Utilizing Cast Antlers for Profiling Quality and Annual Repeatability of Antler Characteristics in a Nutritionally Stable Environment for White-tailed Deer

by

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A thesis submitted to the Graduate Faculty of
Auburn University
in partial fulfillment of the
requirements for the Degree of
Master of Science

Auburn, Alabama
August 8, 2020

Keywords: Antlers, *Odocoileus virginianus*, Repeatability, White-tailed deer, Cast, Shed

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Abstract

Antlers are often used as indicators of management effectiveness in deer populations, and increasing antler size is frequently a management objective. Thus, managers are interested in assessing antler characteristics and annual variation in antler size in individuals within the population. Shed antlers present an annually regenerated, non-invasive data source for antler characteristics from deer populations. We assessed whether shed antlers were representative of the antler characteristics of the male segment of a white-tailed deer population (*Odocoileus virginanus*). We found that detected shed antlers over represented larger antlered, older males, and thus may not be representative of a deer population's antler characteristics. Additionally, annual repeatability of antler characteristics was variable, and the repeatability of several antler traits differed between our study populations. This may suggest differences in investment of antler characteristics in response to differing pressures of competing males and potential mates.

Acknowledgments

I would first like to thank my advisor, Dr. Stephen Ditchkoff, for providing me the opportunity to research the species that has captivated my thoughts since tagging along on my first deer hunt at 4 years old. Steve has provided a tremendous amount of guidance throughout this process, especially in the development of my scientific writing skills. Further, he has given me opportunities for research experience that far exceeded the boundaries of the research project presented here, and for that I will forever be grateful. I would also like to thank my committee members Dr. William Gulsby and Dr. Robert Gitzen for sharing their tremendous knowledge throughout this project. This research would not be where it is today without their input, it is truly appreciated. I would like to thank the Three Notch Wildlife Research Foundation, especially Stewart Carroll for funding this research and Ramin Jackson for all his help with logistics and field work. Additionally, this research would not be possible without the funding of the Auburn Captive Facility provided by PRADCO Outdoor Brands, EBSCO Industries Inc., Code Blue, Moultrie, as well as private individuals.

I have received a lot of help with field work throughout my time here. I owe an immense thanks to Chad Newbolt for all his help with field work at Camp Hill and overall project advice. Thanks to all the graduate and undergraduate students, past and present, who have help with shed hunts and deer captures. I would especially like to acknowledge my DeerLab members who assisted with data collection: Monet Gomes, Jamie Goethlich, Carolyn Moore, Dr. Natascha Ivy-Israel, Jace Steward, Seth Rankins, and Shelby Zikeli.

The great people we surround ourselves with have a lasting impact on who we are, the follow individuals have been those people for me during by time in Auburn. I would like to thank Steve Zenas, Matt McDonough, and Stephen Madre (Ragin Cajun), for sparking my

interest in pigs almost as much as deer, which is saying a lot coming from this deer guy. To the members of Office 3401 (the best office in the building), especially Kent Keene, Evan A. Wheeler, Monet Gomes, and Jamie Goethlich, you guys provided a couple years of constant laughs, great conversations, and support going through the struggle of graduate school together. You all made the office feel like a home, and thankfully, because often times it felt like we lived there. Jamie and Monet, you both have become two of my greatest friends, I will always cherish the help, support, laughs, extensively research discussions, and great times outside of our research.

Finally, very few people get far in life without the support of friends and family. First to Grandpa Deig, thank you for taking me on that first deer hunt in December 1995, which created that first spark and interest in wildlife, you are truly someone I look up too and have taught me much more in life than I will ever be able to thank you for. Kentucky deer camp fostered my incredible interest in white-tailed deer, Uncle Dan and John, my brother Ben, along with Grandpa Deig have been there throughout most of those years and all the great times we had there, thank you. Mom, Ben, and Grandma Deig thank you for all your support and guidance throughout my life, I would not be where I am today without you. Thanks to my Dad, Paula, Grandma and Grandpa Randle, you have all incredibly supportive and provided some great times. Lastly, Cele, thank you for the last few months, I look forward to many more to come!

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List of Abbreviations

ACF   Auburn University's Captive Deer Research Facility

Three Notch   Three Notch Wildlife Research Foundation

QDM   Quality Deer Management

G1…G4   Antler tine length measurements, denoted by a "G" follow by the tine number

H1…H4   Antler circumference measurements, denoted by a "H" follow by the

               circumference number

A1…A7   Antler abnormal point measurements, denoted by a "A" followed by abnormal

               point number

B&C   Boone and Crockett Club

Chapter 1: Utilization of Shed Antlers for Assessing Male Quality in White-tailed Deer

(*Odocoileus virginianus*) Populations

Abstract

Antler measurements from hunter-harvested deer are often used to make assumptions regarding antler characteristics of the population, such as average antler size, and as an index of management success. However, hunter selectivity and antler-based harvest restrictions can bias datasets comprised of hunter harvested animals and may not be representative of the unharvested segment of the population. Previous research suggests that shed antlers may provide managers with a more accurate assessment of population antler characteristics than harvest data. We captured and measured antlers of male white-tailed deer (*Odocoileus* virginianus) housed in the 174-ha Auburn Captive Deer Research Facility over a 7-year period. Antler characteristics of the deer population in this facility were well documented as a result of extensive capture and monitoring efforts. We collected shed antlers over the same time period to assess whether shed antlers were representative of the known male population. We found that larger antlered, older males were overrepresented in our sample of shed antlers due to the greater detection of larger antlers by observers. Specifically, we found that shed antlers were 1.17 and 2.45 times as likely to be detected for each 1 cm increase in main beam length and each point increase in total number of points, respectively. Our results suggest that evaluations of population antler characteristics that use shed antlers may underrepresent young males that possess smaller, less detectable shed antlers.

Introduction

White-tailed deer (*Odocoileus virginianus*) are the most sought after and economically important game species in North America where $18.1 billion in retail sales is generated

annually from 10.9 million hunters throughout the United States (Allen et al. 2013, U.S. Department of the Interior 2014). The immense economic value and hunter interest has resulted in intensive management of populations for sustainable harvest and desired population demographics. The current and most popular management paradigm used throughout much of the white-tailed deer range is quality deer management (QDM; Adams and Hamilton 2011). Although specific management goals are unique to the deer population being managed, QDM prioritizes minimizing harvest of young males, thus increasing the proportion of older, large-antlered males in the population (Hamilton et al. 1995). Therefore, antlers are often used as indicators of management effectiveness, and harvest of large-antlered males is frequently an objective of deer management programs (Demarais and Strickland 2011).

Data generated from harvested individuals constitute a primary source of information for white-tailed deer populations (Roseberry and Woolf 1991). In addition to serving as a measure of success for management programs, antlers can also be used as an index to nutritional availability (e.g., yearling antler beam diameter; Severinghaus and Moen 1983, Rasmussen 1985). However, harvest data have inherit biases associated with hunter selection and younger, smaller antlered males may be underrepresented in the data (Hayne 1984). Additionally, where antler-based harvest restrictions are present, bias associated with data collected from hunter-harvested animals is further confounded. For example, implementation of a selective harvest criteria that protects younger, small-antlered males and permits the harvest of older, large-antlered males may result in overrepresentation of older males relative to their actual representation in the population. Lastly, while harvest data provide information regarding animals that were harvested, they do not provide information on the unharvested segment of the population and may not be representative of true population demographics (Collier and Krementz 2007) or morphometrics.

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Utilizing shed antlers as indicators of population antler characteristics may provide a more accurate measure of population characteristics than harvest data (Ditchkoff et al. 2000; Schoenbeck and Peterson 2014). Shed antlers would afford the additional advantages of providing information on individuals that survived the hunting season and provide a non-invasive technique to acquire population antler measurements. However, as noted by Ditchkoff et al. (2000), the size of a shed antler affects visibility and, thus, detection. Because searches for shed antlers in their study were conducted in food plots (vegetation ≤5 cm high), it is unlikely that visibility of a shed antler would have been impeded. However, while searching for shed antlers in food plots or in other short vegetation types is ideal, it may not be practical depending on vegetative characteristics and demographics of the population of interest. Further, deer simply may not be utilizing short vegetation types in an area or it may not be available. Therefore, we examined whether detected shed antlers represented a random sample of the male segment of the population in an area with mixed vegetative cover types and conditions. The specific objectives of our study were to determine 1) if antler size influenced detection of antlers, 2) if there was a bias towards detection of antlers from certain age classes, and 3) the ages and antler characteristics of males not represented in the shed antler sample.

Methods

Study Area

Auburn University's Captive Deer Research Facility (hereafter "ACF") was a 174-ha facility located in Camp Hill, Alabama, USA. The perimeter of the ACF was enclosed by a 3-m high deer-proof fence in 2007. The captive white-tailed deer population in ACF consisted of wild deer captured within the fence during construction, and their subsequent descendants. Supplemental feed (16-18% protein; Record Rack®, Nutrena Feeds, Minneapolis, MN) was

supplied *ad libitum* year-round at 3 permanent gravity feeders with an additional 4 timed feeders providing 2 kg/day of corn during periods when deer were being actively captured. The deer population was primarily regulated by natural mortalities. An additional 10-15 deer, approximately 6 months of age, were annually captured and released outside of the facility to maintain a desired age distribution and deer density (Newbolt et al. 2017).

