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Relative Fluctuating Asymmetry and Predictive Metrics of Cast Antler Pairs in White-Tailed Deer (*Odocoileus virginianus*)

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Abstract: Antlers are genetically coded to have bilateral symmetry. However, environmental stressors cause asymmetries between antlers. Previous studies have investigated fluctuating asymmetries on harvested white-tailed deer (*Odocoileus virginianus* Zimmermann, 1780). Cast antlers provide underutilized metrics that are not available prior to shedding. The objectives of this study were to quantify relative fluctuating asymmetry (RFA) between age groups and identify the best age-specific pre- and post-cast antler metrics to confirm an antler pair. We hypothesized lower RFA values for post-cast measurements than pre-cast measurements due to a lessened chance for damage when atop the head. Additionally, younger individuals were hypothesized to have higher RFA values due to greater susceptibility to environmental stressors. Cast antler pairs from 196 white-tailed deer were collected in Nebraska. We measured 14 available antler metrics per cast antler side classified by age group. The most symmetric measurements between antler sides included pedicle seal area, main beam length, and circumference. Antlers of older deer were consistently more symmetric than younger deer. When combining the top metrics and testing against random antler pairs, we found an 81.9–92.3% match rate for 1.5 and ≥2.5-year-olds, respectively. Our findings provided a quantifiable method to assign antler pair classifications more confidently while documenting decreased symmetry in younger individuals.

Keywords: cast antler pair; relative fluctuating asymmetry; *Odocoileus virginianus*; white-tailed deer

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1. Introduction

Antlers are perennial, fast-growing, and costly to produce appendages, which represent the individual's quality and condition driven by genetics, age, and nutrition [1,2]. Antler development in most cervids, including white-tailed deer (*Odocoileus virginianus* Zimmermann, 1780), are genetically coded to grow the same on both the right and left sides, with perfect bilateral symmetry, assuming homogenous environments [3–5]. Solberg and Saether observed that the largest, typically older aged bull moose (*Alces alces*) had the greatest symmetry, thus expressing good health and nutrition [6].

Antler asymmetry in cervids occurs in individuals as they cope with environmental stressors that occur prior to and during antler development. These environmental stressors may include climate, pollutants, pathogens, competition, predation, or anything that redirects energy away from growth [7,8]. Antler abnormalities can be caused by several contributing factors that influence antler development, resulting in asymmetry between antler sides during and after complete antler growth (e.g., age, genetics, nutrition, disease, parasites, insects, stress, injury during velvet, or breakage; [7,9]). Hicks and Rachlow found that deformed antlers in elk (*Cervus canadensis*) were not based on genetic factors but were a result of other factors that influenced differences, such as pedicle injury, nutrition, or environmental conditions [10]. Physical injuries such as damage to the skull or pedicles or damage to antlers while in velvet may increase asymmetry in antlers. Injury to a limb can also cause major and minor antler asymmetries, known as contralateral asymmetry, by disrupting the transfer of nutrients towards the injured limb opposite of antler growth [11,12]. Marburger et al. found that all harvested white-tailed deer with leg injuries produced contralateral antler asymmetries [12].

Fluctuating asymmetry is an index of developmental instability, which is an individual's inability to express phenotypic traits due to environmental conditions and can be measured as small deviations from perfect bilateral symmetry [13,14]. Investigations into morphological differences in antlers as they pertain to fluctuating asymmetry have been conducted on many cervid species. Fluctuating asymmetry has been described in moose and fallow deer (*Dama dama*) [6,15,16]. Eggeman et al. observed that fluctuating asymmetry was not a reliable index of environmental variation in elk [17]. Relationships have been investigated between fluctuating asymmetry and genetic diversity in roe deer (*Capreolus capreolus*), sexual selection in red deer (*Cervus elaphus*) and indicators of individual fitness in white-tailed deer [18–20]. These investigations provide insights into antler asymmetries and abnormalities that occur in all individuals, resulting in no antler pair sides being perfectly symmetrical.

It has been suggested that more genetically fit (typically older or more prime) males are less susceptible to environmental stressors and thus have more symmetric antlers [6,16,21]. Baccus and Welch attributed asymmetry in sika deer (*Cervus nippon*) to genetic and developmental processes when investigating main beam length (MBL), tine length (TL), and total points (TP) [22]. Mateos et al. found that older aged red deer males in their prime showed the lowest fluctuating asymmetry, while younger and the oldest age groups had greater fluctuating asymmetries for MBL, TL, and TP [23]. Ditchkoff and DeFreese found no evidence between decreased fluctuating asymmetry and trait size using three-dimensional modeling for white-tailed deer antlers classified by age [20].

