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Environmental and temporal factors affecting record white-tailed deer antler characteristics in Ontario, Canada

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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. We used conditional autoregressive (CAR) models to examine these relationships and found that warmer temperatures the year of harvest were positively associated with larger antlers and more record deer in a given county, while winter precipitation 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.

KEYWORDS white-tailed deer, *Odocoileus virginianus*, antler size, antler morphology, environmental factors, Ontario, hunters, harvest, climate effects, land cover

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 typically only found on males (Rue, 1989; Hewitt, 2011). Antlers have multiple purposes including dominance displays and interactions, weapons against predators and other male Cervidae, and indicators to females that males 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 mature 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 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 approaches can have an effect on antler size and distribution. Across North America, hunter harvest is the primary means of managing white-tailed deer and 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 significant 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, even 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 unique 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 the growing season 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 selective harvest of large-antlered individuals over time has led to a temporal decline in antler size across Ontario.

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). This area 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). However, white-tailed deer exist throughout parts of more central and northern Ontario, including the boreal forest region, and these deer experience harsher winters. To cope with these conditions, deer in these areas inhabit coniferous and mixed woods forests, which offer shelter from excessive 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). Where they overlap, wolves (*Canis lupus*) are the primary predators of white-tailed deer in Ontario, while coyotes (*Canis latrans*) fill that role in their absence, though do not fully replace wolves ecologically (Benson et al. 2017). In addition to climate variation, Ontario's expanding infrastructure and growing population, which has tripled in the last 50 years and has led to an increase in white-tailed deer density and a decline in the availability of their habitat and food per individual (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).

METHODS

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 voluntarily submitted by hunters to FROW from every county in Ontario, except for 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 (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 dating back pre--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.

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 S1, 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. 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 n.d.) 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 S1). For the years not captured by the landcover databases (2012-2014), whichever layer encompassed the year closest 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 S2). The proportion of each landcover type per county was calculated (Table S3), and "other landcover" was dropped in order to interpret the relationship between the response variable and the proportion covariates (see 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 S1). Average county elevation and county size are 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 2025). Each year, the Ontario Ministry of Natural Resources collects 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.

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 among themselves 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). However, we did assess correlations between landcover variables and other covariates. 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 (CAR) 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 S4, available in supporting information.

To assess the number of record deer harvested in each county we used a Poisson regression with a log link and a county area offset to translate the analysis into one of rates of record deer per area. 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 will allow 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 the distribution and ensure the assumptions of the model were met.

For CAR models, we evaluated parameter effects based on the probability of direction (pd) which provided the probability each covariate was either positively or negatively related to antler characteristics (Makowski et al. 2019). Parameters with a probability $\geq$ 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 was sparse pre 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 assessing normality and homoscedasticity of residuals for the Gaussian models, and overdispersion for Poisson and Binomial models. It should also be noted that this data is 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.

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. 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 multiple landcover variables. 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 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 % of Rangeland per county both had 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; β = -0.12, pd = 98.6%), while the temperature of the year of harvest had a moderate probability of having a positive effect (Fig 2; β = 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; β = 0.01, pd = 100%), while precipitation during the winter the year of harvest had a strong probability of having a negative effect (Fig 2; β = -0.01, pd = 97.8%). Precipitation during antler growth 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; β = 0.01, pd = 96.8% and β = 0.01, 96.5%, respectively), and temperature 2 years prior to harvest and the % 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, both of 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 % 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 % 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 % 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 S5, available in Supporting Information).

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). In addition, deer with large antlers are highly sought after as trophies by many recreational hunters. 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 chances of a record deer being harvested (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 months that antler growth is occurring (March-August) positively influenced all antler characteristics (Fig 2), and that rangeland and forest are key landscape components, the amounts of which are correlated to overall greater antler size.

Interestingly, no change in antler size was detected over time in Ontario (Fig. 4), potentially due to the province's position at the northern edge of the white-tailed deer's range. Historically, harsher winters and limited forage could have constrained antler growth, but ongoing warming due to climate change is likely improving habitat suitability by reducing winter severity and extending growing seasons, which could be helping maintain antler size in Ontario. This data set is representative of adult antlered white-tailed deer within Ontario and although not a random sample, the data captures a large range of variation in antler size across the population (Fig S1, available in Supporting Information) and temporal, spatial and environmental influences should 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 will be considered in 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 used suggesting that nearby counties tend to have similar conditions (e.g., temperature). However, a moderate value indicates 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 does 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 in regional hunting interest and behaviour. Notably, hunter behaviour and success which will vary with the amount of roads, dwellings, and with accessibility, while regional differences in the number of hunters and frequency of hunting might also contribute to these spatial patterns (Kilgo et al. 1998, Bonnot et al. 2013).

