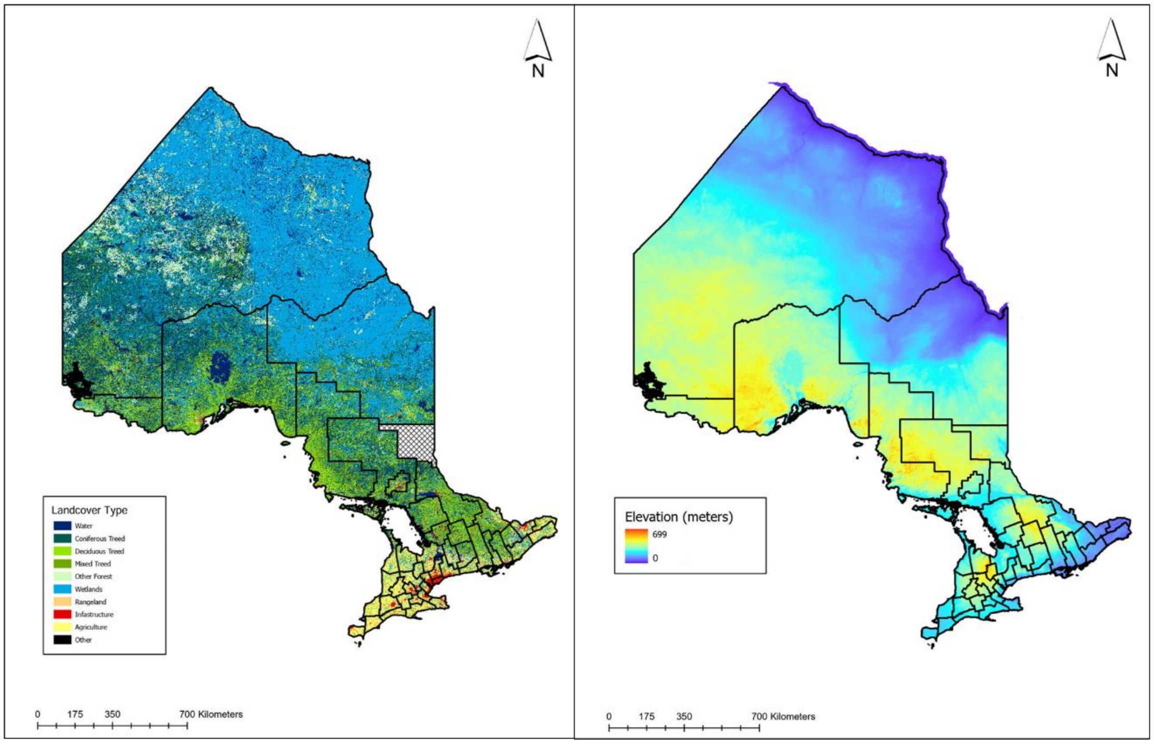

Figure 1. Land cover distribution (Left) and elevation (Right) depicted by county.

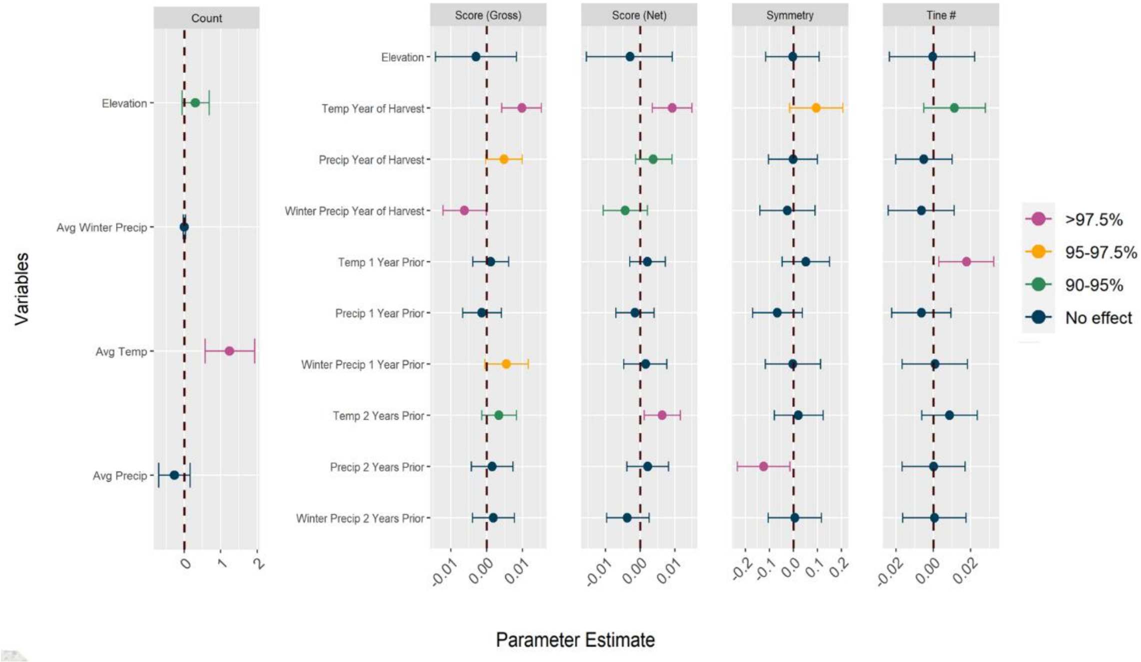

Figure 2. Probability of direction of elevation, temperature, and precipitation on the number of record deer and their antler characteristics. Variables in pink have a high probability affecting the antler trait (>97.5%); variables in Orange have a moderate probability (95 – 97.5%); variables in green have a weak, but present probability (90 – 95%).