The collection of naturally cast (shed) antlers is a popular, less intrusive, yet underutilized means to obtain white-tailed deer individual health, phenotypic, and demographic population information [24–26]. However, because antlers are no longer secured to an individual deer, and the distance between sides can be highly variable, methods are needed to help identify antler pairs that belong to an individual [27]. Protocols have been developed for DNA extraction of soft tissue from cast antlers of South Andean Deer (*Hippocamelus bisulcus*) and white-tailed deer to determine genetic individuality [25,28]. However, these protocols require specialized training and expensive equipment. Major deviations from bilateral symmetry can make it difficult for cast antlers from a specific individual to be paired. Therefore, a more robust, practical method to confidently identify a cast antler pair from the same individual is needed to avoid pseudoreplication within a dataset.

Traditional measurement techniques on harvested deer antlers (recognized by wildlife biologists, property managers, and hunters) are typically taken in accordance with Boone and Crocket Club protocols, which place an emphasis on symmetrical antlers [2,29,30]. A combination of these measurements develops a gross antler score or total antler score (TAS), which has been found to be similar between antler sides in mule deer (*Odocoileus hemionus*), red deer, and white-tailed deer [31–33].

Non-traditional antler characteristics have been investigated to quantify asymmetry. examined non-linear antler characteristics using three-dimensional computer modeling to quantify spatial asymmetry of antler size and shape [20]. Iberian red deer antler branching comparisons have been conducted using 3D CAD modeling to evaluate bilateral symmetry [34]. Additionally, pedicle seal depth (PSD) and pedicle seal area/shape (PSA) are post-cast (only available after antlers are naturally cast) antler metrics that have been found to be consistent between sides and unique to the individual (modifying size, shape, and depth based on the age and health of the individual) [26]. Antler mass (AM) or antler weight has been defined as the best antler metric to describe antler development; however, the lack of trophy deer has prevented this data from being readily obtained on older harvested individuals [31]. Chapman recorded no significant differences in mass between right and left antlers [35]. Therefore, AM and TAS should equally represent the energy invested into each antler side of the individual that produced them. Because standard antler metrics do not account for minor differences and complexities per side (small burrs, beading, pearlation, stickers, or tines $\leq$25.4 mm), AM may represent the best metric to define the energy invested into each side.

To our knowledge, no studies have investigated cast antler metrics to confirm antler pairs in white-tailed deer. Our objectives were to evaluate age-specific, pre-, and post-cast (shed) antler measurements to (1) identify the most symmetrical metrics and (2) quantify how well metrics distinguish antler pairs from other antlers. We hypothesized that (1) post-cast (shed) measurements would have a lower relative fluctuating asymmetry (RFA) value than pre-cast measurements due to a reduced chance of damage when atop the crania (i.e., fewer growth irregularities and shortened timeframe exposed to the environment for mechanical damage to occur) and (2) older deer would have more symmetric antlers than younger deer.

2. Materials and Methods

Naturally cast antler pairs were collected while searching the most probable white-tailed deer habitat in the central Nebraska Platte River valley as part of a long-term (2010–2024) monitoring project [27,36]. Authors investigated and confirmed cast antler pairs based on measurable antler metric similarities between sides (i.e., MBL, circumference, diameter, PSD, pedicle seal shape), and observable antler characteristics (i.e., including but not limited to antler burring, beading, and pearlation patterns), as well as antler coloration, tine basal circumference, and branching angles (Sutton, unpublished data) [24,27,33,37,38]. Pedicle seal shape and depth have the same unique identifiable characteristics as an individual's fingerprint, with the pedicle seal shape aligning on the same plane (orientation) between antler pairs and in subsequent years. We augmented the data set with antler pairs collected from the study area by cast antler-collecting hobbyists if collected during purposeful searches (i.e., seeking cast antlers), and antler pairs met the above criteria. During our 15-year cast collecting effort and antler investigation, authors were only able to match up just over 13% (n = 196) of cast antlers [27], leaving >1000 cast antlers non-matched. While we have a high degree of confidence in the antler pairs that we included in the analysis based on the aforementioned metrics, we acknowledge that an error in misclassifying a pair of antlers could impact the analysis and conclusions.