Open hay fields made up 40% of vegetative cover and consisted of a variety of grass species including Bermuda grass (*Cynodon* spp.), fescue (*Festuca* spp.), big bluestem (*Andropogon* spp.), Johnson grass (*Sorghum* spp.), dallisgrass (*Paspalum* spp.) and bahiagrass (*Paspalum* spp.). The remaining vegetative cover consisted of 13% bottomland hardwoods [oak (*Quercus* spp.)], 26% mixed hardwoods [oak, hickory (*Carya* spp.) and maple (*Acer* spp.)], and 10% pine species, dominated by loblolly pine (*Pinus taeda*). Thickets of sweetgum (*Liquidambar styraciflua*), eastern red cedar (*Juniperus virginiana*), blackberry (*Rubus* spp.), and Chinese privet (*Ligustrun sinese*) comprised the remaining 11%. Mixed forest cover was primarily closed canopy consisting of little understory vegetation, however, canopy gaps along creek bottoms and forest edges created a dense understory. Ample year-round water was provided by two second-order creeks. ACF had an average annual temperature of 15.9 °C and an average annual precipitation of 1,360 mm (National Climatic Data Center 2010).

Shed Antler Searches and Data Collection:

Shed antlers were located annually from 2012-2018 at the ACF using systematic searches and opportunistic detection. We implemented prescribed burning of upland areas on a bi-annual burn rotation and mowing of hay fields and wildlife food plots prior to peak antler casting to aid in the detection of shed antlers. We conducted extensive systematic searches utilizing large volunteer groups from late March through April until the ACF had been extensively covered.

Volunteers were instructed to walk transects in forested areas while holding a spacing of approximately 10 m between transects. We labeled all recovered shed antlers and antlered skulls with the collection year.

Deer captures:

Adult deer (≥6 months) were chemically immobilized and captured annually from 2012-2018. All deer were immobilized using a combined intramuscular injection of Telazol ® (Fort Dodge Animal Health, Fort Dodge, IA; 100 mg/ml given at a rate of 4.5 mg/kg) and xylazine (Lloyd Laboratories, Shenandoah, IA; 100 mg/ml given at a rate of 2.2 mg/kg). We used the antagonist Tolazine ® (Lloyd Laboratories, Shenandoah, IA; 100 mg/ml given at a rate of 6.6 mg/kg; Miller et al. 2004) as a reversal. The chemical immobilization mixture was delivered via 2cc transmitter darts shot from night vision-scoped cartridge-fired dart guns (Pneu-Dart, Williamsport, PA) over feeders. All capture and handlings methods were approved by the Auburn University Institutional Animal Care and Use Committee (PRNs 2008-1417, 2008-1421, 2010-1785, 2011-1971, 2013-2372, 2016-2964, 2016-2985).

We recorded sex, aged animals using tooth replacement and wear (Severinghaus 1949), assigned a unique 3-digit identification number visible on ear tags, and took an ear notch sample for DNA analysis (stored at -78 °C) for all previously uncaptured individuals. We recorded antler measurements according to the Boone and Crockett (hereafter "B&C") scoring system except for inside spread (Nesbitt and Wright 2016). We took antler measurements using a 6.35 mm wide flexible steel tape to the nearest 3.175 mm. These measurements included main beam length, tine lengths, and antler beam circumference measurements. We recorded the number of typical points and the number of total points (the sum of typical and abnormal points). Points (typical and abnormal) were defined as projections ≥2.54 cm in length (any projection <2.54 in length

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was not considered a point and was not recorded). Typical (or normal) points were projections that erupted vertically from the top of the main beam. An abnormal point was defined as those non-typical in location or extra points beyond the normal pattern of points (i.e., those that do not erupt vertically from the top of the main beam). From these antler measurements, we were able to calculate gross B&C score for all captured individuals. We took digital pictures of each individual containing the unique ear tag identification number and antlers, allowing for the identification of shed antlers.

Antler Shed Measurements:

We measured characteristics for each shed antler collected between 2012-2018. Similar to captured males, shed antlers were measured using the B&C scoring system for each shed antler and skulls containing antlers (Nesbitt and Wright 2016). We calculated gross B&C score as a comprehensive variable for overall antler growth and size for a given shed antler. The only aspect of our antler measurements that deviated from the B&C system was that when calculating gross B&C score we did not substitute the last available circumference measurement for any missing circumferences (e.g., if the fourth circumference measurement location was missing on a shed due to breakage, we only included the first three circumference measurements) and did not have an inside spread measure.

Dry mass and wet mass of each antler were measured to determine its specific gravity (relative density). We used a stainless-steel wire brush to clean foreign material from each antler before weighing. Dry mass was recorded on a digital scale to the nearest hundredth of a gram. Subsequently, each antler was suspended from a scale and weighed while being fully submerged and in a container of water. The wet mass measurement resulted from the shed being suspended in water until all air had dissipated from the shed. The wet mass measurement relies on

Archimedes' Principle, in which the buoyant force is equal to the weight of the water displaced by each antler.

Identification of Shed Antlers to Individuals

Shed antlers were assigned to individuals that were present in the population during the year they were cast using several methods. We used capture photos containing the unique ear tag number and antlers to match shed antlers to the individual who cast the antler. We obtained these capture images from 105 adult males during 242 capture (i.e., many males were captured in multiple capture periods). We supplemented capture photos with remote trail camera photos from annual camera population surveys within the ACF. We collected trail camera images annually between late February-early March before antler casting had occurred. We used trail camera photos where ear tag numbers could easily be identified, and antler characteristics used to assign shed antlers to individuals (see Newbolt and Ditchkoff [2019] for a detailed description of trail camera methods). Shed antlers that could not be confidently assigned to an individual were marked as unknown for individual and year shed in our analyses.

Statistical Analysis:

Capture Data

We used Program R for all statistical analyses (version 3.4.1, www.r-project.org, accessed 16 September 2019). We used a series of subsets of the data to compare antler characteristics between the shed antler samples and the overall population. To determine whether antler characteristics influenced detection of a shed antler, we used measurements taken from males captured in the ACF (i.e., measurements taken during capture before the antlers were cast), thus, allowing us to have antler characteristic measurements from shed antler we detected and those we did not detect. Once all shed antlers were identified to an individual, we determined

which males within a given year had shed antlers that were located. We ran linear mixed-effects models (logistic regression; lme) on antler characteristic measurements to determine if antler size influenced the detection of shed antlers. We used the antler characteristic as response variable, whether an antler was detected as our binomial fixed effect, and random effects of year and an year:individual interaction (to account for potentially detecting both antlers from an individual within a year).

Prior to creating candidate models for determination of which antler characteristics were the most important in the successful location of a shed antler, we determined correlation between our parameters using the cor function in Program R (R Core Team 2019) to avoid using >1 highly correlated variable in the same analysis. We expected all antler characteristics to be correlated, however, gross B&C score and main beam length were strongly correlated (Pearson's $r = 0.895$). For evaluation of which antler characteristics were the most important to locating a shed antler, we chose to proceed with main beam length instead of gross B&C score, which we felt would be more important in lifting a shed off the ground and thus, making it more visible to detection. For this analysis we evaluated models with antler characteristics that we thought provided a structural influence on the shed antler that made it easier to detect (i.e., antler characteristics that were most important in exposing an antler from vegetation). We investigated whether detection of a shed was driven by main beam length, total number of points, number of typical points, or length of the second tine (i.e., G-2). We used generalized linear mixed-effects models (logistic regression; glmer) with detection as our binomial response variable, the antler characteristic(s) as our fixed effects, and random effects of year and an year:individual interaction. We compared models using Akaike's information criterion corrected for small

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sample size (AICc) and considered models within 2 ΔAICc competitive (Burnham and Anderson 2002).

Pedigree Data

We used located shed antlers from 2012-2018 and our deer pedigree for ACF to determine if there was an age bias in detected shed antlers and the total percentage of antlers annually recovered from ACF. A detailed pedigree for deer within the ACF provided accurate annual estimates of the number of males and their ages within the population (see Neuman et al. [2016] and Newbolt et al. [2017] for a detailed description of pedigree construction). Using shed antlers, we used generalized linear mixed-effects models (logistic regression; glmer) to determine which age cohorts were represented by detected shed antlers and which were unrepresented compared to their availably in ACF. We specified detection as our binomial dependent variable, male age as our fixed effect, and random effects of year and year:individual interaction. Similarly, to determine the total percentage of shed antlers recovered for a given year, we compared the total number of shed antlers located for each individual male and all antlers that were available within the ACF assuming each male (≥1.5-year-old) shed two antlers annually.

Results

Based upon annual camera surveys and deer captures, we determined there were 113 unique adult males (≥1.5 years old) present in our population between 2012-2018, and this number ranged from 43-63 individuals per year (Table 1). Throughout the study we collected 284 (38%) of available shed antlers within the population. We located between 22 and 47 shed antlers annually, which represented 17–51% of all shed antlers available within the ACF in a given year. Mean annual age of all antler-bearing males in the population was between a low of

3.38 years old and a high of 4.63 years in 2012 and 2017, respectively (Figure 1). In our population, the mean age of deer for which a shed antler was found was 5.39 years (0.13 SE), compared to 3.65 years (0.11 SE) for deer whose antlers were not located. We found that a shed antler was 2.73 (1.83-4.05, 95% C.L.) times as likely to be detected for every 1-year increase in age of the male that shed the antler (p < 0.001).

We captured 105 adult males (≥1.5 years old) that subsequently cast antlers from 2012-2018, many of which were captured in ≥1 year. Of those, we located 176 (36.4%) of their 482 shed antlers (Table 2). Mean age of captured deer for which a shed antler was located was 5.36 years (0.15 SE), compared to 3.77 years (0.14 SE) for deer for which an antler was not located. We found that 8 of the 13 antler characteristics (main beam length, first three circumference measurements, length of the second tine (G2), gross B&C score, and number of total points and typical points) that were measured were significantly greater (p ≤ 0.019) in detected antlers than undetected antlers.