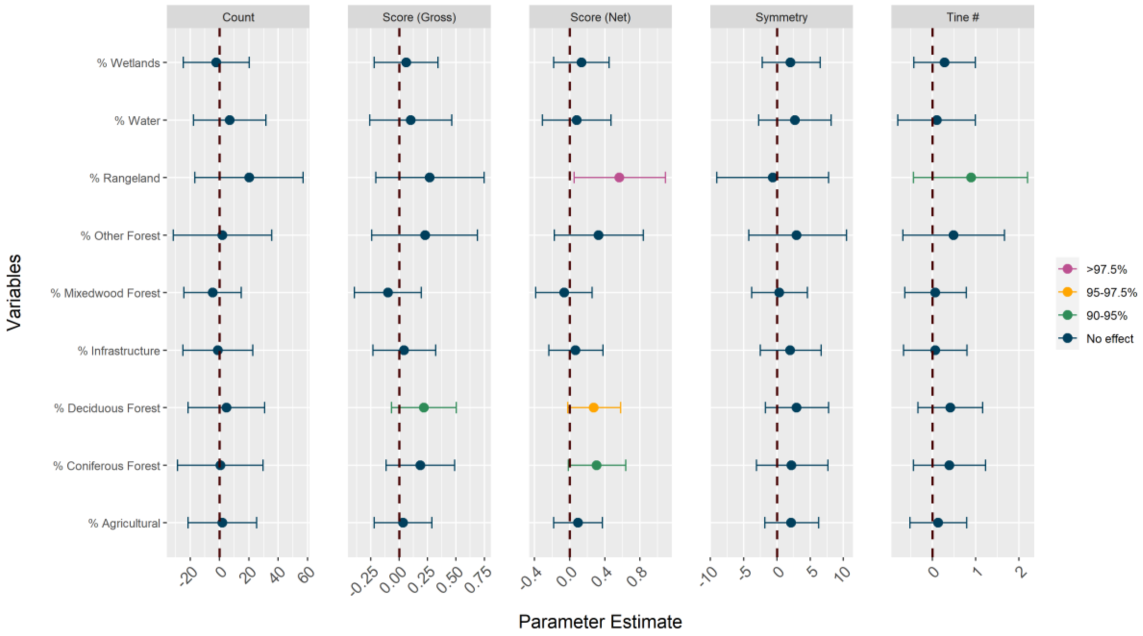

Figure 3. Probability of direction (pd) of landcover proportion on the number of record deer and their antler characteristics. Variables in pink have a high probability affecting the antler trait (>97.5%); variables in Orange have a moderate probability (95 – 97.5%); variables in green have a weak, but present probability (90 – 95%).

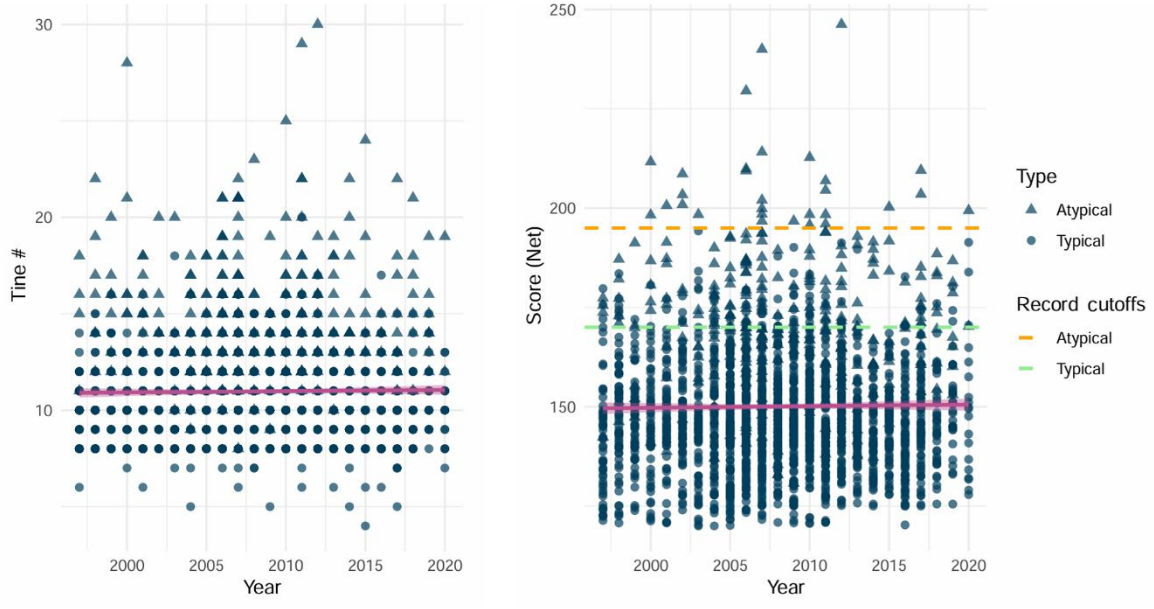

Figure 4. Antler score and tine number over time. Record cutoffs (orange and green) are representative of Boone and Crockett data, depicting the higher minimum cutoff size for record antlers in other parts of North America.