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 the year of harvest a 1°C increase in temperature was associated with a ~1% increase in tine number, a ~10% 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 (Clements et al. 2010, Simard 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 one 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 1mm increase in precipitation was associated with a ~1% increase in net score. Similarly, 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 for blocking excessive snowfall (Government of Ontario 2019). With deer being confined to these yards deer density 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 could strengthen this finding by incorporating direct measurements of snow depth, snow cover duration, or broader indices such as the Winter Severity Index (WSI) 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 probability of harvesting a record deer and are ideal edge habitats (Cain et al. 2019). Forests will 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).

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 in temperature during the year of harvest being associated with an increase in the number of record-sized deer by 1.24 deer in a given county. Similar to antler size, warmer temperatures allow for more forage availability. With more food available, more energy can be allocated to individual deer in a county, presumably allowing more individuals to reach record deer status. The number of record deer harvested was not significantly affected by any landcover covariates (Fig 3); so, while landcover type positively impacts antler size, the overall effect is minor such that it does 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 elevational range is small in the province (0 m – 700 m) and obfuscated when averaged across the 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). The mechanism by which precipitation 2 years prior impacts asymmetry is still unclear. However, 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 S2, available in Supporting Information); however, we see no strong relationship between precipitation and antler size. It is thus still conceivable that high environmental stressors might have long-term impacts on symmetry, even for antlers that are shed annually.

Temporal patterns of record deer

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 S5). 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 vary 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 2007/08 and 2010/11, have coincided with apparent population declines (Ontario Outdoors Magazine Game Forecast 2009, 2011) which would explain a decrease in entries. Still, the number of white-tailed deer in Ontario is 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). This lower density is likely due to Ontario being the northern edge of the white-tailed deer's range, where limited suitable habitat likely has more influence on antlers than harvest pressure or hunting regulations. While Ontario's hunting regulations of being allotted one antlered tag and allocating antlerless tags by lottery could result in lower overall harvest rates compared to other regions, it is not clear if these restrictions make any substantial difference in population dynamics or antler development. Instead, environmental factors associated with climate and habitat likely have a greater influence on population density and antler growth in the province.

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. Combined these conditions could be helping bolster antler size despite pressures that are causing declines elsewhere (e.g.Monteith et al. 2013). With ongoing climate change, we would predict a positive trend in overall antler size if environmental conditions became more favourable for deer and harvest pressures remain like those during our time series.

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 as it relates to maintaining antler size, but we note increased harvest pressure on males in other regions has led to a reduction in age structure, which could impact antler size in the future(Langvatn and Loison 1999, Mysterud 2011). Density dependence also can disproportionately affect 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. It is important to note that these findings are based on hunter-reported data, which could be subject to sampling biases, and are most directly applicable within the Ontario context. Nonetheless, they 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.

ACKNOWLEDGMENTS

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ETHICS STATEMENT

No approval of research ethics committees was required to accomplish the goals of this study.

DATA AVAILABILITY

The antler data that support the findings of this study are available from The Foundation for the Recognition of Ontario Wildlife, Ontario, Canada and were acquired under research agreements for this study. All other model covariates are provided.

CONFLICT OF INTEREST

Authors declare no competing interests.

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FIGURES

Figure 1. Approximate Ontario land cover distribution (Left) and elevation (Right) divided by county.

Figure 2. Probability of direction (pd) of elevation, temperature, and precipitation on the response variables. Variables in pink have a high probability affecting the antler trait (97.5%). Variables in Orange have a moderate probability (95 – 97.5%). And Variables in green have a weak, but present probability (90 – 95%).