There were two competing models (within 2 ΔAICc of best performing model) units that described the relationship between antler characteristics and shed antler detection (Table 3). The top model included main beam length and total number of antler points (Figure 2). For every 1 cm increase in main beam length, a shed antler was 1.17 (1.09-1.28, 95% C.L.) times as likely to be detected (p < 0.001). A shed antler was 2.45 (1.30-4.64, 95% C.L.) times as likely to be detected for each 1-point increase in total antler points (p = 0.005). There was one model that was within 2 ΔAICc of this best performing model (and one slightly outside at ΔAICc = 2.03), however, the additional parameters appear to be uninformative, as the maximized log-likelihoods are essentially identical (Arnold 2010).

Discussion

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While shed antlers of any size may be difficult to see against natural backgrounds, it is not unexpected that larger antlers had greater detectability. Size of an object has been shown to influence detection of cryptic objects in nature. For example, size was found to influence detection of cryptic prey species by predators (Mänd et al. 2006, Remmel et al. 2009, Karpestam et al. 2014). It has also been shown that size of individuals or groups (clusters) of animals and the distance of objects influence sightability probabilities by human observers in wildlife population surveys. This has been observed in aerial surveys of wildlife species, where increased cluster size and distance of the animal species of interest influenced detectability by observers (Caughley 1974, Ransom 2012). Our study utilized line transect sampling methods in which, similar to aerial wildlife surveys, sighting probabilities are influenced by object size and distance (Drummer and McDonald 1987, Otto and Pollock 1990). Under the assumption that our observers held 10-m line transects (thus controlling changes in observer distance to objects), we expected variation in the detection of our shed antlers with variation in antler size under these conditions.

Intuitively, since detection probabilities were greater for larger antlers and antler size increases with age (Roseberry and Klimstra 1975, Schultz and Johnson 1992, Jacobson 1995, Strickland and Demarais 2000, Hewitt et al. 2014), our shed antler sample was biased toward older-age males. Thus, our results suggest shed antlers do not provide an accurate representation of antler size for white-tailed deer populations. However, it should be noted that because the population at ACF is comprised of a high percentage of older, mature males, our results may be somewhat influenced by our population age structure. In contrast, there would be few large antlers available for detection in a population with few mature males, and the sample may be less biased. Additionally, the ACF deer population has a later fawning season (Neuman et al. 2007),

which typically causes males to have smaller antlers at 1.5 years of age (Knox et al. 1991,

Jacobson 1995, Gray et al. 2002). Young males in our population may not have had enough time

by their second breeding season to develop branched antlers, making their shed antlers much

more difficult to detect, especially in tall vegetation.

Main beam length and total number of points were the most important antler

characteristics influencing shed antler detection. Main beam length forms the structure from

which all points vertically erupt. Increased main beam length may aid in detection by making the

antler extend through vegetation and project from the ground or increased main beam length may

simply make the antler easier to detect because it is a larger object. Total points are a

comprehensive variable for all points $\geq$2.54 cm (typical and non-typical points). Therefore,

differences in the total number of points may be influencing antler detection by changing the

physical size of the antler, allowing the shed antler to better protrude from vegetation making

them more visible, or some combination of both.

In contrast to Ditchkoff et al. (2000), our results do not support the hypothesis that shed

antlers are representative of a population. The deer population within the ACF is intensively

monitored. Therefore, we believe it is safe to assume that nearly all males within the population

are known in a given year. Further, because males are captured without regard for antler size

(i.e., volunteers are instructed to dart the first male that presents an opportunity), we believe the

antler characteristics of captured males are representative of the entire male segment of the

population. In contrast, Ditchkoff et al. (2000) assumed shed antlers were representative of their

study population based on antler measurements of shed antlers compared to those of harvested

males. Morphometric characteristics from shed antlers in the ACF suggest that shed antlers

represented older, larger antlered males in greater proportion than their prevalence in the

population. Although this is a non-hunted population, the biases we observed with our shed

antlers (i.e., greater detection of older, larger antlered males) may be similar to harvest data from

populations where younger males are protected from harvest and older males comprise the antler

characteristics represented by the harvest data (e.g., QDM). However, it is important to note a

distinct difference in conducting searches for shed antlers between this study and that by

Ditchkoff et al. (2000). Our objective for this study was to cover the entirety of the ACF, where

Ditchkoff et al. (2000) limited their searches to food plots ranging in size from 1-20 ha,

searching each one at least twice. Vegetation in their study was reported to be typically around 5

cm in height, where the ACF consisted of varying vegetative cover types, of varying height,

therefore, they were likely to have a much greater detectability of shed antlers regardless of size.

Restricting searches for shed antlers to areas of only low vegetation may limit the antler size and

age biases we found. This may be especially important when conducting searches on larger

properties, such as the 18,212-ha property where Ditchkoff et al. (2000) conducted their

searches, as covering the entirety of properties larger than the ACF would take considerable time

and/or personnel.

Although our results indicate that shed antlers are biased towards older and larger

antlered males, there are distinct benefits to using shed antlers instead of harvest data for

assessing male quality. First, shed antlers are a non-invasive source of data for mangers that can

allow for comparisons of antler characteristics between populations, both spatially and

temporally (Ditchkoff et al. 2000, Lopez and Beier 2012). While harvest data provide

information on harvested males, shed antlers provide data on individuals that survived the

hunting and winter seasons, which may be particularly important in the northern extent of the

white-tailed deer range where winter mortality is common (Severinghaus 1947, DelGiudice et al.

2002), and throughout the species range where managers desire to track individual males. Shed antlers provide managers the ability to track annual variation in antler characteristics at the population and individual levels, where harvest data provides measurements for just one antler set for individuals. This allows managers to track annual variation in individuals caused by changes in nutritional conditions, as antlers are a condition dependent trait. For example, pedicle seal depth, which can also only be measured using shed antlers, is the most sensitive antler morphometric to environmental stress in young males, especially in 1.5-year-old males (Bubenik 1990, Peterson et al. 2019). Tracking individual variation can also allow managers the ability to assess the effectiveness of antler-based harvest restrictions. Because shed antlers represent the males remaining after harvest, or the standing crop, they can allow managers to estimate antler characteristics of remaining males post-harvest after implementing new harvest restrictions/regulations. Additionally, shed antlers can provide a source of DNA for deer species without the need to capture or harvest individuals (O'Connell and Denome 1999, Hoffmann et al. 2015). DNA samples can be extracted from shed antlers that are weathered (Lopez and Beier 2012) and old (Hoffmann and Griebeler 2013), providing a means for population genetic studies, even from individuals that are no longer in the population. Lastly, searching for shed antlers takes minimal to no training or previous experience, presenting the opportunity to enlist people with a limited background in biological sciences for data collection.

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Table 1.1 - The annual number, percentage, and mean age of males from detected and non-detected shed antlers at the Auburn University Captive Deer Research Facility (ACF) from 2012-2018.

Year	Individuals [a]	Detected				Not Detected				Total N
		N [b]	% [c]	Mean	SE	N [b]	% [c]	Mean	SE	
2012	43	38	44	4.32	0.18	48	56	2.65	0.21	84
2013	46	47	51	4.86	0.21	45	49	3.01	0.29	92
2014	47	45	58	5.19	0.25	49	52	3.13	0.26	92
2015	48	23	24	6.02	0.38	73	76	3.80	0.27	94
2016	57	40	35	5.93	0.38	74	65	3.43	0.30	108
2017	63	36	29	5.97	0.37	90	71	4.10	0.31	122
2018	63	22	17	6.18	0.56	104	83	4.28	0.28	122
Unknown [d]		33	100							33
Total	113	284	38	5.39	0.13	483	62	3.65	0.11	734

[a] Number of males (≥1.5 years old) present in the population

[b] N = Number of shed antlers

Table 1.2 - Selected antler measurements of captured males at the Auburn University Captive Deer Research Facility (ACF) from 2012-2018.[a]

Detection	Detected					Not Detected					All Captured Males				
				Range					Range					Range	
Antler Characteristic	N	Mean	SE	Min.	Max.	N	Mean	SE	Min.	Max.	N	Mean	SE	Min.	Max.
Main Beam Length [b]	176	49.66*	0.52	25.40	65.41	306	35.63	0.97	2.22	59.37	482	40.75	0.71	2.22	65.41
H-1	176	11.29***	0.14	5.08	17.78	306	8.62	0.19	1.91	20.00	482	9.60	0.14	1.91	20.00
H-2	175	9.55***	0.13	3.49	18.73	241	8.10	0.13	2.86	12.07	416	8.71	0.10	2.86	18.73
H-3	172	8.99**	0.14	4.76	17.15	222	7.66	0.14	2.54	14.92	394	8.24	0.11	2.54	17.15
H-4	147	6.73	0.13	3.49	11.11	156	6.04	0.13	2.86	10.16	303	6.38	0.09	2.86	11.11
G-1	173	9.80	0.28	2.54	19.37	233	8.31	0.25	2.54	20.00	406	8.95	0.19	2.54	20.00
G-2	172	18.74**	0.38	5.08	32.07	221	15.91	0.39	2.54	29.85	393	17.15	0.28	2.54	32.07
G-3	147	13.79	0.46	2.54	24.45	156	12.27	0.42	2.54	26.04	303	13.01	0.31	2.54	26.04
G-4	21	6.15	0.79	2.54	14.61	17	5.42	0.66	2.54	11.43	38	5.82	0.52	2.54	14.61
A-1	35	6.15	0.76	2.54	25.72	25	8.14	1.23	2.54	27.31	60	6.98	0.68	2.54	27.31
Gross Score [c]	176	127.25**	2.00	41.61	193.36	306	84.33	2.75	4.45	169.23	482	100.00	2.11	4.45	193.36
Typical Points	175	2.94***	0.05	1.00	5.00	241	2.60	0.05	1.00	4.00	416	2.74	0.04	1.00	5.00
Total Points	175	3.26***	0.08	1.00	9.00	241	2.71	0.06	1.00	5.00	416	2.94	0.05	1.00	9.00

[a] The measurements represent those from captured males whose antlers were available during the shed hunting period immediately following capture.