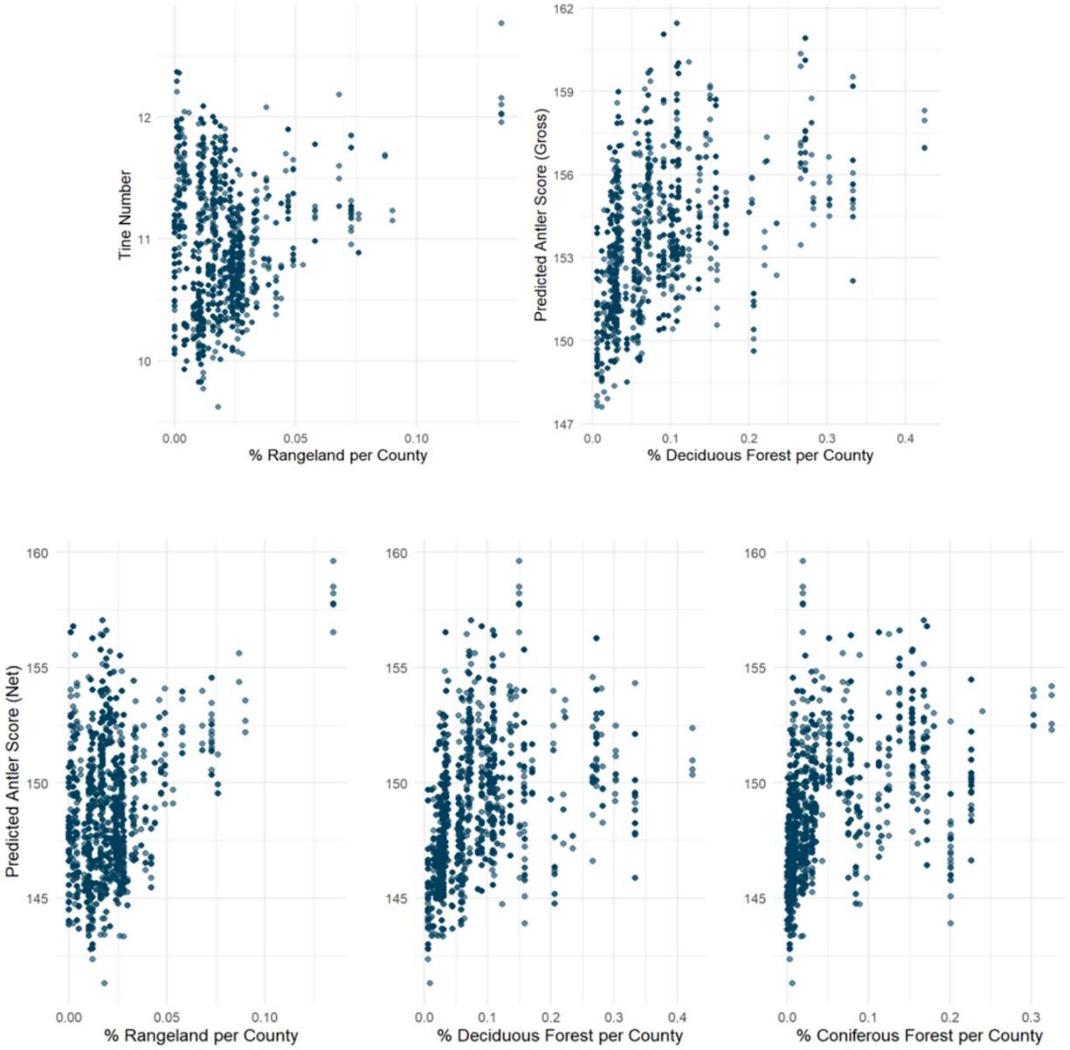

Figure 5. Percent of landcover per predicted antler score and tine number

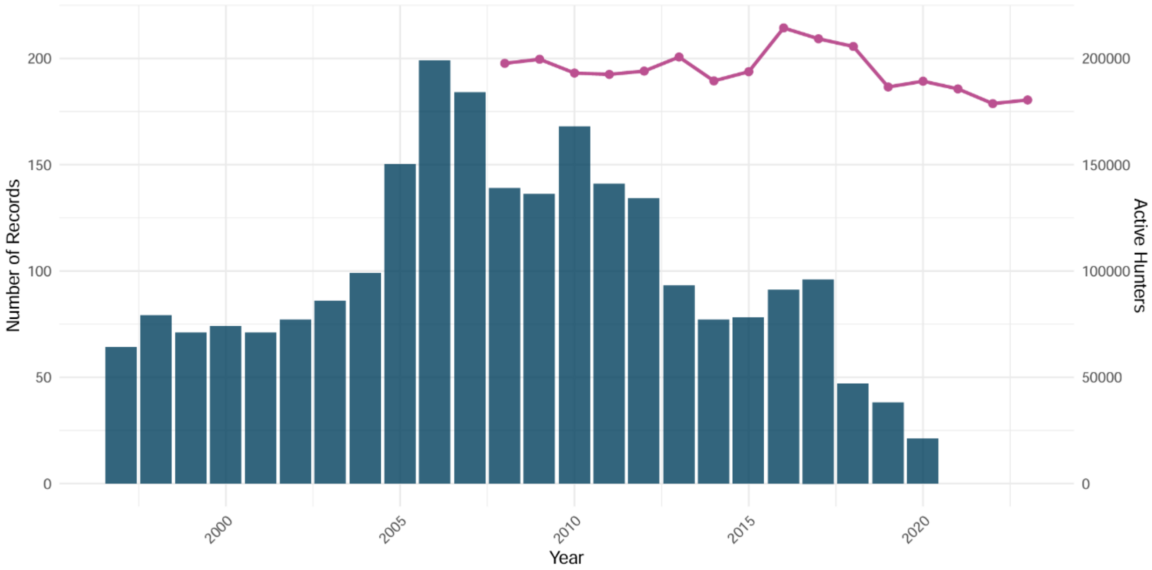

Figure 6. Number of records submitted to the Foundation for the Recognition of Ontario Wildlife (FROW) from 1997 to 2020 (bars) and number of active hunters from 2008 to 2022 (connected points)

CHAPTER 3

DEVELOPMENT AND VALIDATION OF MARKERS ASSOCIATED WITH LEUCISM AND MALOCCLUSIONS IN WHITE-TAILED DEER

3.1 ABSTRACT

The white-tailed deer on Saint Pierre and Miquelon (France) have relatively high rates of two phenotypic traits: leucism (a pigmentation disorder) and malocclusions (jaw deformities). By using previously identified runs of homozygosity (ROHs) presumed to be associated with these traits, we developed SNP assays to genotype markers linked to the traits of interest. A candidate SNP assay for leucism successfully distinguished affected individuals from non-affected individuals, further validating the biological relevance of the previously identified ROH and *LAMTOR2* gene. This leucism-associated SNP assay shows promise as a rapid, scalable, cost-effective tool for screening and managing this trait in both wild and farmed populations. In contrast, the malocclusion assay failed to genotype samples due to poor signal quality; this assay requires further optimization. Future work could focus on developing additional markers and validating these markers in mainland populations.

3.2 INTRODUCTION

Runs of homozygosity (ROHs) are long stretches of consecutive homozygous genotypes that arise from the passing of identical haplotypes to offspring due to inbreeding (McQuillan *et al.*, 2008). Since recessive traits are expressed from homozygosity at specific loci, overlapping ROHs among individuals exhibiting the same trait can help pinpoint the location of recessive, and sometimes deleterious, alleles (Szpiech *et al.*, 2013). Identifying characteristics of ROHs, such as single nucleotide polymorphisms (SNPs) when compared to unaffected individuals, could help reveal variants underlying with traits of interest (Hildebrandt *et al.*, 2009; Sams and Boyko, 2019) or be used for diagnostic assays (Halait *et al.*, 2012; Tietjen *et al.*, 2023).

White-tailed deer on the islands of Saint Pierre and Miquelon (SPM), France (but coastal Canada) have relatively high rates of two traits in the population: leucism and malocclusions. Leucism is a partial to entire lack of pigmentation often resulting in a piebald coat (Reissmann and Ludwig, 2013) and malocclusions are jaw deformities with an incorrect alignment of the maxillary bone and the mandible (Perillo *et al.*, 2015). Although leucism has been classified as a recessive trait (Pereira *et al.*, 2023), the inheritance patterns of malocclusions are not as well known (Cakan *et al.*, 2012). Nevertheless, these traits are assumed to have relatively simple architectures, involving few loci, making ROHs useful for identifying regions of high homozygosity where contributing loci are presumably located (Zhang *et al.*, 2015; Ceballos *et al.*, 2018). Unique ROHs for these traits have already been identified (Cars *et al.*, 2024), with one such ROH in leucistic individuals containing a gene with links to hypopigmentation

(*LAMTOR2*; Bohn *et al.*, 2007), and another ROH in malocclusion individuals containing a gene with links to craniofacial abnormalities (*NPVF*; Yu *et al.*, 2023).

Building on these findings, targeted SNP assays offer a cost effective and high-throughput option for identifying individuals carrying recessive alleles for traits of interest. These assays could be used by wildlife managers or farmers to monitor the genetic health of their herds and manage undesirable traits in large populations. Here, we designed novel SNP assays to identify markers associated with the ROHs underlying leucism and malocclusions.