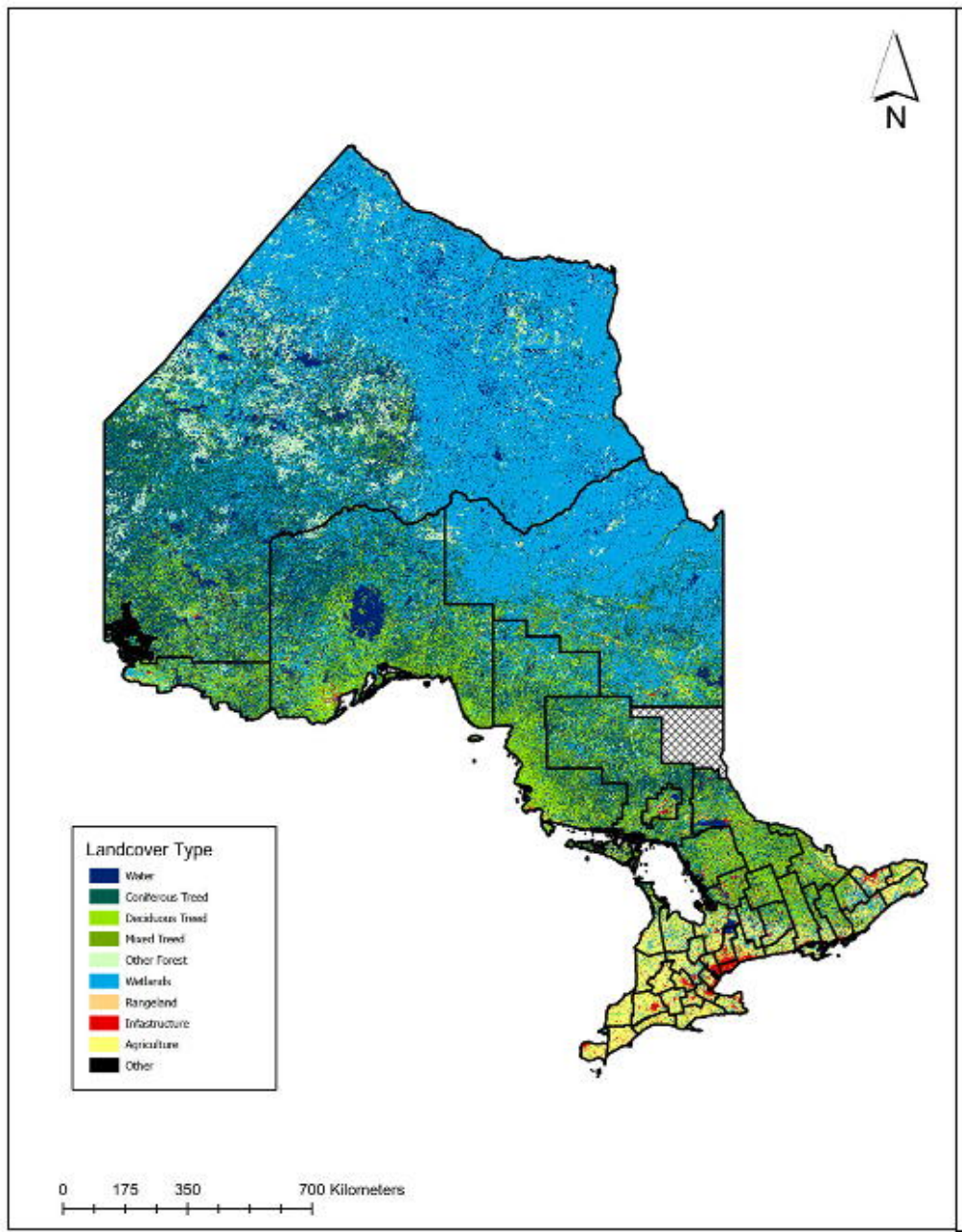
Figure 3. Probability of direction (pd) of landcover proportion on the response variables. Variables in pink have a high probability affecting the antler trait (97.5%). Variables in Orange have a moderate probability (95 – 97.5%). And Variables in green have a weak, but present probability (90 – 95%).