[b] Main beam length, circumferences, and tine lengths are measured in centimeters.

[c] Gross scores are based on the Boone and Crockett Club's scoring system described by Nesbitt & Wright (2016) and scored to the nearest .31 centimeter (cm; 1/8 inch)

* $p \leq 0.05$; ** $p \leq 0.01$; ***$p \leq 0.001$; Significance is tested between the detected and not detected shed antler groups using linear mixed effects models

Table 1.3 - Model suite selection for antler characteristics influencing the detection of shed antlers at the Auburn University Captive Deer Research Facility (ACF) from 2012-2018.

Model	Parameters	Maximized log-likelihood	AICc	Δ AICc	w_i
Main Beam + Total Points	4	-212.697	443.50	0.00	0.51
Main Beam + Total Points + Typical Points	5	-212.608	445.40	1.88	0.20
Main Beam + G2 + Total Points	5	-212.736	445.50	2.03	0.19
Main Beam + G2 + Total Points + Typical Points	6	-212.586	447.40	3.93	0.07
Main Beam + Typical Points	4	-216.016	450.50	7.03	0.02
Main Beam	3	-217.69	452.10	8.59	0.01
Main Beam + G2 + Typical Points	5	-215.891	452.40	8.91	0.01
Main Beam + G2	4	-217.605	454.10	10.61	0.00
G2 + Total Points	4	-219.762	458.30	14.86	0.00
G2 + Total Points + Typical Points	5	-219.719	460.30	16.83	0.00
G2 + Typical Points	4	-222.841	464.90	21.46	0.00
Total Points	3	-224.959	466.80	23.35	0.00
Total Points + Typical Points	4	-224.911	468.80	25.28	0.00
G2	3	-227.307	472.60	29.09	0.00
Typical Points	3	-229.188	475.80	32.28	0.00
Null Model	2	-236.053	488.80	45.31	0.00
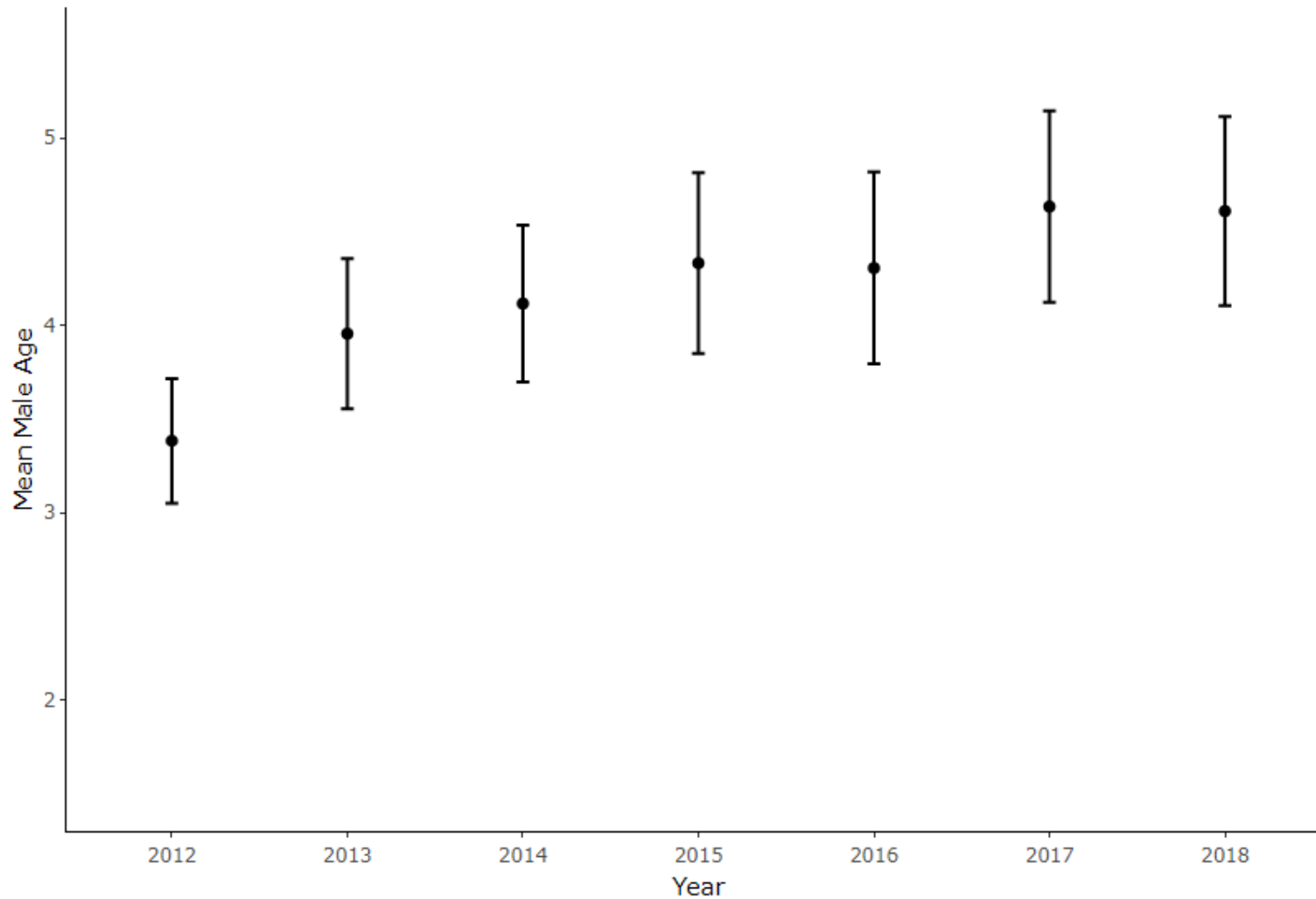
Figure 1.1 – Mean male age of deer that had shed antlers available within the Auburn University Captive Deer Research Facility (ACF) from 2012-2018. Mean ages are from every male of the population that was ≥1.5 years-old within a year. Error bars indicate 95% confidence interval.
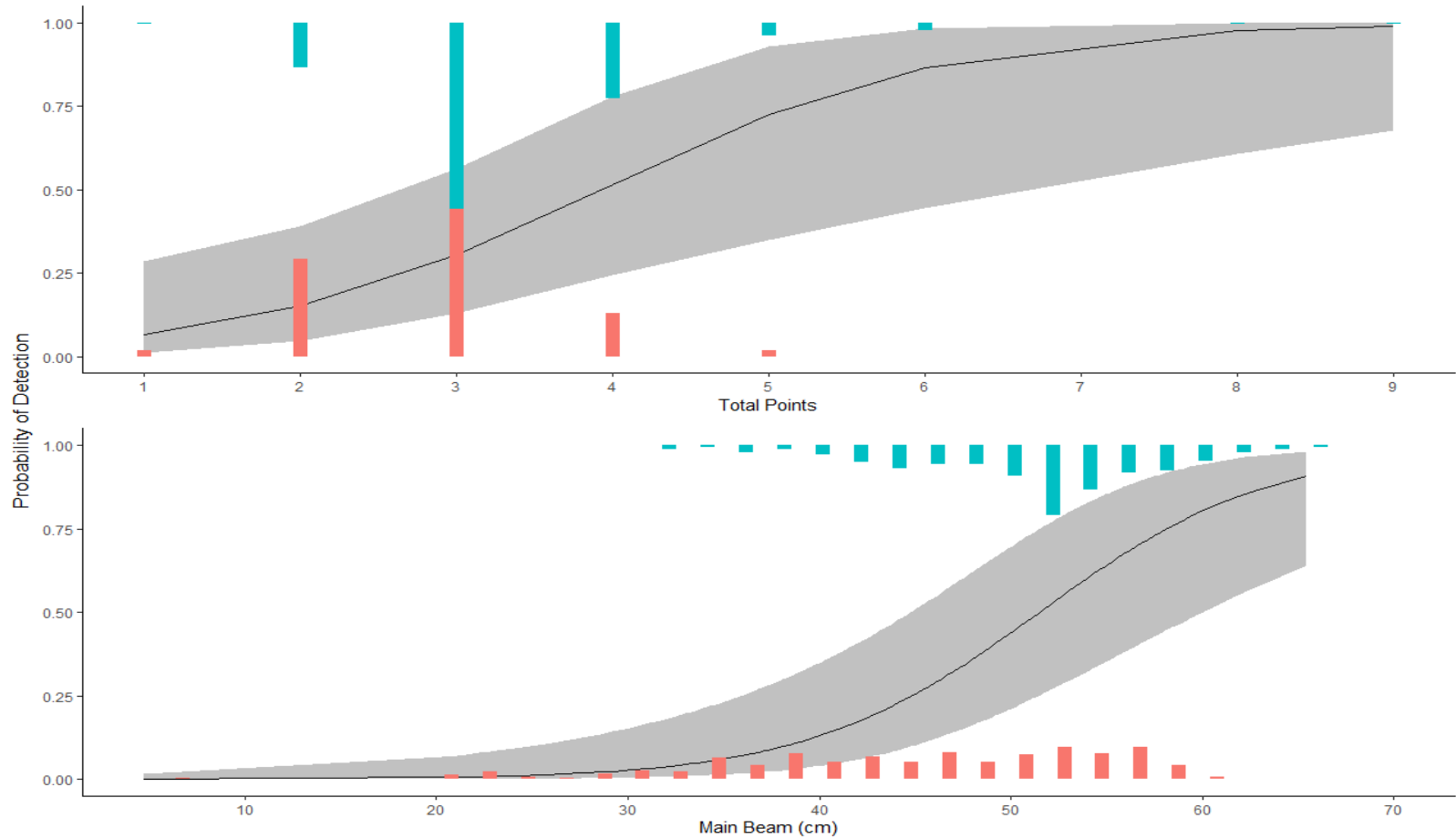
Figure 1.2 – Influence of total number of points (top) and main beam length (bottom) on the probability of shed antler detection. Probability of detection was based on results from the top competing model from the candidate model set evaluated via AICc. The bands represent the 95% confidence envelopes and histograms on top and bottom of each plot represent distribution of the shed antler measurements used to inform the model.

