FLUCTUATING ASYMMETRY OF WHITE-TAILED DEER ANTLERS

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FLUCTUATING ASYMMETRY OF WHITE-TAILED DEER ANTLERS

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THESIS ABSTRACT

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Fluctuating asymmetry has been proposed as an indirect indicator of individual quality. Sexually selected traits, such as deer antlers, are expected to exhibit patterns of decreasing level of fluctuating asymmetry with increasing trait size and decreasing level of fluctuating asymmetry with increasing age. These hypotheses have previously been tested for antlers using linear measures to determine level of asymmetry. However, antlers are complex, 3-dimensional traits making it difficult to quantify all forms of visual asymmetry using linear measures. It is this visual asymmetry that is assessed by potential mates and rivals. Therefore, I created computer models of white-tailed deer (*Odocoileus virginianus*) antlers to measure visual asymmetry, which may have previously been unaccounted for with linear measures. Asymmetry measures of various antler traits were computed from the models by measuring distances from the trait to a vertical and horizontal plane created within the model. There was no association found between

degree of fluctuating asymmetry and trait size, nor was any association found between degree of fluctuating asymmetry and age using either the 3-dimensional measures of asymmetry or traditional, linear measures of asymmetry. These data suggest that fluctuating asymmetry of white-tailed deer antlers is not a reliable indicator of quality.

This method used to measure fluctuating asymmetry in antlers could be expanded for use in measuring asymmetry in many complex 3-dimensional traits. Important landmark points were marked on the features of interest, and then digital photographs were taken of each antler set. These landmark points were labeled and cross-referenced across all the photographs, using the program PhotoModeler, to create 3-dimensional "stick" figures. Distances were taken from the important features to a vertical and horizontal plane that was created using the coordinate points generated by the model. By modeling ten sets of antlers twice using the same photographs, the models were found to be highly repeatable.

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ABSTRACT

Fluctuating asymmetry, random departure from perfect symmetry in bilateral traits, has been proposed as an indirect indicator of individual quality. Sexually selected traits, such as deer antlers, are hypothesized to demonstrate decreasing level of fluctuating asymmetry with increasing trait size and decreasing level of fluctuating asymmetry with increasing age. These hypotheses have been previously tested for antlers using linear measurements to quantify fluctuating asymmetry. However, antlers are complex, 3-dimensional traits making it difficult to quantify all forms of visual asymmetry using traditional, linear measurements. It is this visual asymmetry that would be assessed by potential mates and rivals. Therefore, I created 3-dimensional computer models of white-tailed deer (*Odocoileus virginianus*) antlers to measure visual fluctuating asymmetry. Asymmetry measures of various antler traits were computed using the models by measuring distances from the trait to a vertical and horizontal plane created using coordinate points generated within the model. There was no association found between degree of fluctuating asymmetry and trait size, nor was any association found between degree of fluctuating asymmetry and age using either the 3-dimensional measures of asymmetry or traditional, linear measures of asymmetry. These data suggest that

fluctuating asymmetry of white-tailed deer antlers is not a reliable indicator of quality.

INTRODUCTION

Fluctuating asymmetry is random deviation from perfect symmetry in traits that are normally bilaterally symmetrical. Because these traits arise from the same genome, their optimal condition is assumed to be perfect symmetry (Polak and Trivers 1994). Therefore, a departure from symmetry indicates disruption of normal development, most likely due to genetic or environmental stresses (Parsons 1992). Homozygosity, inbreeding, and mutation are some of the genetic stresses that have been associated with increased fluctuating asymmetry (Møller 1998). Most recent studies have focused on the relationship between environmental stressors and fluctuating asymmetry, and numerous studies have found a positive relationship between parasitism and fluctuating asymmetry (reviewed in Møller 1996). Other environmental stresses that have been studied include nutritional stress, temperature extremes, high population density, and pollutants (reviewed in Møller 1998).

One reason for interest in asymmetry is the proposed association between fluctuating asymmetry and individual quality (Palmer 1996). Variation in the level of fluctuating asymmetry exhibited by different individuals in the same environment allows for an indirect measure of developmental stability (Møller 1998), which is defined as the ability of an individual to buffer detrimental effects of stress during development (Palmer 1996). This measure may in turn reflect an individual's quality or fitness (Møller 1998). While it is assumed that fluctuating asymmetry itself is not heritable, it is also assumed that the ability to overcome developmental stress is at least partially heritable (Palmer 1996).

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This proposed relationship between fluctuating asymmetry and quality has been studied for a variety of different traits. However, not every trait shows an increase in fluctuating asymmetry with increased stress; different traits appear to be under different levels of stabilizing selection. Many morphological traits, especially those used in functions related to survival, are highly canalized, and therefore, are less susceptible to developmental disturbance (Polak 1993). Other traits seem to be much more susceptible to stress. These include characters that are under directional selection, such as ornamental traits (Møller and Pomiankowski 1993).

Ornamental traits and secondary sexual characters have been shown to be important factors influencing mate choice and intrasexual competition in many species (Andersson 1982; Møller 1988; Mateos and Carranza 1997; Pärt and Qvarnström 1997). Also, several studies have documented that females prefer more symmetrical males (Sheridan and Pomiankowski 1997; Schlüter et al. 1998; López et al. 2002). Therefore, it is hypothesized that the symmetry of these ornamental traits may play an important role in mate choice, and hence, have important implications for sexual selection.

If ornamental traits are used in sexual selection, they are expected to provide reliable information about the condition of the bearer (Zahavi 1975; Berglund et al. 1996), and several studies have reported cases of ornamental characters signaling honest information about condition (Møller 1991; David et al. 2000; Velando et al. 2001; Malo et al. 2005). Because ornamental traits are costly to produce and maintain (Kodric-Brown and Brown 1984) only high quality males should be able to produce large, symmetrical ornaments. This leads to the hypothesis that fluctuating asymmetry and sexual selection are related as follows: low levels of fluctuating asymmetry in a male may

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indicate a male's heritable ability to cope with stress, so a female should choose to mate with a more symmetrical male in order to increase her offspring's viability and, in turn, her fitness. An alternative hypothesis, for the case of disease or parasite induced fluctuating asymmetry, is that a female should choose to mate with a more symmetrical male in order to gain the direct benefit of avoiding parasite or disease transmission (Polak 1993). These ideas lead to predicted patterns of fluctuating asymmetry in ornamental traits. It has been hypothesized that level of fluctuating asymmetry will decrease with increasing trait size, because only high quality males will be capable of producing large ornaments (Møller 1992). This is a contrast to the predicted pattern for non-ornamental traits. For these characters, a flat or U-shaped pattern is expected for the relationship between fluctuating asymmetry and trait size (Møller 1992).