We classified the age group for all cast antlers using the MBL antler metric ($\leq$364.0 mm cut-off value defined for this region to differentiate antlers of 1.5-year-old deer from $\geq$2.5-year-old deer [38]). This defined main beam cut-off was developed from deer aged through tooth wear and replacement methods and remained a consistent predictor for age groupings over an eight-year period within the Platte River Valley. If one side of a cast antler pair was above and one below the defined MBL cut-off, we used circumference ($\leq$84 mm) as a secondary antler metric cut-off to differentiate between the 1.5-year-old and $\geq$2.5-year-old age groups (n = 10) [38].

We measured up to 14 available antler metrics for each cast antler per antler pair. Measurements were defined as either pre-cast (n = 11) or post-cast (n = 3; Table 1). Pre-cast antler metrics were defined as measurements that were available to be collected prior to natural antler casting (but could be collected while still attached to the skull plate) following the Boone and Crockett Club scoring system protocols [30]. Pre-cast antler metrics for both 1.5-year-old and $\geq$2.5-year-old cast antlers (when available) included TP and TL (G1-G4; mm), MBL (mm), up to four main beam circumferences (MBC (H1-H4; mm)), and TAS (Table 1). In the case of complete main beam breakage or extensive post-cast vertebrate damage (i.e., one or more antler tips chewed by rodents, deer, or canids; [39,40]) MBL and TAS comparisons were excluded from statistical analysis; however, all non-damaged metrics available for comparison were taken and analyzed [2,41]. Post-cast antler metrics were defined as measurements that could only be collected after antlers were naturally cast and included AM (g), PSD (mm), and PSA (mm). Antler mass values were only compared in the analysis if antler pairs were collected during the same season (fresh vs. fresh or old vs. old) and not between subsequent seasons or in the case of complete main beam breakage or extensive vertebrate damage. Cast antlers were placed at room temperature (22–23 °C) for ≥14 days post-field collection and AM measurements were taken to ensure a standard dry and consistent hygroscopic mass [33,42]. Pedicle seal depth was obtained using digital calipers as described by [33]. Bartoš and Bahbouh investigated seal circumference in red deer; however, the methods were not described [19]. Therefore, we determined the PSA using digital calipers and the following equation: pedicle length/2*pedicle width/2*π (mm).

Table 1. White-tailed deer cast antler pair metrics, combined across age groups that, indicate availability relative to casting (Pre/Post-Cast), metric description, and metric abbreviation. Average (Mean) relative fluctuating asymmetry (Mean RFA), standard error (SE), and sample size (N). Metrics are ordered from most symmetrical to least symmetrical based on average (Mean) RFA.

Pre/Post-Cast	Metric	Abbreviation	Mean RFA	SE	N
Pre-cast	Main Beam Circumference 1	H1	0.034	0.002	193
Pre-cast	Main Beam Length	MBL	0.036	0.002	183
Pre-cast	Main Beam Circumference 2	H2	0.040	0.003	192
Pre-cast	Main Beam Circumference 3	H3	0.047	0.003	177
Post-cast	Pedicle Seal Area	PSA	0.048	0.003	185
Post-cast	Antler Mass	AM	0.065	0.004	169
Pre-cast	Total Antler Score	TAS	0.066	0.005	178
Pre-cast	Main Beam Circumference 4	H4	0.096	0.006	155
Pre-cast	Total Points	TP	0.102	0.010	190
Post-cast	Pedicle Seal Depth	PSD	0.114	0.008	192
Pre-cast	Tine Length 2	G2	0.164	0.014	167
Pre-cast	Tine Length 1	G1	0.181	0.012	164
Pre-cast	Tine Length 3	G3	0.190	0.016	142
Pre-cast	Tine Length 4	G4	0.299	0.027	39

To evaluate the symmetry of antler pairs, we determined relative fluctuating asymmetries to rank the best antler metrics for all cast antler pairs and for those differentiated by age group. Relative fluctuating asymmetry (RFA) was calculated by taking the difference between each characteristic divided by the maximum value: (maximum-minimum)/maximum [2,15]. The lower the calculated RFA value, the more symmetric the antler metric characteristic or the less asymmetry between sides. We used a two-sample t-test to compare 1.5-year-olds and ≥2.5-year-olds' RFA values for both pre- and post-cast antler metrics. Analyses were conducted using R statistical software through RStudio [43,44]. We then identified the five most symmetrical metrics as those with the lowest mean RFA values and variability (Table 1) to understand if the 5 most symmetrical measurements could distinguish antler pairs from non-pairs.