Chapter 2: Repeatability of Antler Characteristics in Nutritionally Stable White-tailed Deer Populations

Abstract

Managers have long been interested in annual variation of antler characteristics for white-tailed deer (*Odocoileus virginianus*). Although an individual's antler size increases with age, annual variation in antler size and conformation has also been associated with annual variation in nutrition. However, none have examined the repeatability (i.e., the intra-class correlation of reproducible measurements of a phenotypic trait over time) of antler characteristics in a nutritionally stable environment. Thus, we evaluated the repeatability of antler characteristics in two Alabama populations of white-tailed deer where natural forage was supplemented with pelletized high-protein feed, supplied *ad libitum*, year-round. We located shed antlers annually from 2012-2018 using both systematic and opportunistic searches. Shed antlers were identified to individuals using trail camera and capture photos and by using microsatellite loci identity analysis. We then quantified antler characteristics including specific gravity, mass, total points, and other measurements used in the Boone and Crockett scoring system. Overall, repeatability estimates for antler characteristics were variable, ranging from moderately low for traits like specific gravity and total points, to high for tine lengths, main beam length, and gross score. We also found differences in repeatability estimates of specific gravity, circumference measurements, and mass between populations. This may suggest a difference in resource utilization for antler characteristics in response to different pressures from competing males and potential mates.

Introduction

Wildlife managers have long been interested in temporal variation of labile phenotypic traits in animals (Nussey et al. 2007). Understanding the extent of individual variation in phenotypic trait expression is important for management and conservation of species and determining potential for phenotypic selection. Discerning phenotypic variation among individuals in a population requires an understanding of how a quantitative trait varies among individuals and how those traits vary temporally (Hayes and Jenkins 1997). Often, phenotypic traits may be expressed multiple times spatially or temporally in an individual's lifetime. Phenotypic traits are influenced by several factors including genetics, age, and environmental factors, making these traits rarely repeatable. Thus, improving our understanding of phenotypic trait variation can allow for a better understanding of genetic potential of these traits and how environmental factors influence the expression of that potential.

Antlers are a sexually selected characteristic that appear to serve as honest advertisements of the possessor's quality and condition (Ditchkoff et al. 2001). Antlers are unique to cervids, and are annually cast and regenerated, where their size and confirmation are partially influenced by annual fluctuations in environmental conditions (e.g., nutrition availability). Variation in an individual's antler size has important implications for advertisement of quality to potential competitors and mates and through intraspecific competition and, thus, sexual selection, because large, branched antlers aid in leverage during male combat in many cervid species (Clutton-Brock et al. 1980, Goss 1995). To be honest advertisements of their bearer's quality, sexually selected traits should be costly to produce or maintain (Zahavi 1975). Antlers are physiologically costly to produce (Ullrey 1983), suggesting that males with less annual variation among antler characteristics may be of greater quality or condition and better able to cope with environmental stressors (Foley et al. 2012). It has been suggested that during periods of nutritional stress, males

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may exhibit an overall reduction in antler size, but preferentially allocate resources to antler characteristics that provide advantages for intraspecific competition (i.e., those that aid in leverage; Mysterud et al. 2005) and/or improve the visual appearance of large antlers for advertising to prospective mates (Foley et al. 2012).

There are also management implications of antler variation for cervid species. Increasing antler size is often an objective of deer management programs, and antler size is used as an indicator of the effectiveness of a management program (Demarais and Strickland 2011). Many management programs, including those of state agencies and private landowners, also use antler traits to inform harvest decisions (Demarais and Strickland 2011). For example, antler-based harvest criteria may be used to protect young males from hunter harvest and, thus, increase the proportion of older, large-antlered males in the population. Thus, it would make sense to base such criteria on antler characteristics less susceptible to annual variation, especially when producing more mature males are the target of the antler restriction (Foley et al. 2012).

Foley et al. (2012) investigated variation of antler characteristics in white-tailed deer (*Odocoileus virginanus*) in a semi-arid environment. They found that varying rainfall and supplemental feed intensity (i.e., none, moderate, intense) influenced annual variation of antler characteristics. However, to our knowledge there has never been an investigation of annual variation in antler size for white-tailed deer populations in a relatively stable nutritional environment. By maintaining a steady nutritional plane, we should be able to better elucidate the influence of genetics on antler repeatability and provide a baseline to compare past and future studies on annual variation of antler characteristics in variable environments. As a result, our primary objective was to assess the annual variation of antler characteristics in two white-tailed deer populations maintained in nutritionally stable environments.

Methods

Study Area

Our study was conducted on two captive white-tailed deer populations in Alabama. Three Notch Wildlife Research Foundation (hereafter "Three Notch") was a 258-ha facility that was enclosed with a 3-m high deer proof fence in 1997. Three Notch was located approximately 10 km east of Union Springs, Alabama, USA in Bullock County. All deer within Three Notch were wild deer contained within the fence at its initial construction and their descendants. Three Notch consisted of mixed vegetative cover types of planted wildlife food plots and mixed forests. Forested habitat varied from dense hardwood stands in creek drainages to open, mature, mixed pine (*Pinus* spp.) hardwood stands in upland areas. There were approximately 140-ha of mixed pine-hardwood stands, 60-ha of mature hardwoods, and 25-ha of pine stands. Hardwood species consisted primarily of oaks (*Quercus* spp.), and loblolly (*Pinus taeda*) and shortleaf pine (*P. echinata*) constituted the vast majority of pine species. Prescribed burning was applied annually on approximately 100-120 ha of upland stands to aid in the detection of shed antlers and improve understory forage availability for deer. Food plots consisted of perennial forage plots of 3.5 ha of ladino clover (*Trifolium repens*) and 6.5 ha of alfalfa (*Medicago sativa*), and 1 ha of cool season plots of winter rye (*Secale cereale*). Supplemental deer feed (20% protein; "Purina Antlermax", St. Louis, MO) was supplied *ad libitum* year-round at 12 permanent feed troughs. Irrigation systems supplemented natural precipitation on the clover and alfalfa food plots. Three Notch averaged 1,400 mm of annual precipitation and had an average annual temperature of 17.3 °C (National Climatic Data Center 2010b). A centrally located 20-ha pond, and the headwaters of the Pea River, provided a consistent and ample year-round water source for deer. For a more detailed description of Three Notch see Glow and Ditchkoff (2017) and Glow et al. (2019). The

deer population at Three Notch was managed through restricted, primarily archery, hunting by the landowner and family members. The harvest was limited to mature males (≥5 years old), and females of any age class. The limited hunting pressure, restrictive harvest, and abundant food resources resulted in a high density population. A 2007 mark-recapture survey (Jacobson et al. 1997) estimated a sex ratio of 2.64:1 (M:F) and a deer density of at least one deer per 1.7 ha (McCoy et al. 2011).

The Auburn University Captive Deer Facility (hereafter "ACF") was established with construction of a 2.6-m high deer-proof fence in 2007. The enclosure was 174 ha and was located in Camp Hill, Alabama, USA. As with Three Notch, the deer population within the facility consisted of wild deer that were captured at the time of fence construction and their subsequent descendants. ACF consisted of two main general vegetative cover types: open hayfields (40%) and mixed forest (60%). The open hayfields were maintained for hay production and consisted a variety of grass species including Bermuda grass (*Cynodon* spp.), fescue (*Festuca* spp.), big bluestem *(Andropogon* spp.), Johnson grass *(Sorghum* spp.), dallisgrass (*Paspalum* spp.) and bahiagrass (*Paspalum* spp.). Mixed forest areas consisted primarily of hardwood species (70%) including oak, hickory (*Carya* spp.) and maple (*Acer* spp.), and pine species (20%) dominated by loblolly pine. Thickets of sweetgum (*Liquidambar styraciflua*), eastern red cedar (*Juniperus virginiana*), *Rubus* spp., and Chinese privet (*Ligustrun sinese*) constituted the remaining 10% of mixed forest. Forested areas were primarily closed canopy with little understory, however, canopy gaps along creek bottoms and forest edges created a dense understory. A second-order creek flowed through ACF, providing a year-round water source. ACF had an average annual temperature of 15.9 °C and an average annual precipitation of 1,360 mm (National Climatic Data Center 2010a). Natural deer forage was supplemented with 3

permanent protein gravity feeders (16-18% protein; Record Rack®, Nutrena Feeds, Minneapolis, MN) throughout the year and 4 timed corn feeders (providing approximately 2 kg/day) during periods when deer were actively being captured as part of other research. The deer population at ACF was maintained for research purposes (Neuman et al. 2016, Neuman et al. 2017, Newbolt et al. 2017) and the population was regulated primarily by natural mortalities. Additionally, a select number of deer (10-15 individuals; ≤6 months of age) were captured annually and released outside of the facility to maintain desired deer density and age cohorts (Newbolt et al. 2017).