Antlers of cervids seem to be well suited to studies of fluctuating asymmetry. Not only are these secondary sexual characters important in intrasexual competition (Clutton-Brock 1982; Goss 1983; Lincoln 1992), dominance (Lincoln 1972; Bowyer 1986), and possibly mate choice (Lincoln 1992), but also rapid development of antlers (Goss 1983) should make them particularly sensitive to stress (Watson and Thornhill 1994). Swaddle and Witter (1997) suggested that rapid growth may prohibit compensational growth feedback between sides of a bilateral trait, thereby making it even more difficult for an individual to produce symmetrical traits. In addition, the deciduous nature of antlers, in most species of cervids, may provide an annual record of the level of stress experienced during antler development. This highlights the potential value of using fluctuating asymmetry of antlers as a relatively easy way to monitor environmental quality.

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Previous studies of antler asymmetry have found positive relationships between fluctuating asymmetry and parasitism (Folstad et al. 1996; Lagesen and Folstad 1998), and several studies have reported support for Møller's (1992) hypothesized negative relationship between fluctuating asymmetry and trait size (Putman and Sullivan 2000; Bowyer et al. 2001; Ditchkoff et al. 2001a). Solberg and Sæther (1993) further hypothesized a decrease in fluctuating asymmetry with increasing age, because only higher quality males will survive to older ages.

While previous studies have examined fluctuating asymmetry of antlers, the most common way of measuring asymmetry was through simple measures of length, width, and circumferences of various parts of the antlers. Although these measures may provide information on level of asymmetry, they do not allow for the measurement of all forms of spatial, visual asymmetry. Antlers are complex 3-dimensional traits, which makes it difficult to quantify fluctuating asymmetry using traditional methods. For example, it is possible for two antler tines of equal length to appear very asymmetrical based on the way they are curved or oriented in space. Two corresponding tines of equal length could appear very different if, for example, one tine was oriented 90° from the ground plane and the other at 45° from ground plane. However, traditional linear measures would consider those two tines to be symmetrical because they have the same length. Visual asymmetry is the type of asymmetry that would most likely be assessed by potential mates or rivals. We used 3-dimensional computer models of white-tailed deer (*Odocoileus virginianus*) antlers to evaluate patterns of both 2- and 3-dimentional fluctuating asymmetry, thereby considering an additional aspect of asymmetry that may have been neglected in earlier studies. Specifically, we tested for the hypothesized

negative relationships between level of fluctuating asymmetry with antler size and individual age. In addition, we compared detected levels of asymmetry between traditional (2-dimensional) and our 3-dimensional measures of fluctuating asymmetry.

MATERIAL AND METHODS

Data were collected from hunter-harvested deer from Tallapoosa and Bullock counties in Alabama, USA during the 2002 and 2003 hunting seasons. In addition, to increase sample size, antler measurements were obtained from various sets of antlers collected in previous hunting seasons. These antlers were still attached to the skull plate. Antlers were measured following guidelines for the Boone and Crockett trophy scoring system (Nesbitt and Reneau 1988). Measurements taken included greatest inside spread of main beams, tine lengths, main beam lengths, and main beam circumferences at the antler bases and between antler tines (not to exceed 4 circumferences measured per antler). The official Boone and Crockett scoring system includes deductions based on antler asymmetry. However, these deductions were not used in this study. Total gross score was calculated for each antler set by adding together tine lengths, main beam lengths, inside spread, and circumference measures. An individual gross score was also calculated for each antler side by omitting the inside spread measure. When possible, we also measured chest girth, body length, body weight, skull length, and tail length on deer collected during the 2002-2003 hunting seasons. Measurements were taken using a flexible measuring tape and were recorded to the nearest mm. In addition, deer were aged using tooth wear and replacement patterns (Severinghouse 1949).

In order to create the 3-dimensional computer models, approximately 12 digital photographs were taken around the circumference of each antler set and from above. The

antlers were first marked with approximately 3 mm dots using paint and/or stickers to provide landmark points for use in modeling. These photographs were then entered into the program PhotoModeler (Eos Systems Inc, Vancouver, BC, Canada). Using between 9 and 12 pictures for each antler set, the landmark points and tips of tines and main beams were marked and cross-referenced between all photographs resulting in a 3-dimensional "stick" model of each antler set. The scale of the model was calibrated using a manual measure of distance between the tips of the right and left G2 tines (second tine erupting vertically from the main beam; Fig. 1). The PhotoModeler program assigned each scaled model point a 3-dimensional (x,y,z) coordinate point. These coordinate point values were labeled to correspond to important antler features (Append. 1) to allow for comparison between individuals. By using the base points of the antlers and a center point (marked between the deer's eyes), a vertical plane between the antlers and horizontal plane at the base of the antlers were created (Fig. 2). Distances were calculated from the horizontal and vertical planes to selected antler features. In addition, the angle between the main beam and the G2 tine was calculated. These calculations were done using Statistical Analysis System (Statistical Analysis Systems 1990).

Absolute asymmetry was calculated as the absolute difference between right and left side antler measurements. From the data generated by the 3-dimensional computer models, absolute asymmetry was calculated for many variables: distance from the horizontal plane to the G1, G2, and tips of the main beam, distance from the vertical plane to the G1, G2, and main beam tips, angle between the G2 tine and the main beam. In addition, absolute asymmetry was calculated for the manual measurements of basal circumference, score, main beam length, and lengths of G1 and G2 tines.

A subset of ten antler sets was modeled twice using the same photographs in order to assess the precision of the measurement technique that utilized the computer models. Differences in lengths of corresponding tines were divided by the average trait size to obtain a percent difference between the two models, thereby allowing us to evaluate repeatability. Accuracy of computer models was evaluated by comparing manually measured tine lengths with the computer modeled tine lengths. This was evaluated using t-tests.

Broken or worn antler points were not included in analyses of asymmetry. Because the data were not normally distributed, asymmetry measures were log transformed. To test for relationships between asymmetry measures a Pearson correlation test was used. Pearson correlations were also used to test for relationships between levels of asymmetry of the manual measurements and asymmetry measures generated with the computer model. In addition, relationships between asymmetry measures and measures of trait size (basal circumference, antler score, and main beam length) and age were compared using Pearson correlation. To test for differences in level of asymmetry between age classes a one-way analysis of variance (ANOVA) was conducted. Due to small sample sizes, deer aged 4.5 years and older were grouped in a single age class. In addition, within each age class antlers were divided into three size classes (low, medium, and high) of approximate equal sample size based on score, and an ANOVA was conducted to test for differences in level of fluctuating asymmetry based on antler size. We found no differences ($P > 0.05$) in asymmetry or morphometric variables across years, so data were pooled from the 2002 and 2003 hunting seasons to increase sample sizes and statistical power.

RESULTS

The percent differences between corresponding measures of repeated models ranged from <0.01 to 4.75%, and absolute differences ranged from <0.01 to 3.86 mm (Table 1). Mean percent differences were less than 1% for all but four variables measured and were less than 2% for all variables measured. All comparisons of tine lengths measured via the computer models versus the corresponding manually measured lengths were different (P > 0.001; Table 2). Mean measurements for computer model lengths were greater than manual lengths, and mean differences ranged from 8.28 to 32.40 mm.