3.3 METHODS

We had complete genomic sequence data for 16 SPM individuals, including the four leucism and seven malocclusion individuals, and nine North American mainland individuals. This data was used for assay design; the original sample collection, DNA, sequencing, and genome analysis (including read quality filtering and mapping to the reference genome) can be found in Cars *et al.* (2024). The positions of four previously identified ROHs for leucism and one previously identified ROH for malocclusions were extracted from previously assembled BAM files (Cars *et al.*, 2024) and a VCF was assembled of these regions using bcftools mpileup (Danecek *et al.*, 2021).

SNPs unique to the trait groups within these ROHs were then identified using Integrative genomics viewer (IGV; Robinson *et al.*, 2011) by visually comparing BAM and VCF files to a reference genome (GCA_023699985.1; Anderson *et al.*, 2022). Assuming the reference genome was from a wildtype animal, variants were considered unique if they were homozygous for the alternate allele in all affected individuals and were heterozygous or homozygous for the reference allele in all unaffected individuals. Candidate SNPs for each trait were selected for assay development. Primers for these candidate SNPs were designed using the rhAmp™ Genotyping Design Tool (Integrated DNA Technologies) and were used to develop genotyping assays.

A total of fifty-six white-tailed deer DNA samples were selected (including all those used in assay development), thirty-three individuals from SPM of which four presented with leucism and seven with malocclusions leaving twenty-two that did not present with the traits of interest, making them phenotypically wildtype for the purpose of this study. An additional twenty-three samples from the North American mainland, part of a larger project (PRJNA830519), were included as control samples, all of which were also phenotypically wildtype. Samples were genotyped were run on the QuantStudio 3 (Thermo Fisher Scientific), with oligo sequences and reaction conditions detailed in Table 1. Genotypes generated from the rhAMP assay were compared to those from the same individual's genome resequencing data.

3.4 RESULTS AND DISCUSSION

A candidate SNP for the leucism assay was found at position 1,514,222 within the ROH on scaffold ref0002511 (ROH position 1,368,616 - 1,525,114). All four individuals with leucism possessed this SNP when compared to wildtype animals. Distinct clusters corresponding to homozygous reference/alternate and heterozygous genotypes were observed with leucism samples being the only ones called as homozygous for the alternate allele (Figure 1). Of the twenty-three samples from the North American mainland, twenty-one were homozygous for the reference allele, one was heterozygous, and one was undetermined – the presumed leucism allele was therefore present in ~2% of mainland samples. Of the 29 SPM individuals that did not present with leucism (both phenotypically normal and malocclusion samples), seventeen were homozygous for the reference allele, eight were heterozygous, and four were undetermined. These results showed 100% match to expected genotypes from the genome sequencing data.

Hence, the leucism assay provided preliminary support for the identified SNP as a potential marker, consistent with previous findings linking pigmentation traits to a single SNP in other ungulate species (Gratten *et al.*, 2006; Reiner, Tramberend, *et al.*, 2020; Reiner, Weber, *et al.*, 2020). The ability to differentiate affected from unaffected individuals based on allele presence suggests the SNP is reflective of the leucism-associated ROH discovered by Cars *et al.* (2024), a finding that strengthens the evidence that this previously identified ROH is biologically meaningful. It is clear that leucism is rare, with anecdotal estimates at <1% on the mainland deer (Matzenbacher, 2023); Hardy-Weinberg theory would predict homozygous genotypes to indeed be quite rare on the mainland (<1%), while notably higher on SPM, consistent with observations. Future validation of the marker in non-island leucistic deer is still needed to determine whether this association extends beyond SPM. In practice, this assay could be used to rapidly screen individuals for the leucism-associated genotype and aid management decisions in populations where leucism may affect visibility to predators or indicate increased homozygosity and inbreeding depression (Brommer *et al.*, 2015; Kardos *et al.*, 2016). It could also give deer farmers a tool to identify and selectively breed for or against the leucism trait based on their desires (Warren, 2025).

For the malocclusion assay one candidate SNP was found at position 792,838 within the ROH on scaffold ref0001199 (ROH position 600,106 - 794,137). Four of seven individuals within malocclusions possessed this SNP and all other samples did not. The malocclusion SNP assay showed poor signal quality and lacked a distinguishable genotype. The failure of the malocclusion assay suggests the design and conditions need further optimization. Potential issues include mismatches between the primers and the genome or low coverage in the target region (Bru *et al.*, 2008; Lefever *et al.*, 2013). As a next step, we recommend screening additional candidate genes and considering increased sequencing depth to better characterize the candidate ROH and identify associated variants with malocclusion.