Shed Antler Collection and Data Collection:

Shed antlers were located annually from 2012-2018 on Three Notch and ACF using systematic searches and opportunistic detection. Upland areas were burned and wildlife food plots and hay fields were mowed prior to peak antler casting to assist in the detection of shed antlers. Extensive systematic searches were conducted utilizing volunteer groups (between 2-15 people) beginning in late March and continuing through April until both study areas had been extensively covered. Forested areas were searched in a series of transects, with volunteers instructed to hold a spacing of approximately 10 m between routes. All shed antlers and antlered skulls were collected and labeled with the collection year.

Shed Antler Measurements:

Physical antler characteristics were measured for each shed antler collected between 2012-2018, and antler measurements used in the Boone and Crockett (hereafter "B&C") scoring system were recorded for each shed antler and skulls containing antlers (Nesbitt and Wright 2016). The physical antler measurements we recorded included: main beam length, tine length(s), smallest circumference measurement between the first tine (G-1) and burr (H-1 measurement in the B&C scoring system), and smallest circumference measurements between

each of the tines up to and including between the third and fourth tine (H-2, H-3, H-4). Thus, there could only be a maximum of four total circumference measurements for each shed antler. If there was no fourth tine (G-4), the fourth circumference measurement (H-4) was recorded as the circumference halfway between the G-3 and the tip of the main beam. If the antler only had two tines (G-1 and G-2) then only three circumference measurements were recorded; those with one tine (G-1) only had two circumference measurements; those with no tine (i.e., spike antlers) only had one circumference measured (halfway between the cornet and the tip of the main beam). The number of typical points and number of total points (the sum of typical and abnormal points) were also recorded. To be considered a point (typical and abnormal) the length of projection had to be ≥ 2.54 cm. Typical (or normal) points were projections ≥ 2.54 cm that erupted vertically from the top of the main beam. An abnormal point was defined as a point erupting in some other manner from the main beam or erupting from another point. Physical antler measurements were used to calculate gross B&C score as a comprehensive variable for overall antler growth and size.

In addition to B&C antler measurements, dry and wet mass of each antler were measured to determine specific gravity (relative density). Each antler was thoroughly cleaned of foreign material using a stainless-steel wire brush before a mass measurement was taken. Dry mass was measured using a digital scale and recorded to the nearest hundredth of a gram. After obtaining a dry mass measure, each antler was weighed using the same scale while being fully submerged and suspended in a container of water. The antler was left suspended until all air had dissipated, resulting in the wet mass measurement. The wet mass measurement is the result of Archimedes' Principle, in which the buoyant force is equal to the weight of the water displaced by each antler. All antler measurements were taken using a 6.35 mm wide flexible steel tape to the nearest 3.175

mm. Similar to Foley et al. (2012), we defined primary antler characteristics as those traits with continuous measures that formed the physical structure of an individual's antler set (i.e., main beam length, circumferences, and tine lengths). All other antler characteristics that were discrete in measure (i.e., number of points), or could not be assessed by outward visual appearance (i.e., specific gravity and mass) were considered secondary antler characteristics.

Genetic Data Collection:

DNA samples were drilled from the base of each antler using a 6.35 mm drill bit designed for drilling through metals. The shavings from a shallow initial drill depth of 1-2 mm were discarded to minimize foreign material in the DNA sample. Drill bits were cleaned and sterilized after each use by first rinsing with a 10% bleach solution (10% bleach/90% De-ionized water), scrubbing with a stainless wire brush, further rinsing with the bleach solution, rinsing with de-ionized water, and allowing the bits to completely dry. Antler shavings were collected until enough was obtained to fill a 1.5-mL microcentrifuge tube (approximately 4-5 mm in drilling depth). Drilling occurred approximately half-way between the coronet and the center of the base (half the radius) as this area was preferred for DNA material (B. Cassidy, DNA Solutions, INC., personnel communication).

Microsatellite Analysis:

DNA Solutions, Inc. (Oklahoma City, OK, USA) conducted all DNA sample isolation, extraction, amplification, and microsatellite marker scoring. The microsatellite panel used was derived from the 21 microsatellite loci panel first developed for white-tailed deer by Anderson et al. (2002) and subsequently refined by DeYoung et al. (2003). The resulting microsatellite panel consisted of 18 total microsatellite loci and 1 sex locus, consisting of 7 tetranucleotide and 12 dinucleotide repeats. Because of minor changes in the panel over time and lack of presence in

our populations, 14 microsatellite loci were used in our analyses (i.e., Cervid1, BM6506, N, INRA011, BM6438, O, BL25, K, Q, D, OarFCB193, P, L, S).

Individual Identification:

For identification of individuals within and across years, we used Cervus 3.0 (Kalinowski et al. 2007). The minimum number of matching loci required to be considered a match was set at Cervus 3.0's default setting of half the number of loci used in the allele frequency analysis (i.e., 7 loci for Three Notch). The identity of individuals for all shed antlers at Three Notch was determined using the microsatellite panel and identity analysis in Cervus 3.0. The identity of individual sheds found at ACF was determined utilizing photos from captures and camera trap surveys. A unique 3-digit ear tag affixed to each deer was used to correctly identify individuals in camera photos. If we could not confidently identify a shed antler to an individual using capture and trail camera photos, that shed antler was marked with the collection year and unknown for identity.

Statistical Analysis:

We compared antler characteristics between populations using only the left antler side (thus accounting for an individual only once per collection year). For each characteristic, we fit linear mixed-effects models with a random effect of individual to account for repeated sampling of individuals across years. To determine the annual reproducibility of antler characteristics, we estimated repeatability (*R*) for Three Notch, ACF, and both study sites combined. Repeatability is estimated as the intra-class correlation (*ICC*) and represents the fraction of total phenotypic variance in the population to the variation among groups (i.e., within individual deer; Stoffel et al. 2017). Program R was used for all statistical analysis (version 3.4.1, www.r-project.org, accessed 16 September 2019). The annual repeatability of antler

characteristics was determined using linear mixed models (LMMs) in the R package "rptR", which allowed for estimation of adjusted repeatability (repeatability estimates taking into account the influence of fixed effects; Nakagawa and Schielzeth 2010, Stoffel et al. 2017). Enhanced agreement repeatability of a given physical antler characteristic for an individual was determined using the collection year and antler side (i.e., left or right) as fixed effects and individual as a random effect. Confidence intervals and standard errors for repeatability were estimated using 1,000 parametric bootstrapped repetitions and statistical significance was tested by likelihood ratio (Stoffel et al. 2017). The range for repeatability estimates is from 0 to 1, where $R = 0$ indicates that the average of repeated measures of individuals are all identical and thus, lacks additive genetic variance (i.e., the variation is entirely within individuals). A repeatability measure of 1.0 would indicate that the given antler characteristic is the same every year and all the variation is among individuals in the population (Hayes and Jenkins 1997). To assess differences in repeatability between our two populations, for each characteristic, we used the 1000 bootstrap samples for each area to derive 1000 bootstrap sample of the difference in repeatability. We then used 2.5 and 97.5 percentiles as empirical confidence limits, and concluded differences were significant at alpha=0.05 if confidence limits excluded 0.

Only individuals that had shed antlers of the same side (i.e., left or right) in subsequent years (e.g., one right shed in 2016 and another right shed in 2017) were included in repeatability analyses. Broken tines or main beams were removed from analyses, as was any antler measurement that would be influenced by a broken main beam or tine. For example, if the first antler tine (i.e., G-1) was broken, then that measurement, the mass measurement, and gross score values were also removed from analysis. Total and typical point values were still included in the analyses if a tine was ≥2.54 cm (the minimum to be considered a point in the B&C scoring

system). Specific gravity values were not removed from the analyses even if the tines and/or main beam were broken on a shed antler.

Results

We located 359 total shed antlers at Three Notch (n = 141) and ACF (n = 216) between 2009-2018, from 90 unique individuals (n = 46 and n = 43 at Three Notch and ACF, respectively). The number of shed antlers included in each repeatability analysis for each antler characteristic, from both study sites, ranged from 359 for total and typical points to 37 for the fourth tine measurement. Most antler characteristics were similar in mean measurements (P > 0.05) for both study locations, however, 2 differed: specific gravity (P < 0.001) and the fourth beam circumference (P = 0.03; Table 1). The number of shed antlers per individual for the 90 unique individuals used in our repeatability analyses (including right and left antler sides), varied from 2 shed antlers to 12 shed antlers, with 2 shed antlers being the most frequent from 38 individuals (Figure 1).