Overall, there were no consistent patterns in correlations among asymmetry measures (Table 3), and correlation coefficients were generally weak, where $r < 0.33$. There were also no consistent correlations between asymmetry measures and variables used to estimate trait size, i.e. mean score, mean main beam length, and mean basal circumference. Age was not significantly correlated ($P \geq 0.083$) with any of the asymmetry measures.

There was no age affect ($P \geq 0.153$) on any measures of asymmetry (Table 4), and there were also no consistent directional trends in mean measures of asymmetry among ages (Table 5) or antler score classes (Table 6). Between the three score classes only two asymmetry variables (labsymbv and labsymsc) were different (Table 4). The log of the absolute asymmetry of the distance from the tip of the main beam to the vertical plane (labsymbv; $P = 0.024$) and the log of the absolute asymmetry of score (labsymsc; $P = 0.004$) were different among score classes.

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DISCUSSION

Antlers are a prominent secondary sexual character in male deer, and fluctuating asymmetry of this trait is hypothesized to provide a reliable signal of individual quality to potential mates (Zahavi 1975; Kodric-Brown and Brown 1984). Assessment of the symmetry of this complex trait by potential mates would be based on visual differences in the conformational shape of a set of antlers, which may or may not correspond to differences in linear measurements of antler traits. There are specific trends in levels of fluctuating asymmetry predicted for sexually selected traits (Møller and Pomiankowski 1993; Solberg and Sæther 1993). However, we found no support for these hypotheses using the 3-dimensional measures of fluctuating asymmetry. Specifically, there was no consistent relationship between antler asymmetry measures and trait size. Secondary sexual characters, like antlers, are costly to produce, and the relative cost to produce equal sized traits is greater for low quality individuals (Zahavi 1977; Grafen 1990). Thus, only high quality individuals are expected to produce large antlers, and since fluctuating asymmetry is an indirect measurement of individual quality (Møller 1998), these high quality individuals are expected to produce symmetrical traits. There was also no evidence to support the hypothesized decrease in level of fluctuating asymmetry with increasing age. Antlers tend to increase in size with increasing age, until a point when the cost of producing larger antlers outweighs the benefits of a larger trait, or until the individual reaches an age of senescence (Clutton-Brock 1982). Individuals that have reached a mature age are expected to be high quality individuals because low quality individuals cannot survive into old age (Solberg and Sæther 1993). Consequently, males of prime age should exhibit lower levels of fluctuating asymmetry than immature males.

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We found no evidence that 3-dimensional asymmetry of antlers honestly signals male quality.

The traditional linear measures of fluctuating asymmetry also failed to reveal relationships between level of fluctuating asymmetry and trait size, and no relationship between level of fluctuating asymmetry and age was detected using manual measurements. The expected patterns of decreasing asymmetry with increasing trait size and increasing age were not supported by data from this study using either measurement technique. While many previous studies have found positive relationships between fluctuating asymmetry and antler size (Putman and Sullivan 2000; Bowyer et al. 2001; Ditchkoff et al. 2001a), other studies have failed to find this hypothesized relationship. Kruuk et al. (2003) found no association between level of antler asymmetry of red deer (*Cervus elaphus*) and trait size or environmental stress. Bartoš and Bahbouh (2006) found that fluctuating asymmetry in red deer decreased with increasing trait size in some measured antler traits but results were not consistent across all traits measured, thereby violating one of the expected patterns of fluctuating asymmetry as an indicator of quality.

Manual measures of asymmetry were not consistently correlated with 3-dimensional measures of asymmetry. If the levels of asymmetry found with both methods were similar, it would have implied that manual measurements were adequate to quantify visual antler asymmetry. However, the lack of consistent trends in the data make if difficult to draw conclusions about the efficacy of our measurements at quantifying visual asymmetry. Our measures of visual asymmetry may possibly document different components of spatial asymmetry than the linear asymmetry measures. Additionally, it is possible that our measures did not adequately address 3-

dimensional asymmetry, or 3-dimensional asymmetry does not follow the same predicted patterns as traditional measures. Regardless of the possible reasons for the lack of associations between asymmetry measures, our data fail to support the hypothesis that fluctuating asymmetry can be used to reliably assess individual quality, as has been predicted for traditional measures of fluctuating asymmetry.

A possible alternative explanation for the lack of support for the hypothesized decrease in fluctuating asymmetry with increased trait size is the lack of natural selection pressures on deer in Alabama. This hypothesis (Solberg and Sæther 1993) was originally formulated with the assumption that animal species operate under natural selection pressures, and high quality individuals will exhibit greater rates of survival than poor quality individuals. In contrast, most white-tailed deer populations are driven by hunting pressure, where the major cause of mortality is hunter harvest. Alabama has deer bag limits that are more liberal than most regions, leading to high hunting pressure on wild deer populations. Considering this, white-tailed deer may be a poor model to test the assumptions of Solberg and Sæther (1993) because individuals that survive to older age classes are going to be a more random cross section of the population (e.g., those that were fortunate enough not to encounter a hunter) rather than those of greater genetic quality. For example, one study with white-tailed deer that did support this hypothesis (Ditchkoff et al. 2001a) was conducted on a unique population where natural selection pressures were greater than human-induced pressures (Ditchkoff et al. 2001b), and hunting pressure and hunting success were minimal (Ditchkoff et al. 1996).

Asymmetry measures of the different antler components were not consistently correlated with each other using either measurement method. This is contrary to

expected findings, as fluctuating asymmetry researchers predict that multiple components of a trait are integrated developmentally and would experience the same stressors during development causing them to exhibit similar patterns of symmetry (Leamy 1993; Whitlock 1996; Palmer and Strobeck 2003); features within a trait would be expected to have the same developmental stability properties and level of stabilizing selection. Variations present in precursor stages of a trait may be expected to perpetuate into later growth stages that arise from it.

The computer models were highly repeatable. Mean differences between the repeated model measurements were well below asymmetry values measured and generally less than 1 mm (ranging from 0.112 mm to 1.74 mm); these values are generally below 1% difference between replicates. Therefore, measurement error was not corrected for in this study. These are similar or lower than levels of measurement error that have been found acceptable in other studies of antler fluctuating asymmetry (Ditchkoff et al. 2001; Kruuk et al. 2003; Bartoš and Bahbouh 2006).

Differences between the manual and computer measured tine lengths can be explained by the disparity in measurement landmarks for the two techniques. For the manual Boone and Crockett-type measurements (Nesbitt and Reneau 1988), tines were measured from the tip of the tine to where the tine intersected the top edge of the main beam. However, to facilitate the construction of the 3-dimensional "stick" model, tine lengths were measured from the tip of the tine to where the tine intersected the middle of the main beam. Therefore, it was expected that computer-generated tine lengths would be greater than manual measurements by approximately half the width of the main beam. In addition, tine lengths calculated from computer models were measured as a straight-

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line distance from tip of the tine to the base of the tine while manual measurements followed the outside curve of tines. The purpose of comparing corresponding measurements from the two techniques was to determine if measurements were similar and differed by approximately half the width of the main beam. Measurements differed by approximately 10-20 mm, which is consistent with half the width of the main beam. Therefore, computer models were scaled and representative of actual size and proportion of antler sets.