To evaluate how well the best five metrics distinguished antler pairs from non-pairs, we compared RFA values for antler pairs to non-pairs within each age group. Comparing antler pairs to non-pairs allowed us to understand how well antler metrics can determine if antlers were a pair or not. To create non-pairs, we randomly chose ten non-matching, right-side antlers from our dataset to compare with each left-side antler for the 1.5-year-old and ≥2.5-year-old age classes. Random antlers were only drawn from within the age group, so, for example, 1.5-year-old left-side antlers were compared to ten random, non-matching 1.5-year-old right-side antlers. We then calculated the empirical cumulative distribution function (ECDF) for antler pairs and non-pairs for the five best measurements in each age group. For each metric, an ECDF allowed us to generate the distribution of RFA values for antler pairs and random antler comparisons to understand how much overlap occurred between their distributions. Using the ECDF, we then identified the value of the RFA that captured 95% of antler pairs for each of the five most symmetrical measurements and compared the percentage of antler pairs (i.e., 95%).

Ninety-five percent was chosen to exclude the upper 5% of antler pairs that may contain extreme measurement differences between the left and right-side antlers. This allowed us to calculate the percentage of antler pairs that were observed at the identified RFA values when accounting for non-pair RFA. We accomplished this by dividing the percentage of antler pairs (i.e., 95%) by the sum of the percentage of antler pairs and non-pairs. We also used the same procedure to combine the five best measurements to understand how this combination of measurements improved the percentage of antler pairs represented at the combined RFA value of those five metrics.

3. Results

Over the course of the 15-year study, 196 cast antler pairs were collected or obtained and measured. Authors accounted for 94 cast antler pairs, while antler-collecting hobbyists augmented the dataset with 102 cast antler pairs. Fresh antler pairs accounted for 73.0% (*n* = 143), old antler pairs in the environment for ≥1 year equaled 22.4% (*n* = 44), and 4.6% (*n* = 9) were collected as a single fresh cast antler and the other antler side collected ≥1 year later within the environment. Of the 196 cast antler pairs in the sample set, we classified 25% (*n* = 49) as cast from 1.5-year-olds and 75% (*n* = 147) as cast from deer ≥2.5 years old.

We found that a subset of fresh and old cast antlers decreased in mass on average by 3.83 ± 0.02% (*n* = 45) and ranged from 2.92 ± 0.02% (*n* = 24) to 4.88 ± 0.03% (*n* = 21), respectively, after being stored at room temperature for ≥14 days. We found that fresh cast antlers collected were 6.24 ± 0.03% (*n* = 8) heavier than the antler side that had remained in the environment for ≥1 year after constant masses were maintained; therefore, fresh/old antler pair mass measurement comparisons were not included within the analysis.

We determined that the most symmetrical antler metrics to define an antler pair based on RFA for both age groups included the MBL, the first three MBC (H1–H3), followed by PSA (Table 1, Figure 1). Total antler score and AM had similar average RFA values, and the least predictive metrics with the greatest variability in RFA to define an antler pair included H4, TP, PSD, and TL (G1–G4; Table 1, Figure 1). Antlers of ≥2.5-year-olds were, on average, more symmetrical than 1.5-year-olds for 12 of the 14 metrics investigated (Figure 1).

Our comparison of antler pairs to non-antler pairs yielded 1640 non-antler pairings to complement 164 antler pairs containing complete records of MBL, H1, H2, H3, and PSA. The first main beam circumference (H1) was the best pre-cast measurement to distinguish antler pairs of 1.5-year-olds, and MBL and H1 were the best pre-cast measurements to distinguish antler pairs of ≥2.5-year-olds (Table 2). When the RFA of H1 was ≤0.061 for 2.5-year-olds, 71% of antler comparisons were pairs, and when the RFA of MBL was ≤0.087 for 2.5-year-olds, 71% of antler comparisons were pairs (Table 2). The pedicle seal area was the best post-cast measurement, as well as the best single metric to distinguish antler pairs for both age groups. When the RFA of PSA was ≤0.086 for 1.5-year-olds, 76% of antler comparisons were pairs (Table 2). When the RFA of PSA was ≤0.122 for ≥2.5-year-olds, 77% of antler comparisons were pairs (Table 2). When we combined the five most symmetrical metrics and the combined RFA was ≤0.477 for 1.5-year-olds, 82% of antler comparisons were pairs. When we combined the five most symmetrical metrics and the combined RFA was ≤0.317 for ≥2.5-year-olds, 92% of antler comparisons were pairs.