Repeatability estimates from both study sites combined ranged from a high repeatability for the third circumference (i.e., H-4; R = 0.66) to a low repeatability for abnormal points (R = 0.04; Table 2). Repeatability estimates were high ($R \geq 0.60$) for main beam length, the first three circumferences, the first tine length, and gross score. Moderate repeatability estimates ($R \geq 0.45 \leq 0.60$) were found for the fourth circumference, the second and third tine lengths, specific gravity, and mass (g). Low repeatability estimates ($R \leq 0.45$) were found for the fourth tine length, abnormal points, and typical and total points. Repeatability estimates between Three Notch and ACF were comparable to each other, except regarding specific gravity, mass (g), and circumference measurements. Specific gravity repeatability estimates were less at Three Notch compared to ACF and both sites combined (Three Notch; R = 0.43; ACF R = 0.69; and

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combined; $R = 0.53$). In contrast, Three Notch had considerably greater mass repeatability estimates than did ACF and both sites combined (Three Notch; $R = 0.73$; ACF $R = 0.45$; and combined; $R = 0.59$). We found statically significant differences in repeatability between our populations (alpha ≥ 0.05) for specific gravity, mass, and the first circumference measurements (H-1 and H-2). Abnormal point repeatability estimates were very low to zero in all three analyses and was the only antler characteristic that was not statistically significant, regardless of study location.

Discussion

Main beam length, tine lengths, and gross score had high repeatability in both populations. Foley et al. (2012) also found high repeatability estimates for these primary antler characteristics in several white-tailed deer populations in Texas under varying environmental conditions. Their repeatability estimates for main beam length were above 0.60 for all populations, and total antler length estimates (a measure of gross B&C score without the inside spread measurement, or approximately twice the measure of our shed antler gross scores) were 0.59 or greater. Sexual traits with high repeatability are likely to be selected by choosy females because they may indicate males that provide genetic benefits to offspring (Garamszegi et al. 2006), and thus, may be potential targets for sexual selection (Gil and Gahr 2002, Sattman and Cocroft 2003). Thus, consistently high repeatability estimates across studies indicates there is strong selective pressure for main beam length and total antler development (e.g., gross score) in white-tailed deer (Foley et al. 2012). Because the primary function of antlers is for mate acquisition through use as ornaments and weapons (Morina et al. 2018), consistently high repeatability suggests these antler traits may play an important role in advertisement and/or combat. For example, antler characteristics, such as main beam length, may increase antler

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strength, provide additional leverage, and increase overall visual appearance of size. For example, larger branched antlers provide additional leverage for pushing (Goss 1995), thus antler strength and size (e.g., longer main beam/tine lengths) may be more beneficial than number of points (Foley et al. 2012).

Number of antler points (total and typical) had low repeatability estimates in our populations compared to other antler characteristics we measured. This is similar to what was reported for white-tailed deer populations in Texas (Foley et al. 2012) and Mississippi (Lukefahr and Jacobson 1998), as well as in red deer (*Cervus elaphus*; Bartos et al. 2007). While our repeatability values for the number of antler points were generally less than those previously reported (Lukefahr and Jacobson 1998, Bartos et al. 2007, Foley et al. 2012), there is a consistent pattern where number of antler points is more variable than other antler traits Differences in annual repeatability between primary antler characteristics and number of points may suggest that antler traits that provide advantages in combat (e.g., main beam length) are more important than number of antler points which may provide little advantage against competitors. Once a set of antlers meets a certain minimum threshold of number of antler points, they have possibly maximized their effectiveness for leverage during combat, and the investment required to grow additional antler points is not worth the minimal increase in combat effectiveness. Intrasexual and intersexual advertisement is partially driven through visual cues, where antler appearance likely plays a role (Lincoln 1972, Clutton-Brock 1982, Ditchkoff and DeFreese 2010). As noted by Foley et al. (2012), there may be minimal difference in the visual appearance between males with similar primary antler traits despite variance in the number of antler points (e.g., a male with 6 antler points may look similar to a male with 8 antler points if all other characteristics are similar). Additionally, there is likely little difference in the ability of a male to generate leverage

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during combat despite differing number of antler points as long as the number of points is above

some minimum threshold. The low repeatability estimates for abnormal points (represented by

the number of total points versus typical points) provides further support for this hypothesis.

According to Foley et al. (2012) variable environmental conditions (e.g., rainfall) should

reduce repeatability of antler characteristics. If this is true, populations experiencing similar

environmental conditions should exhibit similar patterns in repeatability estimates of antler

characteristics. However, we found differences in repeatability estimates for specific gravity,

mass, and beam circumferences between our study populations, despite them experiencing

similar nutritional and environmental conditions. At the ACF, antler circumference measures and

antler mass had low repeatability, compared to Three Notch where we found high repeatability

for these antler traits. We suspect that differences in historical deer management paradigms

between the two study sites led to these differences. Three Notch had been managed for

production of trophy deer for more than 20 years, and the development of large-antlered males

was the management priority. To increase the probability of producing trophy males, the sex

ratio of the population was maintained above 2.5:1 (males:females; McCoy et al. 2011, Glow

and Ditchkoff 2017, Glow et al. 2019). In contrast, the ACF was a research facility that

simulated a naturally occurring wild population, had a sex ratio of approximately 1:1, and had

been in existence for less than 10 years (Neuman et al. 2016, Neuman et al. 2017, Newbolt et al.

2017). Males at Three Notch likely experienced greater intraspecific competition for mates than

males at the ACF because of the highly skewed sex ratio. Additionally, because of the artificially

inflated density of mature males at Three Notch, which is typical in white-tailed deer populations

managed for trophies (Cook and Gray 2003), there was likely greater incidence of agonistic

encounters than is found in other populations. As a result, natural selection would favor males

with antler characteristics that minimize likelihood of antler breakage in that population. Reducing breakage during agonistic encounters and would enable males to maintain competitiveness throughout the breeding season. Conversely, individuals with broken tines and antlers would potentially be at a competitive disadvantage. Minimizing antler breakage would also maintain antler appearance, which would be important for both inter- and intrasexual advertisements. The proportion of spongiosa has been shown to be positively associated with beam circumference in antlers (Miller et al. 1985) and is thought to increase the ability of an antler to withstand impacts during fights (Chapman 1980). Previous research at Three Notch found that males with greater basal circumference (and more spongiosa) and fewer antler points had lower antler breakage rates (Karns and Ditchkoff 2012).

Despite the greater estimates for antler mass and beam circumferences, specific gravity measurements were surprisingly low for Three Notch, while the repeatability for specific gravity at the ACF was the greatest out of all measured antler characteristics for that population. Miller et al. (1985) reported that specific gravity (relative density) of whole antlers decreased with an increase in beam diameter, and thus spongiosa. Because antler size is positively associated with male age (Roseberry and Klimstra 1975, Schultz and Johnson 1992, Jacobson 1995, Strickland and Demarais 2000, Hewitt et al. 2014), we therefore would expect older males to generally have less dense antlers and increased spongiosa (Miller et al. 1985). Decreased density and increased spongiosa provides advantages for older males. It allows for increased antler strength, but also allows older males to possess larger antlers with less mineral demand for antler growth (Miller et al. 1985). We would therefore expect males within a population that experiences greater intraspecific competition to have greater repeatability values for specific gravity than we found at Three Notch. It is possible that we detected at greater number of younger male shed antlers at

Three Notch, which would experience more annual variation in antler growth and thus variation in antler traits. However, data at the ACF suggest that detected shed antlers are biased toward older age classes (Deig 2020), and the relative mature age of males at Three Notch makes this unlikely.

Several factors may have influenced the repeatability of antler traits in our populations and between our populations and those in other studies. As antler size is asymptotic in growth, increasing with age until maximum antler size is achieved (Roseberry and Klimstra 1975, Hewitt et al. 2014), mature males will have inherently less variation in most antler characteristics. We were not able to assess the age of males at Three Notch, however, data from the ACF suggest that detected shed antlers are usually from larger antlered, mature males (Deig 2020), thus we believe the impact of age on our results would be minimal. We also did not account for nutritional variances in natural forage between our two populations that may have caused differences in the expression of antler characteristics between our populations, though the supplemental feed supplied year-round *ad libitum*, should have minimized any influence from variation in natural forage quality. Lastly, restocking of white-tailed deer populations in Alabama may have caused considerable differences in genetic potential for antler expression, thus influencing repeatability. We could not locate any record of restocking in Bullock county (Three Notch), but Tallapoosa had records for restocking in 1956 and 1961-1963 from several origins including Alabama (from Clarke, Marengo and Sumter counties and captive populations), Georgia, and Arkansas (McDonald and Miller 2004). While antler morphometrics from shed antlers were similar for both populations, the potential for genetically mediated annual variation in antler traits caused by selective harvest, being in a closed population, and restocking is certainly a possibility.

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Table 2.1 - Selected antler character measurements of left shed antlers found at the Auburn University Captive Deer Research Facility (ACF) and Three Notch Wildlife Research Foundation (Three Notch) from 2009-2018 used in the repeatability analyses.