Although our data did not support the hypothesis that 3-dimensional asymmetry of antlers could be used as a reliable signal of quality, further study of 3-dimensional measures of asymmetry is warranted as this type of visual asymmetry is likely to be assessed by potential mates or rivals. It is possible that, for this study, environmental conditions were not severe enough to produce distinguishable patterns of asymmetry. Alternatively, if patterns did exist and we were unable to detect them, this type of research may require more sophisticated methods of analyzing and measuring 3-dimensional shape; these methods may provide more sensitive detection of patterns of asymmetry. Laser grids, computed tomography (CT) scans, and magnetic resonance imaging (MRI) have been used to measure asymmetry, although, these methods are very costly.

CONCLUSIONS

We found no support for the hypothesized trends involving fluctuating asymmetry of sexually selected traits. Neither age nor trait size were consistently correlated with levels of fluctuating asymmetry. Based on our results there was no evidence that fluctuating asymmetry provides a reliable indicator of individual quality, and its widespread

application as a useful monitoring tool for environmental quality and population health seems, at best, inconsistent. Several authors (Palmer 1999; Palmer 2000; Jennions and Møller 2003) have suggested that there is bias in the literature toward only positive or expected results in publications relating to fluctuating asymmetry, and others (Houle 1998; Simmons et al. 1999) suggest caution when generalizing conclusions about the relationship between fluctuating asymmetry and sexual selection. Early enthusiasm for fluctuating asymmetry as an indicator of individual quality may have been overstated due to unbalanced reporting of studies with positive results. Therefore, future work on this topic will determine the strength and validity of fluctuating asymmetry hypotheses.

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Table 1. Absolute and percent differences between measures from repeated computer models for selected antler traits.

Measurement[a]	Absolute difference (mm)					Percent difference				
	$\bar{x}$	SE	n	Min	Max	$\bar{x}$	SE	n	Min	Max
lengthg1r	0.629	0.129	8	0.154	1.122	0.749	0.117	8	0.167	1.269
lengthg1l	0.702	0.177	10	0.145	2.024	0.725	0.120	10	0.176	1.406
lengthg2r	0.835	0.200	10	0.001	2.007	0.535	0.115	10	0.001	1.116
lengthg2l	0.786	0.213	10	0.115	1.980	0.467	0.104	10	0.081	0.986
lengthg3r	1.321	0.272	7	0.611	2.154	1.756	0.537	7	0.550	4.753
lengthg3l	0.913	0.228	6	0.368	1.933	0.961	0.158	6	0.594	1.570
distg1tip	0.676	0.149	8	0.016	1.152	0.618	0.147	8	0.010	1.113
distg2tip	0.112	0.111	10	<0.001	1.110	0.043	0.042	10	<0.001	0.421
distg3tip	1.049	0.561	6	0.116	3.636	0.378	0.184	6	0.051	1.105
distg1base	1.063	0.405	8	0.142	3.190	0.694	0.239	8	0.127	1.98
distg2base	1.062	0.401	10	0.155	3.834	0.301	0.110	10	0.046	1.095
distg3base	1.162	0.510	6	0.077	3.271	0.323	0.125	6	0.018	0.753
rg1h-tip	0.594	0.122	8	0.136	1.003	0.800	0.242	8	0.093	1.827
lg1h-tip	0.880	0.235	10	0.086	2.012	0.723	0.157	10	0.084	1.390
rg1v-tip	0.965	0.251	8	0.268	2.349	1.784	0.447	8	0.610	3.914
lg1v-tip	0.591	0.163	10	0.015	1.420	0.907	0.259	10	0.025	2.622

Table 1. Continued.

| Measurement[a] | Absolute difference (mm) | | | | | Percent difference | | | | |
	$\bar{x}$	SE	*n*	Min	Max	$\bar{x}$	SE	*n*	Min	Max
rg2h-tip	0.946	0.354	10	0.039	3.858	0.362	0.115	10	0.014	1.109
lg2h-tip	1.245	0.401	10	0.028	3.190	0.427	0.130	10	0.011	0.961
rg2v-tip	1.630	0.322	10	0.083	3.208	1.355	0.247	10	0.071	2.357
lg2v-tip	1.245	0.401	10	0.028	3.190	1.489	0.406	10	0.035	4.452
distmb	0.950	0.345	10	0.010	3.357	0.486	0.123	10	0.005	1.127
angleg2r	0.472	0.194	7	0.034	1.315	0.609	0.230	7	0.048	1.562
angleg2l	0.417	0.126	9	0.029	1.207	0.633	0.236	9	0.036	2.341

[a] Descriptions of abbreviations are found in Appendix 1.

Table 2. Mean differences (mm) between manual and computer-generated measurements of antler dimensions and corresponding statistical tests for difference from parity.

Measurement[a]	$\bar{x}$	SE	n	t	P
lengthg1r	28.260	0.964	108	29.33	<0.001
lengthg2r	8.277	1.759	121	4.71	<0.001
lengthg3r	13.516	2.444	89	5.53	<0.001
lengthg4r	16.958	1.878	12	9.03	<0.001
lengthg1l	32.402	1.039	104	31.20	<0.001
lengthg2l	9.871	1.083	121	9.11	<0.001
lengthg3l	16.072	3.301	88	4.87	<0.001
lengthg4l	14.169	0.977	14	14.50	<0.001

[a] Descriptions of abbreviations are found in Appendix 1.

Table 3: Correlation matrix of relationships between measures of fluctuating asymmetry of antler traits, trait size, and age.

		labsymg2h[a]	labsymg2v	labsymg1h	labsymg1v	labsymbh	labsymbv	labsymg2a	labsymc1	labsymsc	labsymmb	lg1symm	lg2symm	avc1	avscore	avmb
labsymg2v	r	0.261														
	P	0.001														
	n	97														
labsymg1h	r	0.081	-0.057													
	P	0.485	0.629													
	n	76	75													
lasymg1v	r	0.097	0.301	0.012												
	P	0.375	0.005	0.916												
	n	85	84	84												

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Table 3: Continued.

		labsymg2h[a]	labsymg2v	labsymg1h	labsymg1v	labsymbh	labsymbv	labsymg2a	labsymc1	labsymsc	labsymmb	lg1symm	lg2symm	avc1	avscore	avmb
labsymbh																
	r	0.167	0.181	0.121	0.023											
	P	0.127	0.097	0.289	0.832											
	n	85	85	79	87											
labsymbv																
	r	0.164	0.248	0.030	0.100	0.116										
	P	0.133	0.022	0.794	0.358	.247										
	n	85	85	79	87	102										
labsymg2a																
	r	-0.143	0.075	0.174	-0.007	-0.126	0.085									
	P	0.280	0.574	0.204	0.955	0.332	0.516									
	n	59	59	55	62	61	61									

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Table 3: Continued.