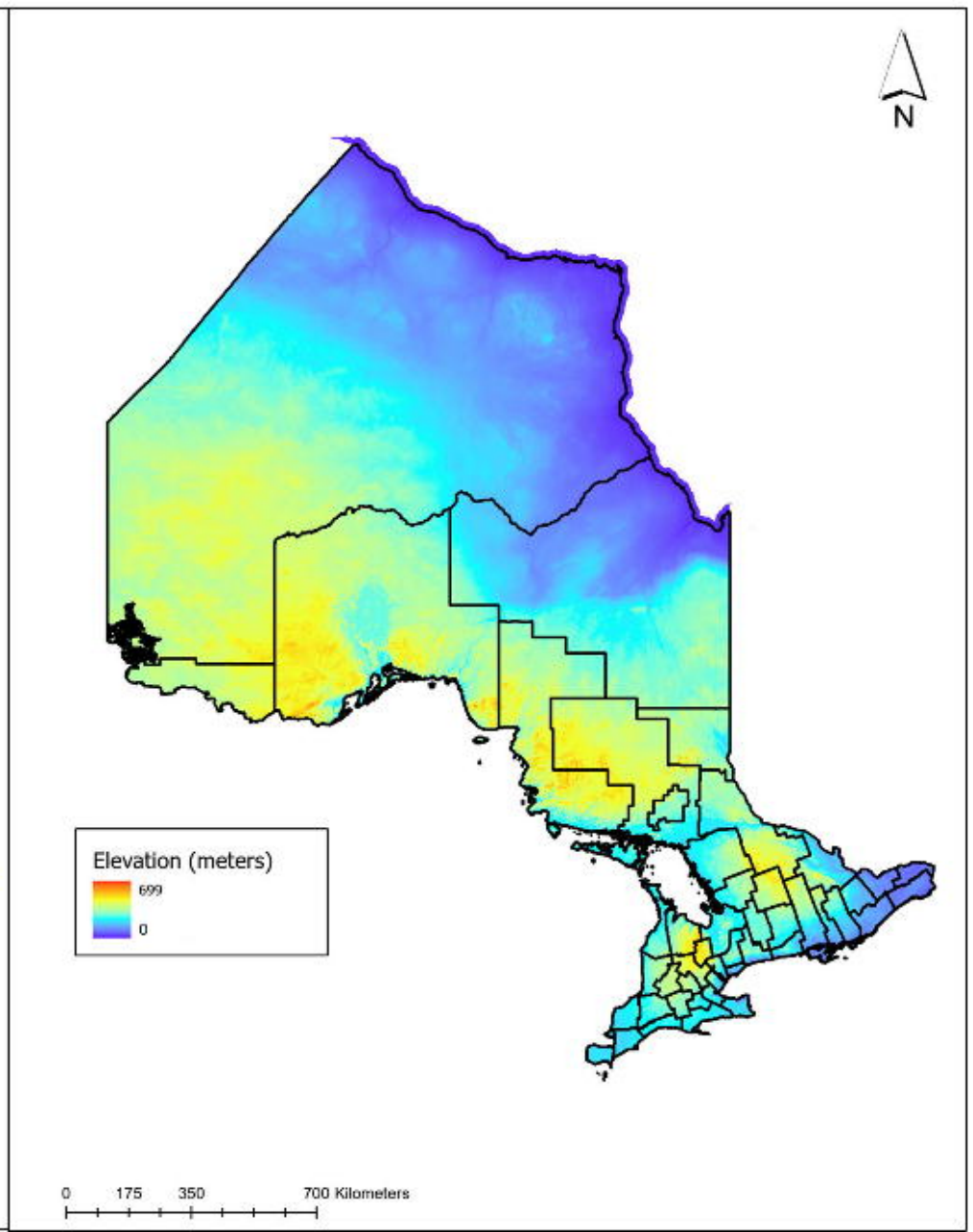
Figure 4. Change in antler score and tine number over time. Cutoffs are representative of Boone and Crockett data, depicting the higher cutoff size for record antlers in other parts of North America.

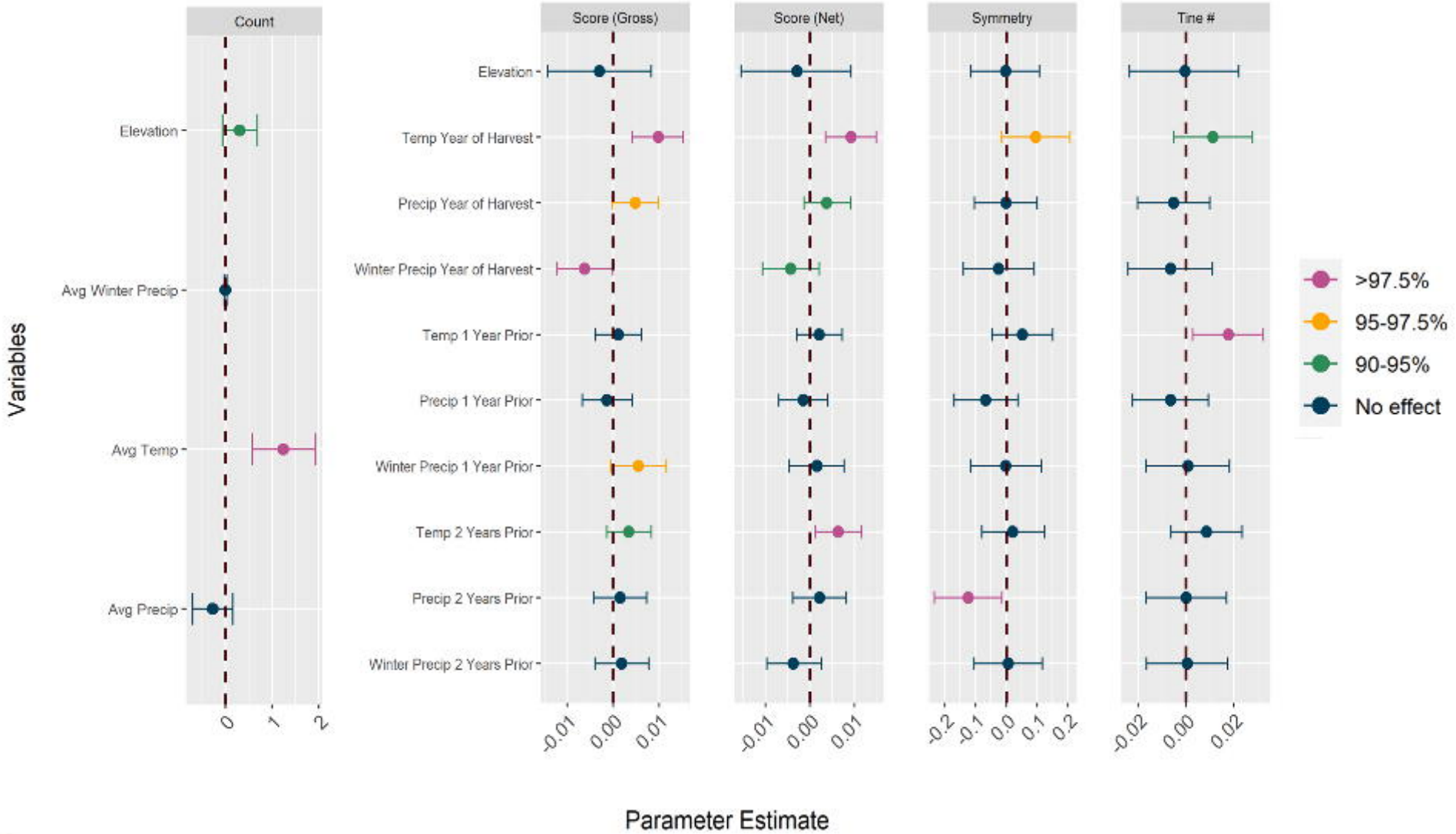
Figure 5. Percent of significant landcover per predicted antler score and tine number