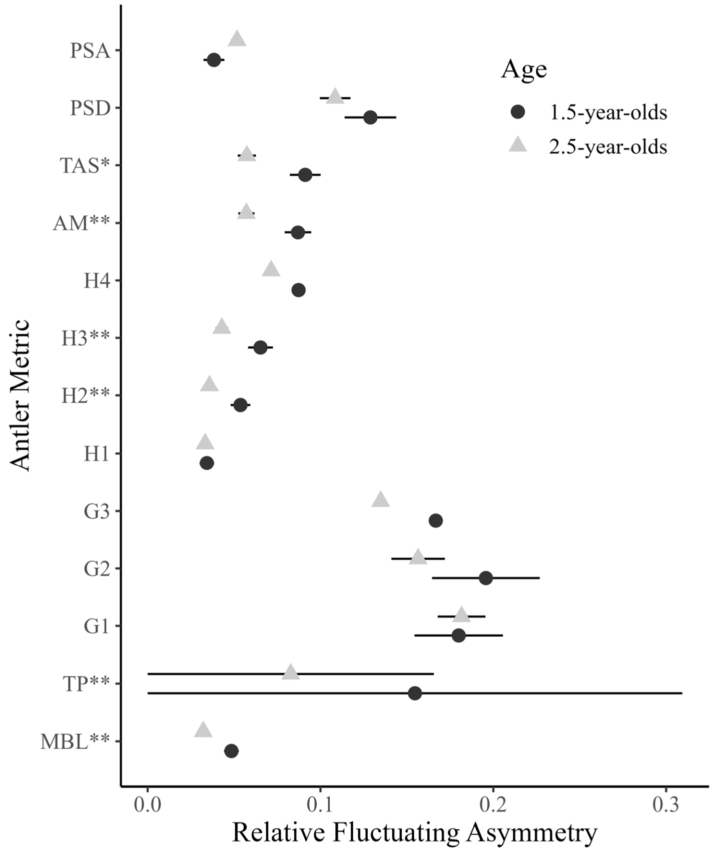

Figure 1. Average relative fluctuating asymmetries, with 95% confidence intervals, of antler metrics for antler pairs of 1.5-year-olds and ≥2.5-year-olds for white-tailed deer. All averages indicated mean values, besides medians for H4 and G3, due to insufficient sample size in at least one age group (<30 antler pairs). G4 was not plotted due to the low sample size for both age groups. Asterisk(s) represent the *p*-value for each t-test used to compare between age groups when each group had ≥30 antler pairs and a Wilcoxon rank sum test when either age group had <30 antler pairs. (* <0.05, ** <0.001). Post-cast antler pair metrics are listed first, followed by pre-cast antler pair metrics. Antler metric description can be found in Table 1.

Table 2. The percentage of antler match pairs compared to the random, non-pairs, at the 95th percentile for each of the 5 most symmetrical antler metrics (as identified by relative fluctuating asymmetry; 95% RFA) and the combination of the 5 most symmetrical antler metrics for each age class. The percentage of antler pairs (Percent Correct) was calculated by dividing 95% (Antler Match %) by the sum of (Antler Match %) and (Non-Match %). Antler metric description can be found in Table 1.

Age Class	Antler Metric	95% RFA	Antler Match %	Non-Match %	Percent Correct
1.5-year-olds	MBL	0.129	95	54	64
	H1	0.103	95	50	66
	H2	0.181	95	75	56
	H3	0.174	95	47	70
	PSA	0.086	95	30	76
	Combined	0.477	95	21	82
≥2.5-year-olds	MBL	0.087	95	39	71
	H1	0.061	95	38	71
	H2	0.097	95	45	68
	H3	0.124	95	48	66
	PSA	0.122	95	29	77
	Combined	0.317	95	8	92