	labsymg2h[a]	labsymg2v	labsymg1h	labsymg1v	labsymbh	labsymbv	labsymg2a	labsymc1	labsymsc	labsymmb	lg1symm	lg2symm	avc1	avscore	avmb
labsymc1															
r	0.017	0.444	-0.008	0.267	0.267	0.209	0.172								
P	0.869	0.000	0.942	0.007	0.007	0.036	0.157								
n	96	95	92	102	101	101	69								
labsymsc															
r	-0.006	-0.097	0.132	0.069	0.213	0.058	0.099	0.126							
P	0.955	0.352	0.212	0.488	0.033	0.567	0.413	0.112							
n	96	95	92	102	101	101	70	160							
labsymmb															
r	0.012	0.217	0.266	0.176	0.206	0.107	0.212	0.327	0.278						
P	0.911	0.047	0.018	0.102	0.037	0.286	0.101	0.000	0.001						
n	85	85	79	87	102	102	61	142	142						

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Table 3: Continued.

	labsymg2h[a]	labsymg2v	labsymg1h	labsymg1v	labsymbh	labsymbv	labsymg2a	labsymc1	labsymsc	labsymmb	lg1symm	lg2symm	avc1	avscore	avmb
lg1symm															
r	0.151	0.049	0.124	0.114	0.018	-0.091	-0.017	0.117	0.211	0.263					
P	0.211	0.493	0.000	0.119	0.627	0.035	0.618	0.155	0.037	0.014					
n	70	70	84	82	72	72	52	98	99	87					
lg2symm															
r	0.241	0.049	0.124	0.114	0.018	-0.091	-0.017	0.117	0.141	0.242	0.213				
P	0.018	0.638	0.293	0.306	0.871	0.412	0.897	0.225	0.141	0.015	0.055				
n	96	96	74	83	84	84	59	110	111	100	82				
avc1															
r	0.115	0.231	-0.040	0.233	0.237	0.194	0.115	0.345	0.142	0.061	-0.004	0.012			
P	0.267	0.024	0.704	0.019	0.017	0.052	0.347	0.000	0.074	0.474	0.968	0.899			
n	96	95	92	102	101	101	69	161	160	142	98	110			

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Table 3: Continued.

	labsymg2h[a]	labsymg2v	labsymg1h	labsymg1v	labsymbh	labsymbv	labsymg2a	labsymc1	labsymsc	labsymmb	lg1symm	lg2symm	avc1	avscore	avmb
avscore															
r	0.000	-0.033	-0.029	0.047	0.142	0.092	-0.169	0.174	0.107	-0.045	-0.067	0.645	0.925		
P	0.997	0.785	0.819	0.719	0.238	0.448	0.266	0.073	0.268	0.645	0.555	0.555	0.000		
n	71	71	66	61	71	71	45	107	108	108	78	86	107		
avmb															
r	0.128	0.081	-0.009	0.099	0.208	0.172	-0.080	0.101	0.153	-0.086	-0.003	0.025	0.876	0.958	
P	0.245	0.463	0.935	0.361	0.036	0.085	0.539	0.230	0.070	0.306	0.977	0.803	0.000	0.000	
n	85	85	79	87	102	102	61	142	142	143	87	100	142	108	
age															
r	0.255	0.039	0.112	0.132	0.247	0.101	-0.354	0.161	0.084	-0.057	-0.052	-0.062	0.661	0.707	0.694
P	0.118	0.815	0.535	0.423	0.124	0.536	0.083	0.246	0.552	0.696	0.766	0.692	0.000	0.000	0.000
n	39	39	33	39	40	40	25	54	53	50	35	43	54	39	50

[a] Descriptions of abbreviations are found in Appendix 1.

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Table 4. Results from ANOVA comparing degree of fluctuating asymmetry in selected traits of white-tailed deer antlers among age and score classes.

Variable	Age class			Score class		
	F	P	d.f.	F	P	d.f.
labsymg1h[a]	0.27	0.846	3, 29	2.68	0.085	2, 30
labsymg1v	0.51	0.680	3, 35	0.12	0.887	2, 36
labsymg2h	1.38	0.265	3, 35	0.56	0.576	2, 36
labsymg2v	0.15	0.927	3, 35	1.16	0.325	2, 36
labsymbh	1.87	0.153	3, 36	0.08	0.925	2, 37
labsymbv	0.82	0.490	3, 36	4.16	0.024	2, 37
labsymg2a	1.05	0.390	3, 21	0.30	0.741	2, 22
labsymc1	0.57	0.639	3, 50	0.23	0.799	2, 51
labsymsc	1.12	0.355	3, 35	6.44	0.004	2, 36
labsymmb	0.42	0.740	3, 46	0.40	0.672	2, 47
lg1symm	0.72	0.546	3, 31	0.78	0.465	2, 32
lg2symm	0.78	0.514	3, 39	0.22	0.803	2, 40

[a] Descriptions of abbreviations are found in Appendix 1.

Table 5: Absolute asymmetry of selected antler traits among 4 age classes (1.5, 2.5, 3.5, and >4.5 years of age).

Variable	1.5			2.5			3.5			4.5 +		
	$\bar{x}$	SE	n	$\bar{x}$	SE	n	$\bar{x}$	SE	n	$\bar{x}$	SE	n
absymg1h[a]	6.085	3.414	2	17.199	3.746	16	37.838	18.340	9	15.702	3.929	6
absymg1v	8.358	0.870	2	17.011	3.701	19	15.600	4.226	10	28.689	9.167	8
absymg2h	8.676	0.989	2	23.748	3.342	19	25.945	7.224	10	34.798	7.097	8
absymg2v	20.557	12.105	2	33.190	5.968	19	40.144	10.788	10	51.655	18.418	8
absymbh	43.455	-----	1	25.407	5.754	20	22.044	3.514	11	44.449	9.46	8
absymbv	5.919	-----	1	28.796	5.601	20	44.094	11.571	11	35.101	10.647	8
absymg2a	14.685	-----	1	11.655	4.787	13	5.807	2.044	7	3.103	1.493	4
absymc1	4.714	1.229	7	5.870	1.736	23	6.071	1.787	14	8.600	2.349	10

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Table 5. Continued.

Variable	1.5			2.5			3.5			4.5 +		
	$\bar{x}$	SE	n	$\bar{x}$	SE	n	$\bar{x}$	SE	n	$\bar{x}$	SE	n
absymsc	85.333	24.722	6	55.235	12.121	17	53.250	14.844	8	91.625	24.035	8
absymmb	24.167	10.480	6	31.364	6.728	22	25.083	8.699	12	19.800	4.756	10
g1symm	8.667	6.667	3	22.000	4.366	16	16.375	5.092	8	38.250	29.811	8
g2symm	21.250	11.778	4	24.850	4.208	20	19.778	8.263	9	33.000	13.710	10
avc1	63.500	5.118	7	88.239	4.315	23	101.821	5.390	14	116.800	4.459	10
avscore	422.833	45.460	6	869.382	81.144	17	1058.380	114.285	8	1329.560	51.167	8
avmb	256.083	18.182	6	404.273	19.076	22	456.042	22.998	12	539.500	19.066	10

[a] Descriptions of abbreviations are found in Appendix 1.