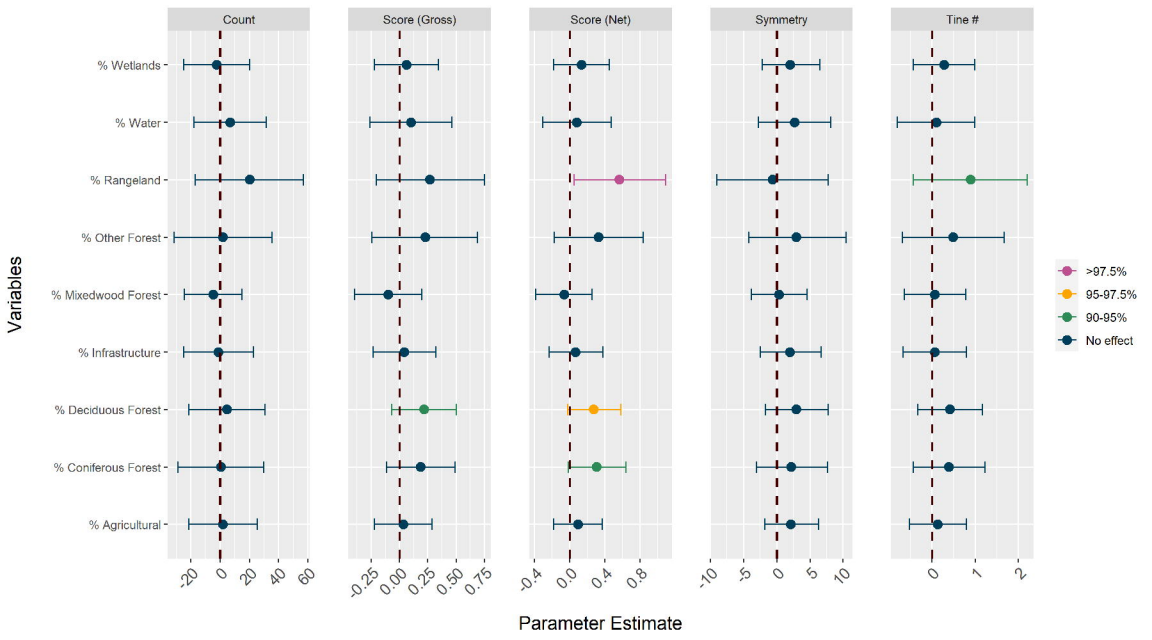
Figure 6. Number of records submitted to the Foundation for the Recognition of Ontario Wildlife (FROW) from 1997 to 2020 (blue) and Number of active hunters from 2008 to 2022 (pink)