4. Discussion

Apart from caribou or reindeer (*Rangifer tarandus*), normal antler configuration in ungulates exhibit bilateral symmetry, as both sides share the same genes and under homogenous conditions, external effects on the development of both sides should be the same [3,4,45,46]. Antler shape is largely due to genetic factors, whereas size is related directly to nutrition and age. Evaluating RFA is a valuable tool to understand the developmental impacts of stress in ecological communities [13]. We found that naturally cast white-tailed deer antler metrics of individuals $\geq$2.5 years old were reliably more symmetric than 1.5-year-olds, which is consistent with previous investigations. Within the literature, it has been reported for harvested cervids that antler metrics of older individuals in good physical condition have larger antlers and typically lower RFA values than younger smaller antlered individuals within the same population [6,17,47,48]. Jones et al. reported that white-tailed deer males $\geq$2.5 years old allocate more energetic resources to antler production than yearlings, which is consistent with our findings, which had lower RFA values for $\geq$2.5-year-olds [49]. These findings suggest that older individuals may be more suited to cope with environmental stressors during antler development than younger individuals [6,50].

Contrary to our hypothesis, pre-cast antler metrics primarily had the lowest RFA compared to post-cast antler metrics. Antlers grow from the base to the tip, with the tip being the newest growth [35]. Pre-cast measurements, despite being highly ranked, would have had lower RFA values if taken immediately following antler velvet shedding and hardening prior to extensive rubbing and antler breakage [51]. Antler bone growth occurs rapidly, and previous studies suggest that larger-bodied older deer grow antlers faster; therefore, the older antler growth has less time for errors to occur between sides [52,53]. We observed that the most consistent measurements between antler sides were related to the oldest antler growth for both pre- and post-cast antler metrics and consisted of the first three MBC, MBL, and PSA. This is likely due to the antler base and main beam being the first growth initiated, which is the oldest, resulting in more resistance to damage [39]. Conversely, we observed higher RFA metrics in TL and TP, which coincides with the tip of the antler while in velvet, being the newest growth and described as the most important tissue (influencing antler size and shape) with damage occurring during this critical growing period producing antler irregularities [54].

The lowest identified RFA values for pre-cast metrics included H1 and MBL, while the best post-cast metric was PSA. Bartoš and Bahbouh made similar observations in red deer and reported MBL being the lowest RFA (RFA: 0.03), which is in line with our results that ranged between 0.03 and 0.05 RFA for younger and older deer, respectively [19]. Main beam length and circumference contain the strongest, most compact bone growth; therefore, metrics are less susceptible to environmental impacts such as insect and parasite damage and late-season extreme environmental conditions, which may impact antler finishing prior to velvet shedding [26,55]. The basal circumference (H1) remained consistently the best pre-cast identifier of an antler pair despite the potential for inconsistent measurements due to irregular and coarse antler pearlation or burring. This suggests that both the right and left antlers wear evenly throughout the velvet shedding process, antler rubbing, signpost marking, and sparring or fighting during pre- and post-rut (breeding season). Evidence of shifting symmetry between new and old antler growth was revealed when investigating the RFA of MBC (H1-H4) for both age groups. With the decrease in circumference from base to tip, RFA values consistently increased as measurements moved up the main beam (H1–H4) from oldest to newest growth and thus became less predictive metrics. Similar to antler circumference, PSA increases with age [35]. Healthy pedicles are essential to normal antler growth, with trauma and injury typically resulting in abnormal antler growth in subsequent years [10]. The antler pedicle seal is typically the most telling qualitative marker when attempting to define an antler pair, confirmed by being the best post-cast antler metric based on RFA values for both age groups. The pedicle seal's shape is rarely a perfect circle, and the oblong or oval shape located on the cast antler base is oriented in the same direction (or plane) and typically a mirror image on both antler sides. However, these qualitative characteristics are difficult to quantify. We only identified one study that investigated the shape of the pedicle seal. Bartoš and Bahbouh reported that red deer seal circumference (RFA: 0.05) had the lowest RFA, which was equivalent to our PSA (RFA: 0.05) findings for all age groups combined [19]. Despite being an acceptable metric to investigate, the lack of research in this area provides an opportunity for more discovery.