Table 6: Absolute asymmetry measures of selected antler traits of white-tailed deer among 3 antler score classes (low, medium, and high).

Variable	Low			Medium			High		
	$\bar{x}$	SE	n	$\bar{x}$	SE	n	$\bar{x}$	SE	n
absymg1h[a]	18.765	4.876	17	44.934	21.311	7	9.838	3.142	9
absymg1v	19.729	3.818	24	20.207	9.479	6	14.522	4.123	9
absymg2h	28.100	3.699	22	21.476	4.345	8	24.017	8.315	9
absymg2v	40.864	8.010	22	44.519	12.230	8	25.692	7.417	9
absymbh	29.871	4.589	23	32.593	13.004	8	22.432	4.122	9
absymbv	42.640	6.658	23	31.833	9.817	8	12.479	4.870	9
absymg2a	9.473	3.788	17	9.127	2.565	5	4.194	0.676	3
absymc1	6.125	1.009	32	7.000	3.527	11	6.00	1.800	11
absymsc	85.353	11.630	17	36.182	11.419	11	69.182	20.531	11
absymmb	29.143	5.738	28	30.909	9.410	11	16.182	3.083	11
g1symm	26.938	14.734	16	25.111	6.281	9	15.800	5.918	10
g2symm	26.000	7.118	22	26.000	7.433	10	23.455	4.981	11

[a] Descriptions of abbreviations are found in Appendix 1.

Figure 1. Diagram showing the typical anatomical features of a white-tailed deer antler.
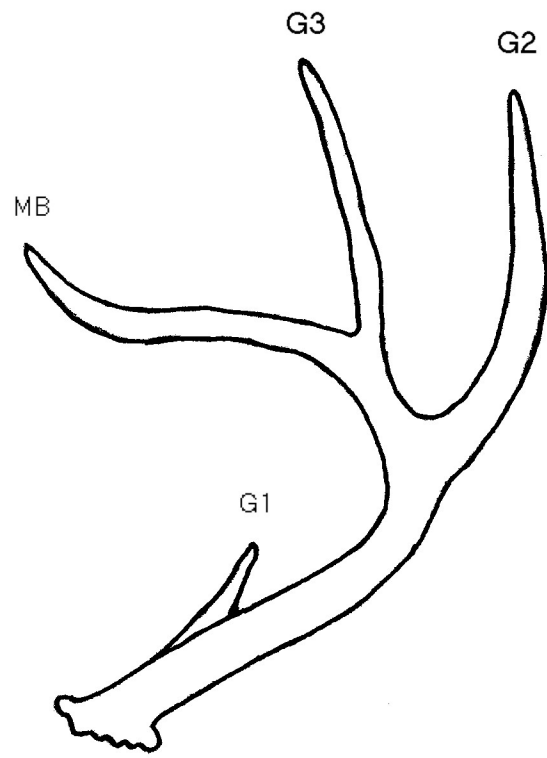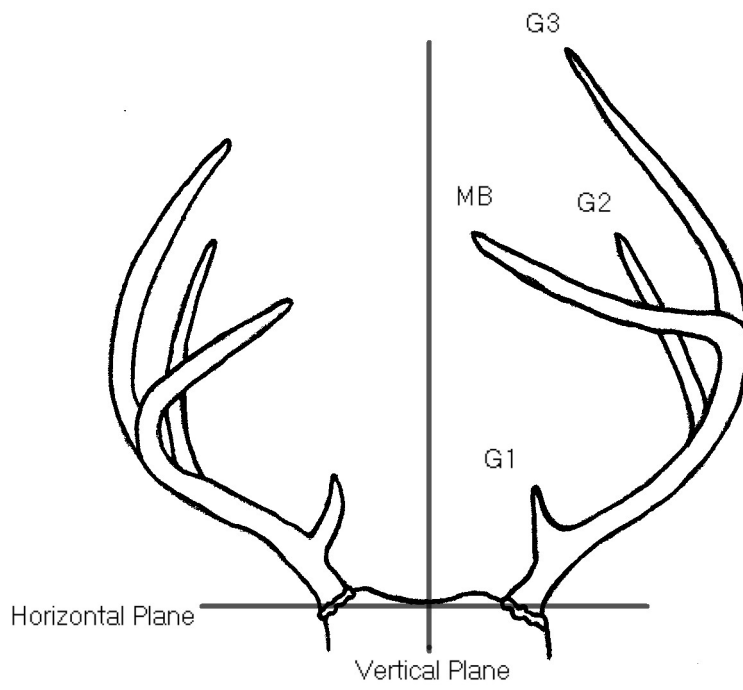
G3 G2

MB

G1

Figure 2. Diagram showing vertical and horizontal planes used to measure 3-dimensional asymmetry of white-tailed antler traits.

II. QUANTIFYING ASYMMETRY IN COMPLEX 3-DIMENSIONAL TRAITS

ABSTRACT

Fluctuating asymmetry has been proposed as an indirect indicator of individual quality. In most studies of fluctuating asymmetry, simple measures, such as length and width, were measured. These simple measures may be adequate for simple, 2-dimensional traits, but for complex 3-dimensional traits important aspects of visual, spatial asymmetry may have been ignored. Visual, perceptible asymmetry is the type of asymmetry likely to be important in studies of sexual selection. Therefore, we used 3-dimensional computer models to quantify this type of asymmetry in white-tailed deer antlers, a complex sexually selected trait. This method used to measure asymmetry in antlers could be expanded for use in measuring asymmetry in many complex 3-dimensional traits. To construct the computer models important landmark points were marked on the features of interest, and then digital photographs were taken of each antler set. These landmark points were labeled and cross-referenced across all the photographs, using the program PhotoModeler, to create 3-dimensional "stick" figures. To quantify visual asymmetry, distances were taken from the important features to a vertical and horizontal plane that was created using the coordinate points generated by the model. By modeling ten sets of antlers twice using the same photographs, the models were found to be highly repeatable.

INTRODUCTION

Fluctuating asymmetry, random variation from perfect symmetry in bilateral traits (Van Valen 1692), has been proposed as a quantifiable indicator of developmental stability, which is defined as the ability of an individual to buffer the harmful effects of stress experienced during development (Palmer 1996). By comparing the level of fluctuating asymmetry between individuals of a population an indirect estimate of individual quality can be obtained. Because bilateral traits arise from the same genes, their expected, optimal condition is perfect symmetry (Polak and Trivers 1994). Therefore, any deviation from perfect symmetry is attributed to the individual's inability to counteract the effects of genetic or environmental stress experienced during development (Parsons 1992). Individuals exhibiting lower levels of fluctuating asymmetry are theorized to have a greater ability to develop optimally despite the stresses experienced during development. Consequently, these individuals are considered higher quality (Møller and Pomiankowski 1993). In contrast, individuals exhibiting greater levels of fluctuating asymmetry are considered lower quality due to inability to cope with stress during development. While fluctuating asymmetry has been studied for both ordinary morphological traits and ornamental traits, Møller and Pomiankowski (1993) hypothesized that degree of fluctuating asymmetry should be greater in ornamental traits, which are subject to directional selection. In contrast, ordinary morphological traits, especially those used in functions related to survival, are more canalized and subject to stabilizing selection (Møller and Pomiankowski 1993), and are therefore, less susceptible to developmental disturbance (Polak 1993).