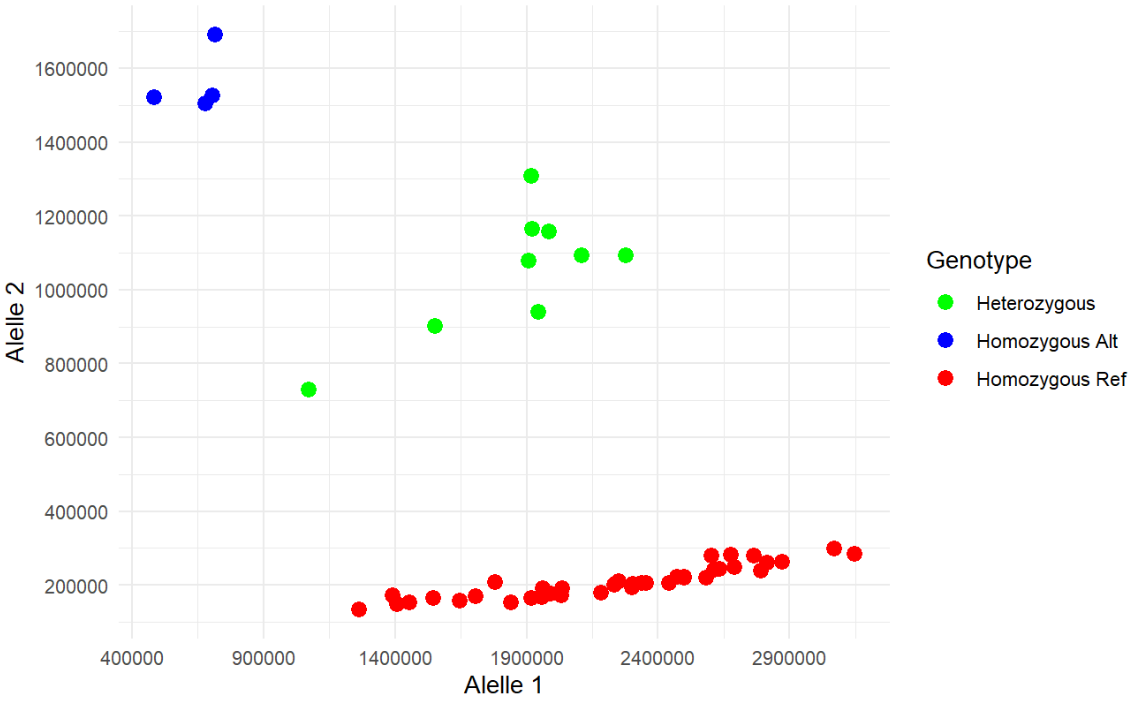

Figure 1: Genotype clustering of a candidate SNP for leucism in white-tailed deer (position 1,514,222 within an ROH on scaffold ref0002511: 1,368,616–1,525,114). Each point represents one individual, with clusters corresponding to homozygous reference (red), heterozygous (green), and homozygous alternate (blue) genotypes. All four leucistic individuals were homozygous for the alternate allele. Among controls, mainland deer (n = 23) included 21 homozygous reference, 1 heterozygous individual and 1 undetermined individual, while Saint Pierre and Miquelon deer (n = 29) included 17 homozygous reference, 8 heterozygous individuals, and 4 undetermined individuals. No controls were homozygous alternate.

Table 1: Designed primer sequences for the rhAMP genotyping assay. F = FAM-labeled forward primer (allele 1) and V = VIC-labeled forward primer (allele 2). ASP = Allele-Specific Primer; LSP = Locus-Specific Primer. Sequences are listed 5’ → 3’.

Primer	**Primer Sequence**
Leucism_ ASP1	/rhAmp-F/ATTCAATCTCTGGTCAGGGAGrCTAAG
Leucism _ASP2	/rhAmp-V/ATTCAATCTCTGGTCAGGGAArCTAAG
Leucism_ LSP	GCCCTTTTGTCTCTTTTGAATTGGTTACrATTGT
Malocclusion_ ASP1	/rhAmp-F/GACCAGAACTATAAACTCCAATrGAGGA
Malocclusion_ ASP2	/rhAmp-V/GACCAGAACTATAAACTCCAACrGAGGA
Malocclusion_ LSP	GCTCAGTCATTTGAATATAGCAAGCrATTGT

CHAPTER 4

GENERAL DISCUSSION

4.1 SUMMARY OF FINDINGS

In Chapter 2, I evaluated how environmental factors, such as climate and habitat composition, influence the antler characteristics and distribution of record-scoring white-tailed deer across Ontario. Through the use of conditional autoregressive (CAR) models, I found that warmer temperatures were positively associated with all antler characteristics (size, shape and symmetry) and a greater number of record-scoring deer. This is likely attributed to warmer conditions that promote plant growth resulting in more forage availability for the deer and therefore more energy allocated to antler growth (French *et al.*, 1956; Hatfield and Prueger, 2015). Interestingly, higher winter precipitation was linked to smaller antlers, suggesting that harsh winter conditions (in the form of more snowfall) limit forage availability and increase energy demands, likely depleting energy reserves (Lesage *et al.*, 2001; Patterson and Power, 2002). Further, as predicted, land cover was found to influence antler characteristics; specifically forest and rangeland were positively associated with increased antler size and tine number, likely due to forage quality and preferred habitat structure of white-tailed deer (Hewitt, 2011; Cain *et al.*, 2019). This study is among the first in Cananda to explicitly link environmental variation to antler expression using long-term, province-wide hunter harvest records, providing new insights into how climate and habitat interact to shape traits in white-tailed deer.

Contrary to my predictions, I did not observe a decline in antler size over the past few decades, a pattern documented at the continental scale (Monteith *et al.*, 2013). One hypothesized reason is that Ontario's colder winters limit access to nutritious food which contrasts many parts of North America which, with warmer climates, have longer growing seasons and therefore more high-quality food (Sontheimer *et al.*, 2024). Colder temperatures could be preventing deer in Ontario from achieving their full antler growth potential as less energy can be directed towards antler growth (Lesage *et al.*, 2001; Sontheimer *et al.*, 2024). This suggests that antler size trends in white-tailed deer vary according to local environmental conditions or harvest regimes and are not uniform across their range.

Shifting focus to genetic factors, in Chapter 3 I looked within previously identified runs of homozygosity (ROHs) to uncover diagnostic mutations behind phenotypical abnormalities (leucism and malocclusions) in an isolated population of white-tailed deer. I found a diagnostic single nucleotide polymorphism (SNP) for leucism within the same ROH as the candidate gene *LAMTOR2* (Cars *et al.*, 2024), further validating that this ROH is biologically relevant. The assay I designed from this SNP was successful in genotyping individuals with leucism with all four individuals being homozygous for the alternate allele. Furthermore, the majority of individuals that genotyped as heterozygous were from Saint Pierre & Miquelon (SPM). This follows expectations because, given the high number of individuals presenting with leucism, many should also be carriers of the allele.

A potential diagnostic SNP was also found for malocclusions within the same ROH as the candidate gene *NPVF* (Cars *et al.*, 2024). The assay I designed from this SNP was, however, not successful in genotyping individuals with malocclusions. It is likely that the assay design and conditions need further optimization. Differences in assay performance between the two traits highlight the importance of validating candidate SNPs and assay conditions before broader application.

4.2 CONCLUSIONS AND FUTURE DIRECTIONS

The models in Chapter 2 provided strong support that variation in environmental conditions across Ontario counties influences antler size, morphology, and the distribution of record-scoring white-tailed deer. While antler size has shown no significant change in Ontario from 1980 to 2022, suggesting that harvest practices have been effective, it is important to remain cautious as intensified hunting pressure in other jurisdictions has been linked to shifts in age demographics, specifically reducing the presence of older, larger males (Langvatn and Loison, 1999; Mysterud, 2011). Higher population densities, and thus increased competition for food, can also disproportionately impact larger males who expend much of their energy during the breeding season and often enter winter with reduced fat reserves (Lesage *et al.*, 2001; Keyser *et al.*, 2005). A decrease of larger, older males within the population could result in a loss of important genetic variation and lower breeding success (Milner *et al.*, 2007; Coltman, 2008; Mysterud, 2011). As a result, the population could become less able to adapt to challenges such as disease, harsh weather, or habitat changes, ultimately weakening its long-term health and resilience (Milner *et al.*, 2007). Therefore, protecting key habitat features and maintaining balanced population densities will not only support the population's stability, but also ensure sustainable hunting opportunities which will benefit local economies and conservation funding. For this reason, I recommend continued monitoring of harvest practices to ensure that population dynamics and habitat limitations do not compromise the long-term sustainability of Ontario's deer population.