Similar to PSA, PSD is a protected, visibly telling post-cast antler characteristic to define an antler pair. In general, measurements close to the head (basal circumference) were more symmetrical; however, the PSD fell within the lower end of the metrics evaluated to define an antler pair. The higher RFA observed for this metric could be due to the process in which osteoclasts weaken the connection of the antler from the skull as it breaks free (likely influenced by antler mass and mechanical force). While we did not encounter antler pair pedicle seals classified as irregular or "dirty sheds", we found that these measurements were sensitive to variation between sides [46,56]. While PSD has been defined as a consistently sensitive metric to evaluate environmental stress in white-tailed deer, we found that based on higher-than-expected RFA values, perhaps the measuring technique described, is difficult to consistently replicate, resulting in variation between measurements [26,33]. Future studies should investigate a more consistent method to obtain detailed PSD metrics, such as scanning to create 3-dimensional computer images to take more accurate digital measurements [20]. We found that this metric was still visually a good indicator but not as symmetrical as several other metrics. Antler mass and TAS have been recommended as continuous variables to accurately represent antler development, growth, and size and should equally represent the antler growth invested in both sides by the individual [31,32,57,58]. We found that AM (post-cast) and TAS (pre-cast) were indeed equivalent measurements reflected by RFA values for both age groups. However, both were, at best, an average indicator of an antler pair. Our findings were similar to observations of AM between sides by McCollough, and high RFA values (0.32) reported by Bartoš and Bahbouh [19,59]. Antler TL and TP consistently had the highest RFA values and, therefore, were the worst metrics to define an antler pair, compounded by antler point breakage prior to antler casting. Differences in white-tailed deer TL and TP could be due to these metrics being the latest antler growth representing greater physical energy exerted in securing sufficient critical minerals than growth first initiated (MBL and MBC; [60]). Total point RFA values were lower (RFA: 0.08–0.16 for $\geq$2.5-year-olds and 1.5-year-olds, respectively) than identified by Bartoš and Bahbouh in red deer (RFA: 0.27) [19]. In future investigations, this could represent a stronger metric if only non-broken matching tine lengths and total typical points formed (despite length) were examined and counted.

We found that, for the most part, in white-tailed deer, the oldest or the first initiated antler growth metrics (MBL, H2, H3) were more symmetric for $\geq$2.5-year-olds than 1.5-year-olds, with the exception of H1. The H1 antler MBC metric is the genesis of new antler growth from the pedicle atop the skull plate, and therefore it should be the strongest, most resistant to damage and injury, resulting in the most symmetric measurement as we observed in both age groups. This may explain the lack of discernable differences between age groups for this metric. Ditchkoff et al. however, found that smaller antlered (RFA: 0.08) deer had significantly higher RFA values for basal circumference than both medium (RFA: 0.05) and large (RFA: 0.06) antlered deer [47]. As antlers increase in size with age, the dense and larger diameter antlers continue this symmetric growth along the main beam and subsequent circumference measurements (H1-H4 [35]). Like our findings, Demarais and Strickland observed that white-tailed deer MBL between sides had the greatest percent asymmetry in yearlings (>14%) compared to 2- to 7-year-olds (5–6%) while Ditchkoff et al. also observed that RFA for MBL was significantly greater for smaller (RFA: 0.15) antlered deer than medium (RFA: 0.09) and large (RFA: 0.05) antlered deer [47,61]. These observations remain consistent in other cervids, including roe deer, fallow deer, and red deer [23,62]. For these consistent metrics Gómez et al. suggested that these differences between age groups may be attributed to heavier-bodied older individuals growing antlers faster and thus allowing less time for errors to occur between sides [52]. While TAS and AM were equivalent metrics to each other, we observed significant differences between age groups (1.5-year-olds; RFA: 0.09, 0.09 respectively and ≥2.5-year-olds; RFA: 0.06, 0.06 respectively). Our findings for TAS were similar to Ditchkoff et al., as smaller, younger antlered deer (RFA: 0.18) had significantly higher values than larger, older antlered deer (RFA: 0.07) [47].