Applications of fluctuating asymmetry have been suggested in conservation and behavioral ecology. Monitoring of fluctuating asymmetry has been proposed as a potential tool to assess habitat or environmental quality (Leary and Allendorf 1989; Hill 1995). Furthermore, level of fluctuating asymmetry in sexually selected traits has been proposed as a possible signal of quality used by potential mates for sexual selection and by potential combatants in intrasexual competition (Møller and Pomiankowski 1993). Therefore, there is much interest in fluctuating asymmetry for its potential as an easily measured indicator of quality.

Due to the small magnitude of differences attributed to fluctuating asymmetry precise and accurate measurement techniques are required for its detection (Palmer 1996). Measurement error can be a confounding problem in detecting fluctuating asymmetry. Palmer and Strobeck (1986) reported that measurement error contributed between 10 to 76% of directional asymmetry found in the studies they reviewed.

In many previous studies, fluctuating asymmetry was measured for relatively simple two-dimensional traits, such as insect wings (Polak 1993; Leung and Forbes 1997) and bird feathers (Møller and Högland 1991; Bize et al. 2004). The most commonly assessed measurements were linear measures such as length and width. While these measures may adequately describe levels of asymmetry in these simple traits, they may be inadequate for other more complex 3-dimensional traits. These complex traits can vary not only in length and width but also in shape and conformation; it is possible for two objects of similar length to appear very different due to differences in shape, such as curvature. For example, it is possible for tines of equal length on deer antlers to appear very different if, perhaps, one was oriented 90° from the ground plane and a

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corresponding tine on the other side was oriented 45° from the ground plane. According to simple length measures, these two tines would be considered symmetrical, but appear asymmetrical. Therefore, traditional measurement methods may overlook an important component of fluctuating asymmetry in these traits.

We used white-tailed deer (*Odocoileus virginianus*) antlers as a model to address the challenge of measuring fluctuating asymmetry in a 3-dimensional trait. Antlers are a complex, secondary sexual trait involved in intrasexual competition and possibly mate choice (Clutton-Brock 1982). There have been previous studies of antler asymmetry for a few different species using traditional measurement techniques, such as length, circumference, and weight (Solberg and Sæther 1993; Folstad et al. 1996; Ditchkoff et al. 2001; Kruuk et al. 2003; Bartoš and Bahbouh 2006). However, these studies may have overlooked important elements of spatial asymmetry in antlers. Therefore, antlers are an ideal trait for comparison of measurement techniques.

Our objective was to develop and assess a method to reliably and accurately measure 3-dimensional asymmetry. We entered digital images of the trait into a computer program to create a virtual model of the antlers, thereby allowing for measurement of a variety of antler traits. We also used coordinate points generated by the model to construct a vertical plane between the antlers and horizontal plane at the base of the antlers so that visual, spatial asymmetry could be quantified by measuring the distance from selected antler features to the planes. Traditional, linear measures of antler traits were also taken to allow comparison between the techniques.

MATERIAL AND METHODS

Data were collected from hunter-harvested deer from Tallapoosa and Bullock counties in Alabama, USA during the 2002 and 2003 hunting seasons. In addition, to increase sample size, antler measurements were obtained from various sets of antlers collected in previous hunting seasons. These antlers were still attached to the skull plate. Antlers were measured following guidelines for the Boone and Crockett trophy scoring system (Nesbitt and Reneau 1988). Measurements that were taken included spread between G2 tines, tine lengths, and main beam lengths. These measurements were taken using a flexible measuring tape and were recorded to the nearest mm.

In order to create the 3-dimensional computer models, approximately 12 digital photographs were taken around the circumference of each antler set and from above. The antlers were first marked with 3mm dots using paint and/or stickers to provide landmark points for use in modeling. The dots were placed along the center of the main beam and tines making sure to mark the points were the base of the tines intersected the main beam. Dots were placed approximately every 50 mm in order to ensure representation of the curves of the antlers; where the antlers showed high levels of curvature the marks were placed closer together. In addition, a dot was placed directly between the deer's eyes for later use in constructing the vertical and horizontal planes. The images were then entered into the program PhotoModeler (Eos Systems Inc, Vancouver, BC, Canada). Using between 9 and 12 images for each antler set, the landmark points and tips of tines and main beams were marked, labeled, and cross-referenced between all photographs resulting in a 3-dimensional "stick" model of each antler set. To accurately represent the size of the antlers, the scale of the model was calibrated using a manual measure of

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distance between the tips of the right and left G2 tines (second tine erupting vertically from the main beam; Fig. 1). The PhotoModeler program assigned each scaled model point a 3-dimensional (x,y,z) coordinate point, resulting in approximately 40-60 modeled points per antler set depending on the complexity of a given set of antlers. These coordinate point values were labeled to correspond to important antler features (Append. 1) to allow for comparison between individuals. Coordinate points were exported to SAS (Statistical Analysis Systems 1990) for analysis.

By using the base points of the antlers and a center point (marked between the deer's eyes), a vertical plane between the antlers and horizontal plane at the base of the antlers were calculated (Fig. 2). Base points were marked for both the right (a_R) and left (a_L) antlers along the outside of the main beam and at the base where the antler erupts from the skull. A midpoint (m) calculated using these two base points is the origin of the coordinate system.

$$\vec{m} = \frac{\vec{a}_R + \vec{a}_L}{2} \qquad\qquad (1)$$

The y axis runs between the two antler bases. The x axis runs from the origin toward the nose, and the z axis runs from the origin up between the two antlers perpendicular to the x axis. Therefore, the x-y plane is the horizonal plane, and the x-z plane is the vertical plane. The unit vector in the y direction ($\hat{y}$) was calculated using the following equation:

$$\hat{y} = \frac{\vec{a}_L - \vec{a}_R}{\left\| \vec{a}_L - \vec{a}_R \right\|} \cdot \qquad\qquad (2)$$

In order to approximate viewing angle of antlers by other deer x and z axes were shifted up by a correction angle (θ). For this study the correction angle used was 15°. The unit vector in the uncorrected z direction ($\hat{z}_{UNC}$) was calculated by the following equation:

$$\hat{z}_{UNC} = \frac{(\bar{b} - \bar{a}_R) \times \hat{y}}{\|(\bar{b} - \bar{a}_R) \times \hat{y}\|},$$

(3)

where b is the center point marked between the deer's eyes. The unit vector in the uncorrected x direction ($\hat{x}_{UNC}$) was calculated using the following equation:

$$\hat{x}_{UNC} = \hat{y} \times \hat{z}_{UNC}.$$

(4)

The equation for the horizontal plane (N_H) with the angle correction (θ) is as follows:

$$\bar{N}_H = (-\sin\theta)\hat{x}_{UNC} + (\cos\theta)\hat{z}_{UNC}.$$

(5)

The vertical plane (N_V) was calculated as follows:

$$\bar{N}_V = \hat{y}.$$

(6)

So given modeled point (p) on a set of antlers, the distance from that point to the horizontal plane (d_H) is

$$d_H = \bar{N}_H \bullet (\bar{p} - \bar{m}).$$

(7)

The distance from a modeled point (p) to the vertical plane (d_B) is

$$d_B = \bar{N}_V \bullet (\bar{p} - \bar{m}).$$

(8)

Perpendicular distances were calculated from the horizontal and vertical planes to selected antler features and distances of tines were calculated. In addition, the angle between the main beam and the G2 tine was calculated. These calculations were done using SAS (Statistical Analysis Systems 1990).