With climate change continuing to alter seasonal patterns and increase yearly temperatures, it is possible that we could see a positive trend in the antler size of

Ontario's white-tailed deer. Future work could expand this dataset in upcoming years to see if the current trends remain true for Ontario's record deer. Additionally, I believe that it would be useful to perform this same analysis with harvest data from across Canada. This would allow the exploration of other northern climates and terrain. For example, we could strengthen our understanding of the influence of elevation on record deer distribution if we looked at Alberta which has an elevation that reaches over 3,750 m and greater topographic relief compared to Ontario (Yamazaki *et al.*, 2017). Further, analysis from eastern Canada could highlight the influence of maritime conditions, and prairie regions, such as Saskatchewan, could offer insight into grassland habitats with more extreme temperature variations and lower precipitation levels (Ecological Stratification Working Group, 1995)

Future work could also incorporate studies estimating the heritability of antler traits (Jamieson *et al.*, 2020) to examine how genetic and environmental factors interact to influence antler growth in white-tailed deer. This approach would allow for a more comprehensive understanding of antler development by investigating the interactions both factors on antler traits. Such work could reveal how specific environmental conditions modify genetic effects or if certain genotypes are more responsive to favorable conditions, which could help to clarify the mechanisms driving variation in antler traits across different populations and landscapes.

Further, Chapter 3 detailed the successful development of an assay to detect the leucism-associated genotype on Saint Pierre & Miquelon (SPM) and explores its potential for broader application. In wild populations, the assay could help guide management strategies where leucism may heighten predation risk or indicate underlying inbreeding concerns (Brommer et al., 2015; Kardos et al., 2016). In agricultural settings, it offers deer farmers a means to incorporate the leucism trait into their selective breeding programs enabling more precise selection for desired traits (Warren, 2025).

Future work could incorporate mainland animals with leucism into the assay to confirm that the mutation found is shared across populations. With white-tailed deer on SPM having been introduced fairly recently, it is unlikely that a mutation causing leucism arose independently of the mainland and it was more likely present in the founding population (origine archives SCM, 1953; Daniel L. Hartl, 1980). Therefore, finding the same SNP genotype in mainland leucistic deer would further validate its association with the trait across the species.

In all, my thesis investigated the environmental and genetic factors driving trait variation in white-tailed deer populations across multiple geographic contexts. By combining environmental modeling and population genomic analysis, I have highlighted how both external conditions and internal genomic architecture shape phenotypic diversity. Specifically, I highlighted how variation in climate and habitat composition across Ontario counties is associated with differences in antler size, morphology, and the distribution of record white-tailed deer. I also identified markers and developed an assay that will allow for the identification of trait carrying individuals without the need for whole-genome sequencing.

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APPENDIX

CHAPTER 2

Table S1: Description of response and predictor variables included in spatial models of white-tailed deer antler traits in Ontario, Canada.

	Description	**Units**	**Spatial/temporal resolution and extent**	**Reference**
Response				
Tine no.	Number of antler points per deer rack (both antlers)	Count	Individual, harvested 1997–2022	(Foundation for the Recognition of Ontario Wildlife, 2015)
Gross Score	Total antler score (Measurements of size + points)	Points	Individual, harvested 1997–2022	(Foundation for the Recognition of Ontario Wildlife, 2015)
Net Score	Gross score adjusted for asymmetry	Points	Individual, harvested 1997–2022	(Foundation for the Recognition of Ontario Wildlife, 2015)
Symmetry	Measure of left-right antler symmetry	Yes or No (0/1)	Individual, harvested 1997–2022	(Foundation for the Recognition of Ontario Wildlife, 2015)
Record Deer per County	The number of record deer harvested in each Ontario county	Count	County-level, Single value per county (1997–2022)	(Foundation for the Recognition of Ontario Wildlife, 2015)
Predictor				
Temp.	yearly difference from county average during antler growing season (March – August)	Degrees Celsius (°C)	County-level, annual 1997–2022; also 1 and 2 years prior	(Hutchinson *et al.*, 2009; Hopkinson *et al.*, 2011; McKenney *et al.*, 2011)
Precip.	Average precipitation during antler growing season (March – Aug)	Millimeters (mm)	County-level, annual 1997–2022; also 1 and 2 years prior	(Hutchinson *et al.*, 2009; Hopkinson *et al.*, 2011; McKenney *et al.*, 2011)
Winter Precip.	Average winter precipitation (Jan – March)	Millimeters (mm)	County-level, annual 1997–2022; also 1 and 2 years prior	(Hutchinson *et al.*, 2009; Hopkinson *et al.*, 2011; McKenney *et al.*, 2011)
Landcover	Proportion of each landcover type per county (agriculture, forest types, rangeland, water, wetlands, infrastructure)	Percentage (%)	County-level; raster 15 m resolution; years 1999–2011 (OLC v and 2015–2020 (OLC v1.	(Land Information Ontario, 2023; 'Ontario Land Cover Version 1.0 - Overview')
Elevation	Average county elevation	Metres (m)	County-level, Single value per county	(TessaDEM v1.2, 2024)
County Si	Area of the county	Kilometers Squared (km^2)	County-level, Single valu per county	(Government of Canada, 2022)
Deer Abundanc	Relative index of white-tailed deer per county	Deer seen per	County-level, averaged 2 2023, Single value per county	(Government of Ontario, 2025b)

Table S2: Raw climate and land cover variables (Excel booklet)

Table S3: Landcover classification organization

Coarse Classification	**1999**	**2015**
Water	Clear Open Water, Turbid Water	Water
Other	Shoreline, Disturbance, Cliff and Talus, Alvar, Sand Barren and Dune, Sand, Gra Mine Tailings, Extraction, Bedrock	Alvar, Dune, Barren
Wetlands	Mudflats, Marsh, Swamp, Fen, Bog	Coniferous treed swamp, Mixed wood treed swamp, Deciduous treed swamp, Transitional treed swamp, Thicket swamp, Bog, Fen, Marsh
Other Forest	Heath, Sparse Treed, Treed Upland, Plantations - Treed Cultivated, Hedge Ro Tallgrass Woodland	Sparse treed, Transitional Forest, Hedge row
Deciduous Forest	Deciduous Treed	Deciduous forest
Mixed Forest	Mixed Treed	Mixed wood forest
Coniferous Forest	Coniferous Treed	Coniferous forest
Rangeland	Open Tallgrass Prairie, Tallgrass Savannah	Prairie, Savanah, Meadow, Shrubland
Infrastructure	Community, Infrastructure	Built up area-pervious, Anthropogenic, Transportation
Agriculture	Agricultural and Undifferentiated Rural Land Use	Cropland, Hay-pasture

Table S4: Comparison of Land Cover Types (%) in Ontario, 1999–2011 vs. 2015–2020.