Antler TL showed no difference, lacked consistency between age groups, and was one of the least predictive RFA metrics to define an antler pair. Our lack of consistency between age groups and high standard errors for this metric was likely due to antler breakage. Ozoga and Verme found that dominant white-tailed deer males in older age classes typically had higher antler breakage, while Miller et al. and Karns and Ditchkoff reported that younger individuals with more TP and smaller diameters were more susceptible to antler breakage [46,63,64]. Despite no differences in TL between age groups, due to high variability in TP, we did find that white-tailed deer ≥2.5-year-olds had lower RFA values (RFA: 0.08) for TP than 1.5-year-olds (0.16) which was similarly observed by Matoes et al. in red deer but differed from Ditchkoff et al. who found no difference between TP in white-tailed deer between antler size and age groups (RFA: small 0.13; medium 0.11; large 0.14) [23,47]. We did not quantify antler tine breakage as we followed Boone and Crocket Club measuring protocols, which only measure and record tines ≥25.4 mm, however G2 being the lowest TL RFA value is consistent with findings by Karns and Ditchkoff in which G2 was the least susceptible to breakage [33,39]. Including broken tines likely influenced pre-breakage RFA values for TL and TP. Future studies should document cast antler tine breakage and evaluate RFA values for broken and non-broken matching tines between age groups to better understand the impact on symmetry for this metric. We found that PSA for 1.5-year-olds was one of the only metrics to have a slightly higher RFA for ≥2.5-year-olds. This is somewhat surprising, as one would assume that this is one of the least impacted metrics as it is protected atop the skull most of the year, and this metric should be a comparable metric to H1, which showed nearly identical RFA values for both age groups. While we found no significant differences between age groups for PSD, ≥2.5-year-olds had slightly lower RFA values than 1.5-year-olds. We assumed that older, healthier individuals would have higher testosterone levels and, therefore, deeper PSD, resulting in a more symmetric measurement [2,26,65]. This, however, was not the case. While both PSA and PSD are visually telling qualitative indicators of an antler pair, the higher PSD RFA values for both age groups suggest that this is a difficult metric to obtain consistently (i.e., prone to measurement error).

Combining our top five most symmetrical metrics provided a quantitative method to confidently determine antler pairs. Older deer had more symmetry among the five most symmetrical metrics, which led to a greater percentage of pairs represented within the 95th percentile of combined RFA values for ≥ 2.5-year-old antler pairs than 1.5-year-old antler pairs. Younger deer were less symmetrical, which is compounded across the top five most symmetrical metrics, leading to a lower representation of antler pairs within the 95th percentile of combined RFA values for 1.5-year-old antler pairs. Both the combined RFA values for ≥2.5-year-olds (92%) and 1.5-year-olds (82%) provide high levels of confidence in determining antler pairs, even though our study treated all opposite side antlers within an age class as potential pairs.

This study serves as a baseline and reinforces the utilization of naturally cast antlers in future investigations to compare data spatially and temporally between age groups, populations, regions, and environmental conditions. As long-term data is collected across different geographic areas and environmental conditions, the symmetry of age-specific antler metrics can be compared to our study to better understand the patterns of symmetry within white-tailed deer antler metrics. Comparing the measurements of cast antlers allowed us to compare and capture the impacts of realized natural wear on symmetry for a more realistic assurance at identifying cast antler pairs while documenting differences in the symmetry between age groups. Although we have a high degree of confidence in the antler pairs included in the analysis, we acknowledge that an error in misclassifying a pair of antlers could impact the conclusions drawn. The probability of error is reduced when other factors are considered, as were in this study, including non-traditional and descriptive antler pair characteristics along with distance apart [27,33]. Further research should consider using both the combined RFA scores and these other factors to evaluate whether they can determine antler pairs at a greater rate than we found in this study. Our results were based on naturally cast antlers remaining in the environment. Without further investigation, we do not know how selective harvest pressures for or against symmetry may have impacted results (e.g., potential bias against the harvest of deer with broken antlers). While beyond the scope of our study, future studies should investigate the correlation between asymmetry and environmental factors to explore the possibility of using antler symmetry as an index of environmental quality. Indeed, environmental conditions have been shown to impact white-tailed deer antler metrics (e.g., pedicle seal depth), but implications of asymmetry have not been considered [26]. Similarly, the possible connection between antler symmetry and both population and individual health and fitness should be further explored [18–20].

Our findings provide a practical, quantifiable, and innovative method to confidently assign an antler pair classification using pre- and post-cast antler measurements. We documented the oldest antler growth was the most symmetric, reaffirming asymmetry in younger individuals while justifying the use of naturally cast antlers as a less intrusive means to evaluate antler growth in free-ranging white-tailed deer. Maintaining these historical datasets provides insight into antler symmetry geographically over time as it pertains to the selective harvest of cervids and environmental impacts [24,29,33]. Future studies should investigate more non-traditional antler characteristics, including those that are difficult to quantify. These RFA metrics should include matching non-broken antler tines, point of each antler tine branching from the main beam, matching basal tine circumference, branching tine angles (Sutton, unpublished data), and more descriptive, yet not widely defined in the literature antler characteristics between antler sides like pearlation, burring pattern or wear, antler coloration, visibly calcified veins, and upper anterior cupping where the G1 branches) [37].

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