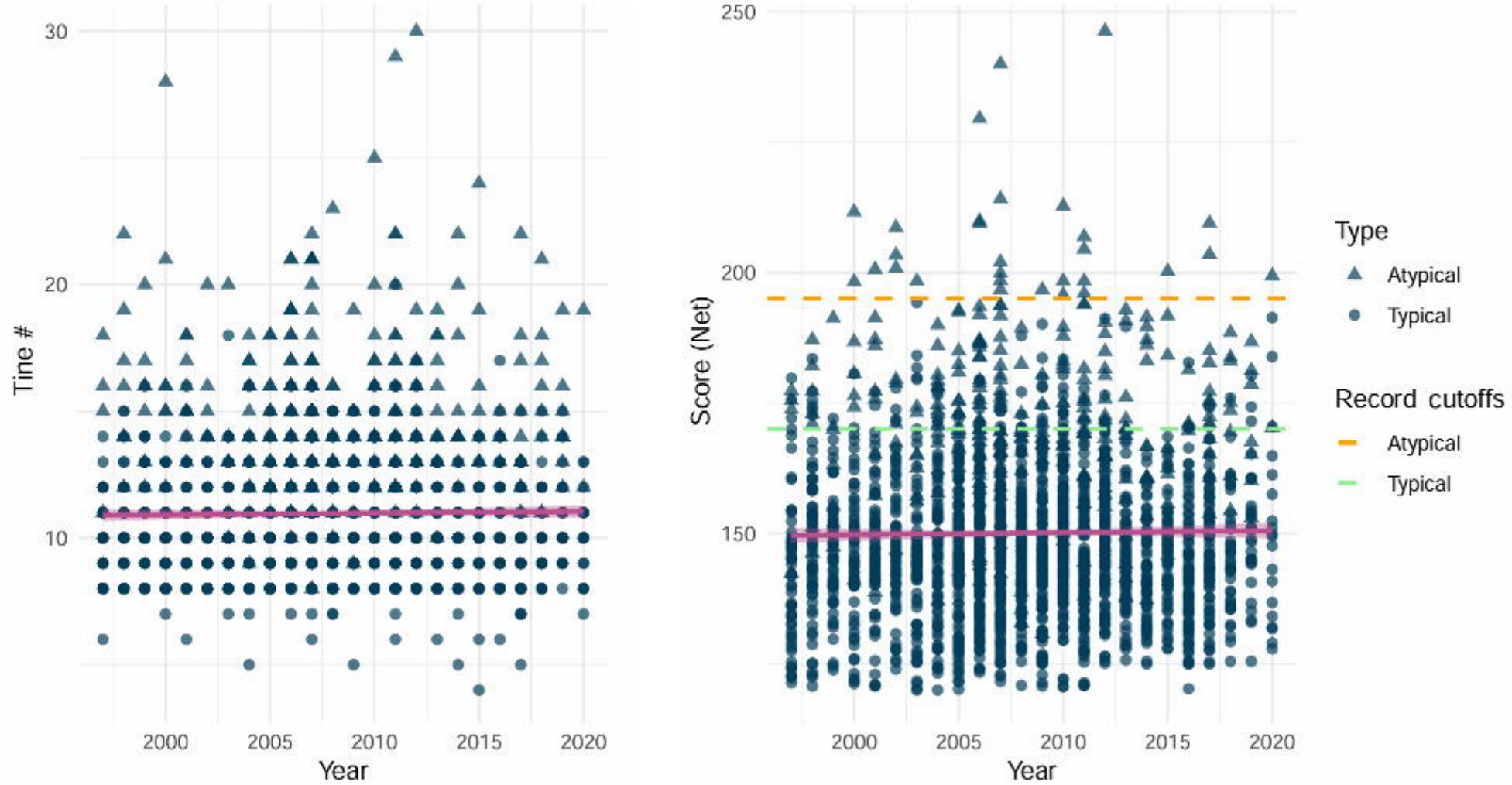
APPENDIX A. SUPPLEMENTAL

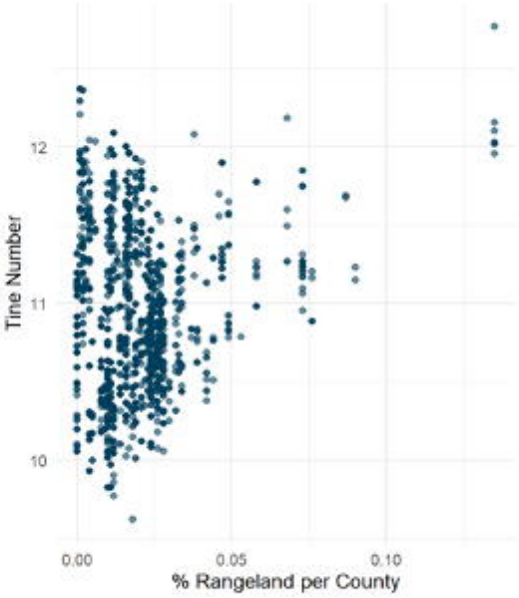

N
Landcover Type
Water
Coniferous Treed
Deciduous Treed
Mixed Treed
Other Forest
Wetlands
Rangeland
Infastructure
Agriculture
Other
0 175 350 700 Kilometers