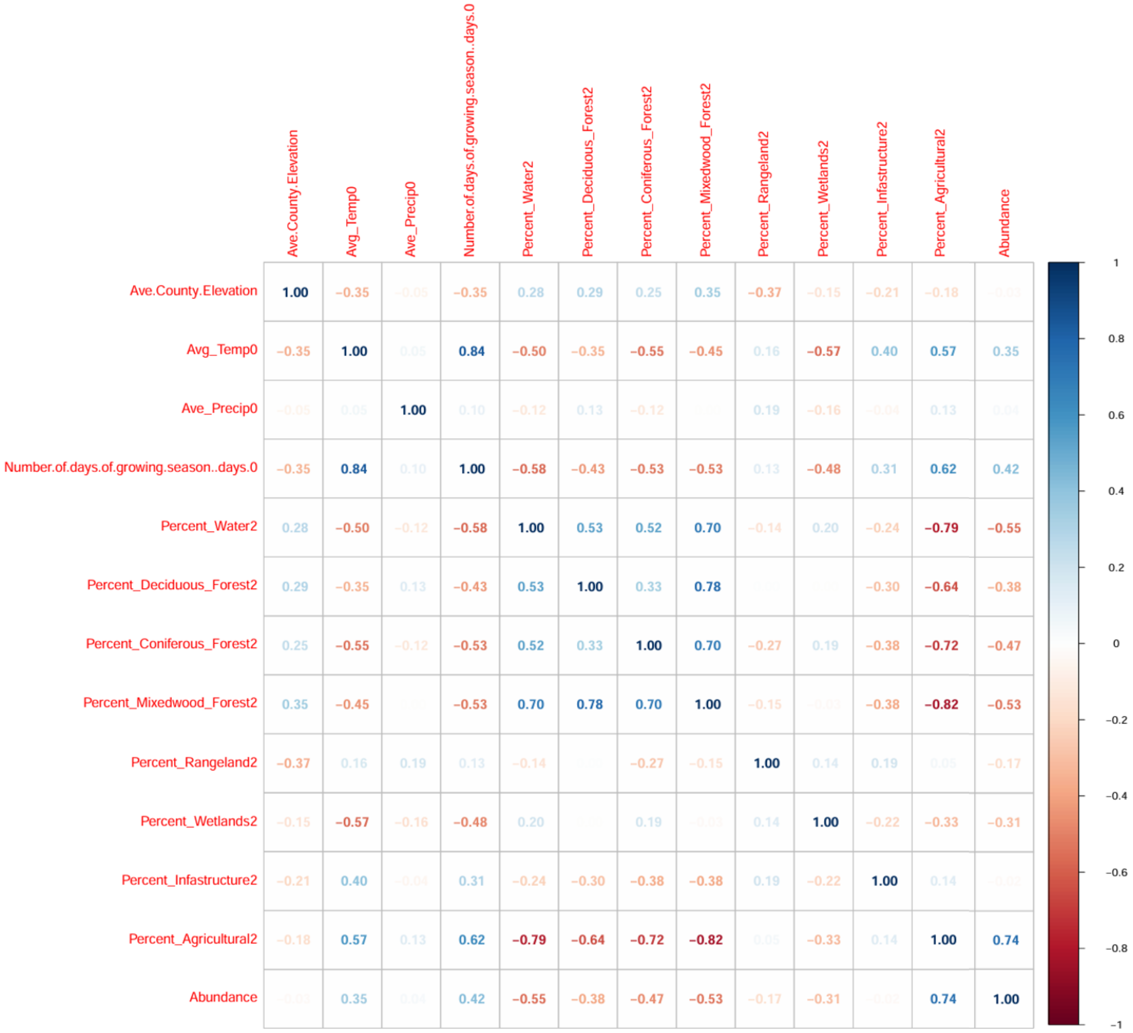
Year	**Water**	**Decid. forest**	**Con. forest**	**Mixed forest**	**Other Forest**	**Rangeland**	**Wetlands**	**Infra -structure**	**Agri -culture**
1999-2011	4.51%	7.53%	5.77%	9.86%	8.64%	1.68%	10.38%	7.62%	36.94%
2015-2020	5.10%	12.66%	6.09%	10.46%	1.34%	3.34%	13.40%	10.49%	36.91%

Table S5: Predictor variables used in each model

Response	***Predictors***
Record deer count	*Avg. elev. + avg. temp. + avg. prec. + avg. prec. winter + avg. # growing days + % water + % dec. forest + % conif. forest + % mixed wood forest + % other forest + % rangeland + % wetlands + % infrastructure + % agriculture + abundance + offset(area)*
Antler tine #	*Avg. elev. + Δ temp + avg. prec. + avg. prec. winter + # growing days + Δ temp (1 yr prior) + avg. prec. (1 yr prior) + avg. prec. winter (1 yr prior) + # growing days (1 yr prior) + Δ temp (2 yrs prior) + avg. prec. (2 yrs prior) + avg. prec. winter (2 yrs prior) + # growing days (2 yrs prior) + % water + % dec. forest + % conif. forest + % mixed wood forest + % other forest + % rangeland + % wetlands + % infrastructure + % agriculture + abundance*
Antler symmetry (0/1	*Avg. elev. + Δ temp + avg. prec. + avg. prec. winter + # growing days + Δ temp (1 yr prior) + avg. prec. (1 yr prior) + avg. prec. winter (1 yr prior) + # growing days (1 yr prior) + Δ temp (2 yrs prior) + avg. prec. (2 yrs prior) + avg. prec. winter (2 yrs prior) + # growing days (2 yrs prior) + % water + % dec. forest + % conif. forest + % mixed wood forest + % other forest + % rangeland + % wetlands + % infrastructure + % agriculture + abundance*
Score (gross/net)	*Avg. elev. + Δ temp + avg. prec. + avg. prec. winter + # growing days + Δ temp (1 yr prior) + avg. prec. (1 yr prior) + avg. prec. winter (1 yr prior) + # growing days (1 yr prior) + Δ temp (2 yrs prior) + avg. prec. (2 yrs prior) + avg. prec. winter (2 yrs prior) + # growing days (2 yrs prior) + % water + % dec. forest + % conif. forest + % mixed wood forest + % other forest + % rangeland + % wetlands + % infrastructure + % agriculture + abundance*
Score and Antler Tine # (Temporal)	*Year*

Table S6: Model results of the change in Ontario's white-tailed deer antler characteristics over time (1980-2022).