Study Site	Three Notch					ACF					Combined Sites				
				Range					Range					Range	
Antler Characteristic	N	Mean	SE	Minimum	Maximum	N	Mean	SE	Minimum	Maximum	N	Mean [d]	SE	Minimum	Maximum
Main Beam Length [a]	84	49.34	0.76	29.53	62.23	103	48.82	0.61	29.21	62.87	187	49.05	0.48	29.21	62.87
H-1	93	10.53	0.20	5.08	15.56	112	10.14	0.13	6.99	13.97	205	10.32	0.11	5.08	15.56
H-2	91	8.84	0.14	4.76	11.75	112	8.82	0.12	5.08	12.38	203	8.83	0.09	4.76	12.07
H-3	90	8.47	0.17	3.18	11.43	110	8.43	0.14	5.08	12.38	200	8.45	0.11	3.18	12.38
H-4	81	6.60	0.17	3.49	10.48	96	6.11	0.14	3.49	10.16	177	6.33[*]	0.11	3.49	10.48
G-1	71	9.34	0.35	3.18	16.83	100	9.12	0.32	2.54	16.51	171	9.20	0.24	2.54	16.83
G-2	83	18.58	0.56	3.81	32.70	108	18.57	0.40	2.54	28.26	191	18.58	0.33	2.54	32.70
G-3	68	15.52	0.63	2.54	27.62	87	14.15	0.55	3.18	24.13	155	14.75	0.42	2.54	27.62
G-4	11	8.25	1.03	2.54	12.38	7	6.08	1.55	3.18	14.92	18	7.41	0.88	2.54	14.92
Abnormal Point	11	11.55	3.67	2.86	44.13	22	6.47	1.10	2.54	25.40	33	8.16	1.45	2.54	44.13
Specific Gravity	91	1.63	0.01	1.40	1.83	112	1.56	0.01	1.25	1.79	203	1.59[***]	0.01	1.25	1.83
Mass [b]	53	548.92	30.77	94.82	1052.42	106	528.62	17.76	147.43	1001.02	159	535.38	1.56	94.82	1052.42
Gross Score [c]	55	49.39	1.55	13.75	72.38	91	48.47	0.90	21.25	63.75	146	48.82	0.81	13.75	72.38
Typical Points	93	2.89	0.08	0.00	4.00	112	2.93	0.05	1.00	4.00	205	2.91	0.04	0.00	0.00
Total Points	93	3.08	0.09	0.00	5.00	112	3.15	0.06	1.00	5.00	205	3.12	0.56	4.00	5.00

[a] Main beam length, circumferences, and tine lengths are measured in centimeters.

[b] Mass is measured in grams to the nearest .01 gram

[c] Gross scores are based on the Boone and Crockett Club's scoring system described by Nesbitt & Wright (2016)

[d] * $p \leq 0.05$; ** $p \leq 0.01$; *** $p \leq 0.001$; Significance is tested between the Three Notch and ACF populations using linear mixed effects models (LMMs)

Table 2.2 - Repeatability estimates for antler characteristics (SE) for individuals from shed antler found at the Auburn University Captive Deer Research Facility (ACF) and Three Notch Wildlife Research Foundation (Three Notch) from 2009-2018.

Antler Characteristic	Three Notch			ACF			Combined Sites		
	$N (SA)$ [a]	R (SE) [b]	P [c]	$N (SA)$	R (SE)	P	$N (SA)$	R (SE)	P
Main Beam	46 (129)	0.599 (0.075)	< 0.001	43 (201)	0.610 (0.067)	< 0.001	89 (330)	0.612 (0.048)	< 0.001
H-1	46 (141)	0.726 (0.055)	< 0.001	43 (216)	0.490 (0.065)	< 0.001	89 (357)	0.621 (0.044)	< 0.001
H-2	46 (139)	0.746 (0.054)	< 0.001	43 (216)	0.537 (0.065)	< 0.001	89 (355)	0.637 (0.046)	< 0.001
H-3	46 (138)	0.717 (0.062)	< 0.001	44 (214)	0.620 (0.065)	< 0.001	89 (352)	0.663 (0.047)	< 0.001
H-4	43 (119)	0.680 (0.072)	< 0.001	42 (183)	0.534 (0.077)	< 0.001	85 (302)	0.583 (0.057)	< 0.001
G-1	44 (114)	0.655 (0.075)	< 0.001	43 (191)	0.653 (0.066)	< 0.001	87 (305)	0.649 (0.051)	< 0.001
G-2	46 (131)	0.608 (0.075)	< 0.001	43 (201)	0.566 (0.071)	< 0.001	89 (332)	0.595 (0.051)	< 0.001
G-3	42 (102)	0.718 (0.067)	< 0.001	42 (163)	0.526 (0.085)	< 0.001	84 (265)	0.563 (0.061)	< 0.001
G-4	11 (20)	0.627 (0.200)	0.0012				20 (37)	0.443 (0.193)	0.014
A-1	13 (20)	0.000 (0.237)	1.000	19 (36)	0.118 (0.190)	0.299	32 (56)	0.038 (0.136)	1.000
Specific Gravity	46 (137)	0.431 (0.091)	< 0.001	43 (216)	0.672 (0.062)	< 0.001	89 (353)	0.535 (0.057)	< 0.001
Mass (g)	39 (83)	0.750 (0.065)	< 0.001	43 (201)	0.445 (0.070)	< 0.001	82 (284)	0.581 (0.050)	< 0.001
Gross Score [d]	39 (87)	0.689 (0.076)	< 0.001	43 (170)	0.593 (0.072)	< 0.001	82 (257)	0.646 (0.051)	< 0.001
Typical Points	46 (141)	0.472 (0.089)	< 0.001	42 (216)	0.329 (0.080)	< 0.001	89 (357)	0.423 (0.059)	< 0.001
Total Points	46 (141)	0.356 (0.094)	< 0.001	43 (216)	0.342 (0.078)	< 0.001	89 (357)	0.364 (0.059)	< 0.001

[a] N = Number of individuals included for each antler characteristic; SA = number of shed antlers included for each antler characteristic

[b] Repeatability estimates are enhanced agreement repeatabilties as described by Stoffel et al. (2017) using the Program R package "rptR"

[c] P-values indicate statistical significance from a null hypothesis of R = 0.

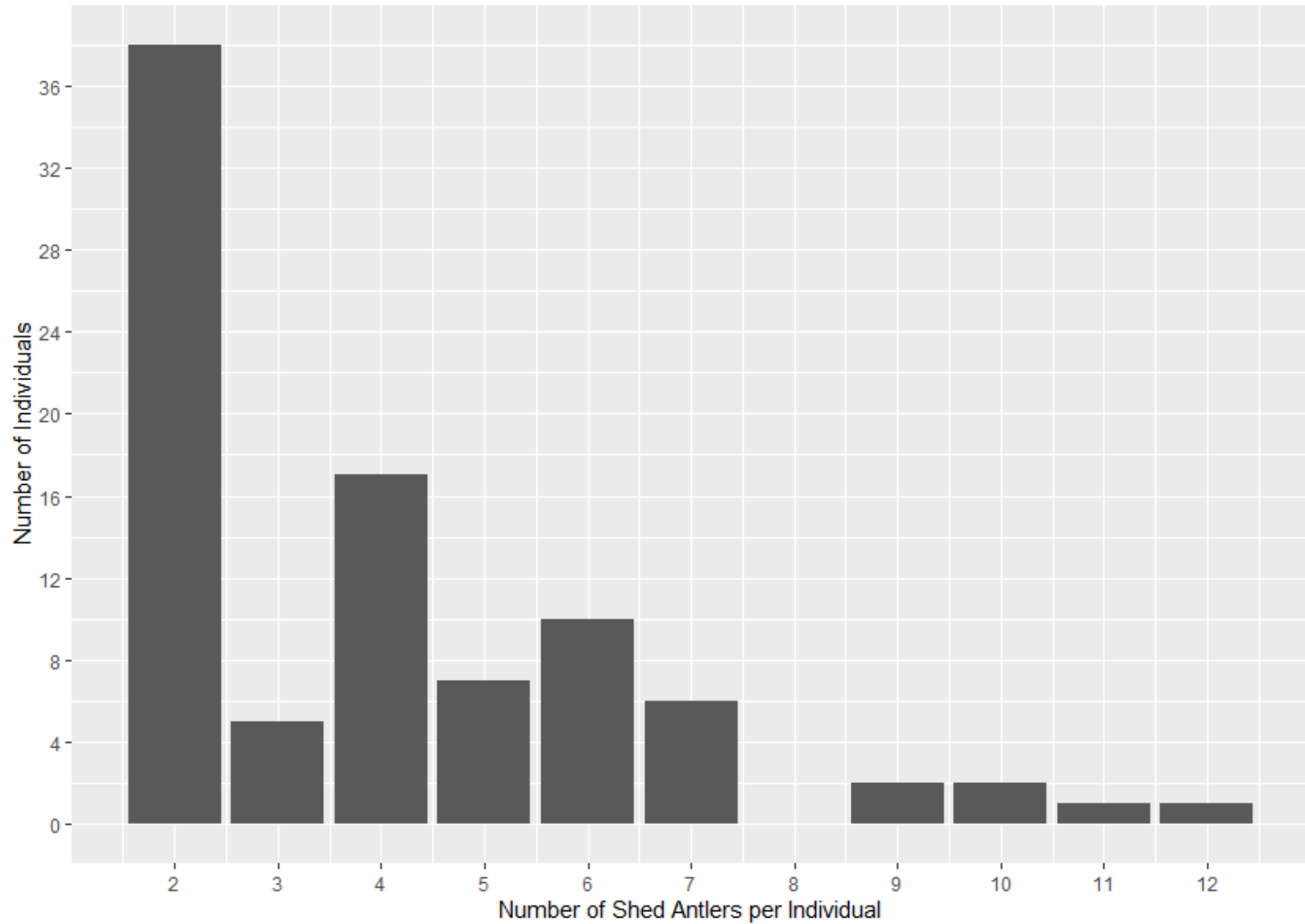[d] Gross scores are based on the Boone and Crockett Club's scoring system described by Nesbitt & Wright (2016)

Figure 2.1 - The frequency of shed antlers per individual (right and left antler sides) used in the repeatability analysis. Shed antlers were located between 2009-2018 at the Three Notch Wildlife Research Foundation (Three Notch) and the Auburn University Captive Deer Facility (ACF).