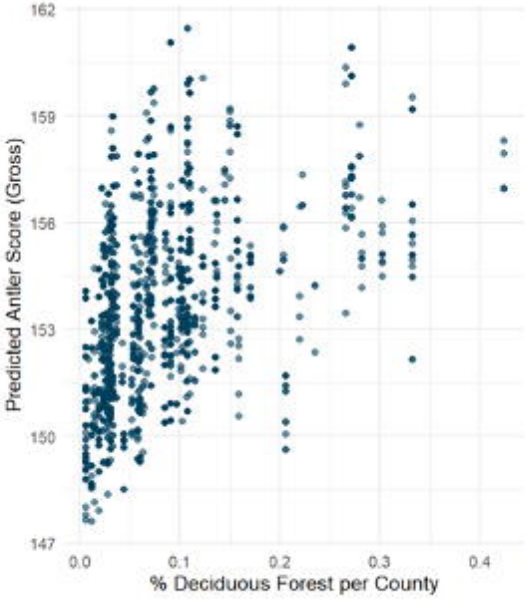

N
Elevation (meters)
699
0
0 175 350 700 Kilometers

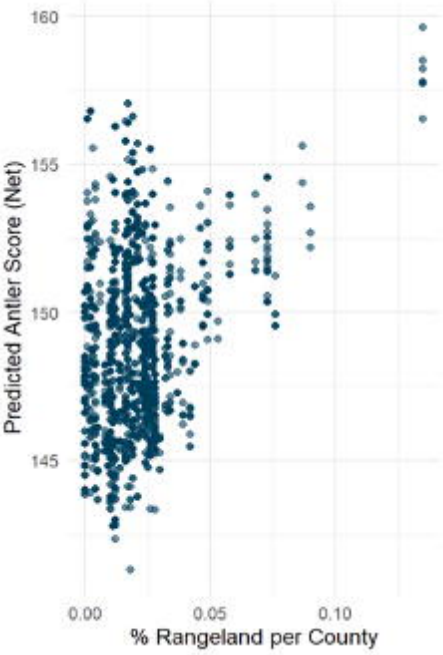

Count
Score (Gross)
Score (Net)
Symmetry
Tine #
Variables
Elevation
Avg Winter Precip
Avg Temp
Avg Precip
Temp Year of Harvest
Precip Year of Harvest
Winter Precip Year of Harvest
Temp 1 Year Prior
Precip 1 Year Prior
Winter Precip 1 Year Prior
Temp 2 Years Prior
Precip 2 Years Prior
Winter Precip 2 Years Prior
0
1
2
-0.01
0.00
0.01
-0.2
-0.1
0.0
0.1
0.2
-0.02
0.02
>97.5%
95-97.5%
90-95%
No effect
Parameter Estimate

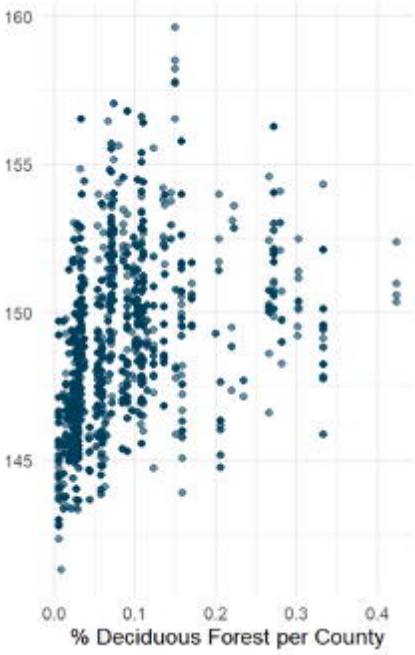

Count
Score (Gross)
Score (Net)
Symmetry
Tine #
% Wetlands
% Water
% Rangeland
% Other Forest
% Mixedwood Forest
% Infrastructure
% Deciduous Forest
% Coniferous Forest
% Agricultural
Variables
-20
0
20
40
60
-0.25
0.00
0.25
0.50
0.75
-0.4
0.0
0.4
0.8
-10
-5
0
5
10
0
1
2
Parameter Estimate
>97.5%
95-97.5%
90-95%
No effect

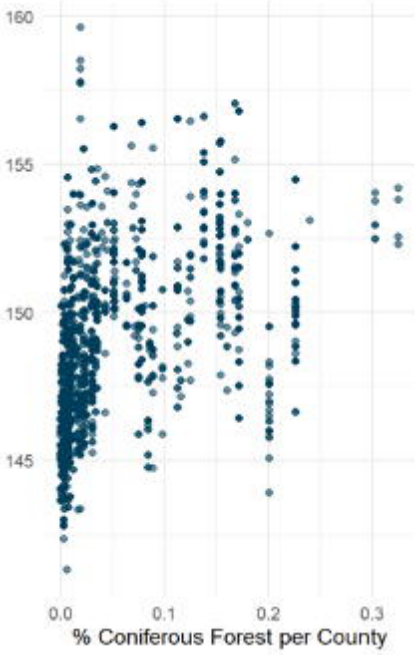

30
20
10
Tine #
2000
2005
2010
2015
2020
Year
250
200
150
Score (Net)
2000
2005
2010
2015
2020
Year
Type
Atypical
Typical
Record cutoffs
Atypical
Typical