Model	**Coefficient**	**p-value**	**β**
Tine number	Year	0.594	0.001
Gross score	Year	0.501	0.039
Net score	Year	0.997	-2.462 e-04



	Ave.County.Elevation	Avg_Temp0	Ave_Precip0	Number.of.days.of.growing.season..days.0	Percent_Water2	Percent_Deciduous_Forest2	Percent_Coniferous_Forest2	Percent_Mixedwood_Forest2	Percent_Rangeland2	Percent_Wetlands2	Percent_Infastructure2	Percent_Agricultural2	Abundance
Ave.County.Elevation	1.00	−0.35	−0.05	−0.35	0.28	0.29	0.25	0.35	−0.37	−0.15	−0.21	−0.18	−0.03
Avg_Temp0	−0.35	1.00	0.05	0.84	−0.50	−0.35	−0.55	−0.45	0.16	−0.57	0.40	0.57	0.35
Ave_Precip0	−0.05	0.05	1.00	0.10	−0.12	0.13	−0.12	0.00	0.19	−0.16	−0.04	0.13	0.04
Number.of.days.of.growing.season..days.0	−0.35	0.84	0.10	1.00	−0.58	−0.43	−0.53	−0.53	0.13	−0.48	0.31	0.62	0.42
Percent_Water2	0.28	−0.50	−0.12	−0.58	1.00	0.53	0.52	0.70	−0.14	0.20	−0.24	−0.79	−0.55
Percent_Deciduous_Forest2	0.29	−0.35	0.13	−0.43	0.53	1.00	0.33	0.78	0.00	0.03	−0.30	−0.64	−0.38
Percent_Coniferous_Forest2	0.25	−0.55	−0.12	−0.53	0.52	0.33	1.00	0.70	−0.27	0.19	−0.38	−0.72	−0.47
Percent_Mixedwood_Forest2	0.35	−0.45	0.00	−0.53	0.70	0.78	0.70	1.00	−0.15	−0.03	−0.38	−0.82	−0.53
Percent_Rangeland2	−0.37	0.16	0.19	0.13	−0.14	0.00	−0.27	−0.15	1.00	0.14	0.19	0.05	−0.17
Percent_Wetlands2	−0.15	−0.57	−0.16	−0.48	0.20	0.03	0.19	−0.03	0.14	1.00	−0.22	−0.33	−0.31
Percent_Infastructure2	−0.21	0.40	−0.04	0.31	−0.24	−0.30	−0.38	−0.38	0.19	−0.22	1.00	0.14	−0.02
Percent_Agricultural2	−0.18	0.57	0.13	0.62	−0.79	−0.64	−0.72	−0.82	0.05	−0.33	0.14	1.00	0.74
Abundance	−0.03	0.35	0.04	0.42	−0.55	−0.38	−0.47	−0.53	−0.17	−0.31	−0.02	0.74	1.00

Fig S1: Correlation matrix showing relationships among predictor variables used in spatial models

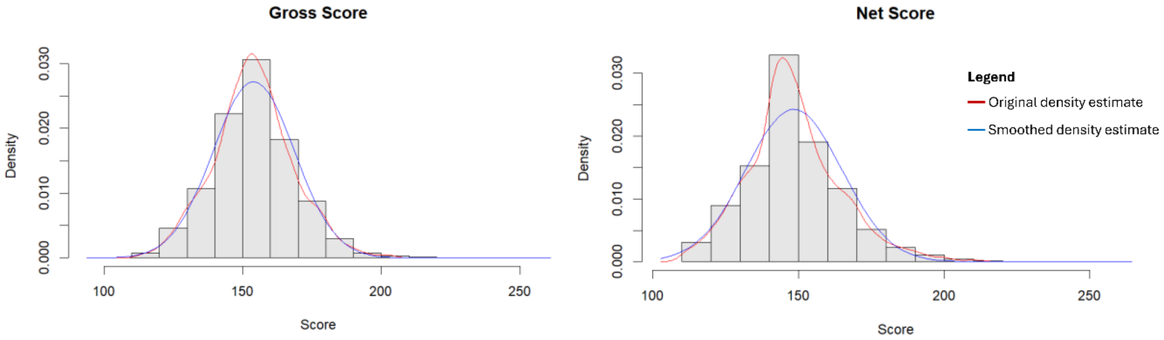


Fig S2: Frequency distribution of the scores of record white-tailed deer. Red line: the estimate using the default bandwidth, capturing more detail in the distribution. Blue line: the estimate using a larger bandwidth to produce a smoother curve

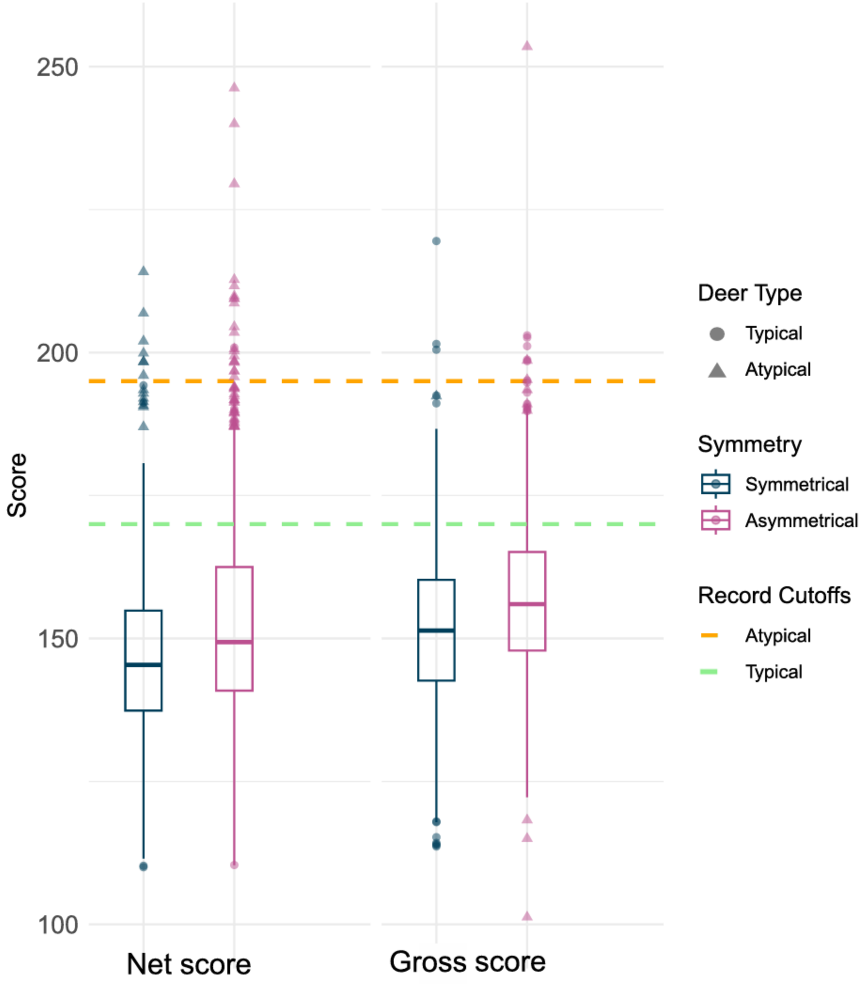


Fig S3. Boxplots of the distribution of scores for symmetrical vs asymmetrical antlered record deer