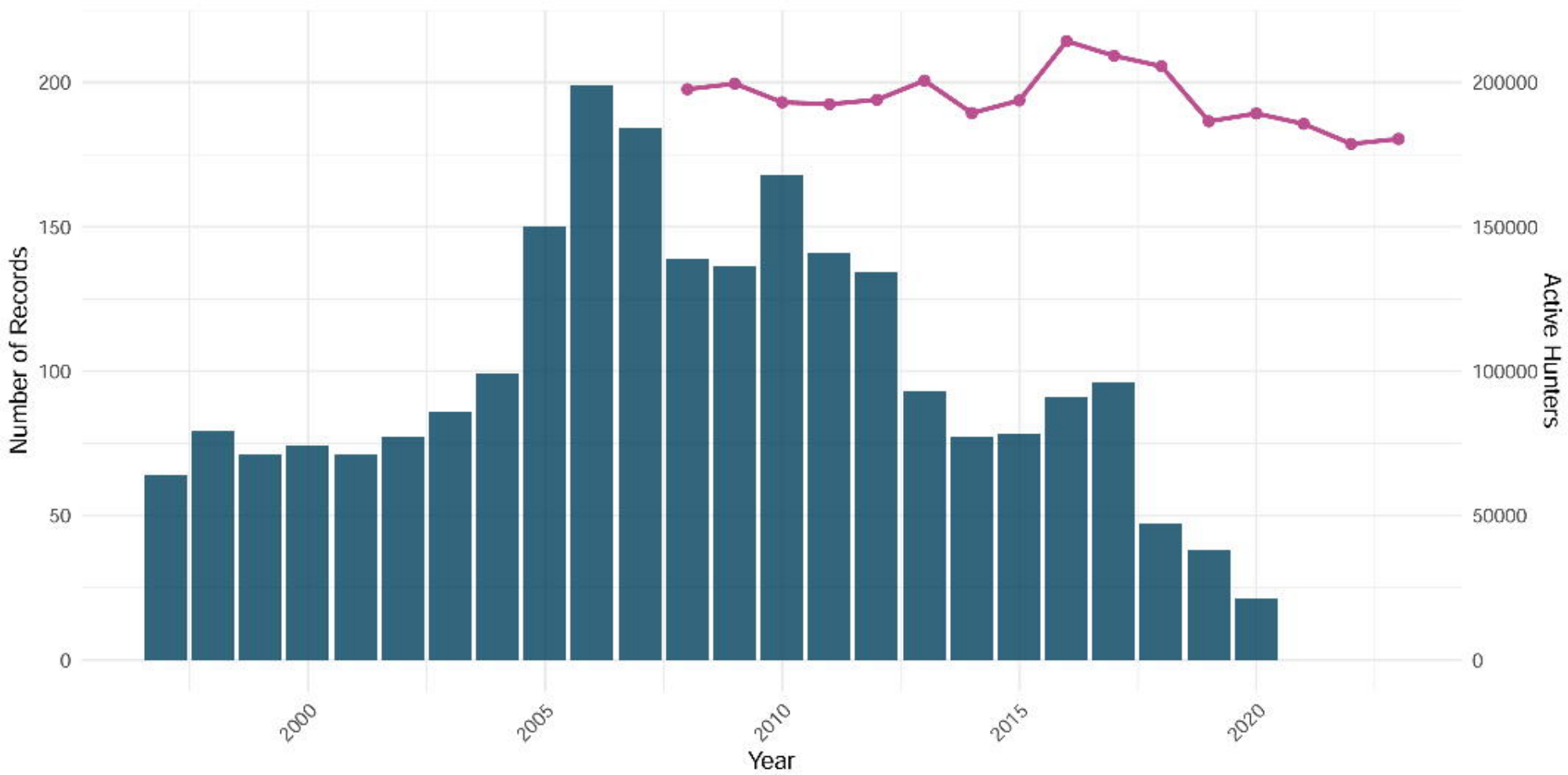

Tine Number
12
11
10
0.00
0.05
0.10
% Rangeland per County


Predicted Antler Score (Gross)
162
159
156
153
150
147
0.0
0.1
0.2
0.3
0.4
% Deciduous Forest per County


Predicted Antler Score (Net)
160
155
150
145
0.00
0.05
0.10
% Rangeland per County


160
155
150
145
0.0
0.1
0.2
0.3
0.4
% Deciduous Forest per County


160
155
150
145
0.0
0.1
0.2
0.3
% Coniferous Forest per County


Number of Records
Active Hunters
Year
0
50
100
150
200
0
50000
100000
150000
200000
2000
2005
2010
2015
2020