Absolute asymmetry was calculated as the absolute difference between right and left side antler measurements. From the data generated by the 3-dimensional computer models, absolute asymmetry was calculated for many variables: distance from the horizontal plane to the tips of the G1, G2, and main beam, distance from the vertical

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plane to the tips of the G1, G2, main beam, and angle between the G2 tine and the main beam.

A subset of ten antler sets was modeled twice using the same photographs in order to assess the precision of the measurement technique that utilized the computer models. Differences in lengths of corresponding tines were divided by the average trait size to obtain a percent difference between the two models, thereby allowing us to evaluate repeatability. Accuracy of computer models was evaluated by comparing manually measured tine lengths with the computer modeled tine lengths. This was evaluated using t-tests. Broken or worn antler points were not included in any analyses.

RESULTS

Percent differences between corresponding measures of repeated models ranged from <0.01 to 4.75%, and absolute differences ranged from <0.01 to 3.86 mm (Table 1). Mean percent differences were less than 1% for all but four variables measured and were less than 2% for all variables measured. Length of the right G3 tine (lengthg3r; $\bar{x}$ = 1.756%), distance from tip of the right G1 tine to the vertical plane (rg1v-tip; $\bar{x}$ = 1.784%), distance from the tip of the right G2 tine to the vertical plane (rg2v_tip; $\bar{x}$ = 1.355%), distance from the tip of the left G2 tine to the vertical plane (lg2v-tip; $\bar{x}$ = 1.489%) were all greater than 1% mean difference between repeated models. Tine lengths measured via the computer models were greater ($P > 0.001$) than corresponding manually measured lengths (Table 2), and mean differences ranged from 8.28 to 32.40 mm.

DISCUSSION

This method of measuring asymmetry addresses an important aspect of asymmetry that has been unmeasured in most studies of complex traits. Visual, spatial asymmetry is the type of asymmetry that a potential rival or mate would most likely regard when selecting a mate or opponent. Only asymmetry that can be perceived by an individual is likely to be important during sexual selection. This modeling method provides a relatively simple, cost-effective way to quantify spatial asymmetry. While there are more sophisticated methods to measure and analyze visual asymmetry, such as laser grids, computed tomography (CT) scans, and magnetic resonance imaging (MRI), these methods are very costly and impractical for field studies.

The amount of time required to acquire the photographs and produce the models was somewhat prohibitive. Marking and photographing each antler set took approximately 20 minutes because of the number of photographs required and awkward nature of photographing and manipulating a large carcass. This time constraint could preclude use of this technique for assessing 3-dimensional asymmetry on antlers of live animals because of stress associated with prolonged restraint or tranquilization. Creating each computer model took approximately 90 minutes because of the difficulty in cross-referencing a large number of data points between numerous pictures. Each data point then had to be labeled and exported to a data file. Therefore, overall handling time for each antler set was considerable; however, analysis of generated data was relatively straightforward.

Antler sets that were very simple, such as spikes or forked antlers, were unable to be modeled using PhotoModeler because there were not enough data points for the

computer program to generate a 3-dimensional model. Therefore, this limitation, at least for this computer program, may in part determine the types of traits for which this technique is well suited; complex 3-dimensional traits such as antlers and skulls seem appropriate. Conversely, more simple traits, such as horns, could be marked with numerous landmark points, more than necessary to depict the traits shape, in order to provide enough data to model.

The computer models were highly repeatable. Mean differences between repeated model measurements were well below asymmetry values and generally less than 1 mm (ranging from 0.112 mm to 1.74 mm); these values are generally below 1% difference between replicates. These are similar or lower than levels of measurement error found acceptable in other studies of antler fluctuating asymmetry (Ditchkoff et al. 2001; Kruuk et al. 2003; Bartoš and Bahbouh 2006). Some of the imprecision in the percent differences may have arisen because the tips of antlers are somewhat blunt. Therefore, when marking these landmarks in the computer program it was more difficult to mark the exact same point on each photograph. This may have resulted in some error, but this did not seem to be a problem when marking the landmarks represented by dots. In addition, the base points marked on the antlers were often shadowed by the antlers and thus more difficult to see clearly in all the photographs. Traditional, manual measurements are generally taken to the nearest mm. Therefore, our computer measures, in general, also had the same margin of error that is inherent in the manual measures; both the computer models and manual measures have approximately the same level of precision.

The differences between the manual and computer measured tine lengths can be explained by the disparity in measurement landmarks for the two techniques. For the manual Boone and Crockett-type measurements, tines were measured from the tip of the tine to where the tine intersected the top edge of the main beam. However, to facilitate the construction of the 3-dimensional "stick" model, tine lengths were measured from the tip of the tine to where the tine intersected the middle of the main beam. Therefore, it was expected that computer-generated tine lengths would be greater than manual measurements by approximately half the width of the main beam. This discrepancy was especially pronounced in the G1 tines because of the thicker width of the main beam toward the base of the antlers and because of the more acute angle with which G1 tines often grow out from the main beam. Thus the modeled lines crossed the main beam at an angle increasing the distance from the tip of the tine to the center of the main beam relative to other tines. In addition, tine lengths calculated from computer models were measured as a straight-line distance from tip of the tine to the base of the tine while manual measurements followed the outside curve of tines. The purpose of comparing corresponding measurements from the two techniques was to determine if measurements were similar and differed by approximately half the width of the main beam. Measurements differed by approximately 10-20 mm, which is consistent with half the width of the main beam. Therefore, computer models were scaled and representative of actual size and proportion of antler sets.

CONCLUSIONS

Our method of measuring asymmetry was both precise and accurate enough for use in studies of fluctuating asymmetry. It allows spatial asymmetry of complex traits to

be quantified and analyzed by a relatively inexpensive, simple method. This method also allows for spatial asymmetry to be studied in the field, which may not be possible with methods utilizing large machines, for example MRI. Studies of visual fluctuating asymmetry may have important implications for studies of sexual selection and habitat monitoring and could provide new insight about hypotheses related to fluctuating asymmetry.

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Table 1. Absolute and percent differences between measures from repeated computer models for selected antler traits.

| Measurement | Absolute difference (mm) | | | | | Percent difference | | | | |
	$\bar{x}$	SE	*n*	Min	Max	$\bar{x}$	SE	*n*	Min	Max
lengthg1r[a]	0.629	0.129	8	0.154	1.122	0.749	0.117	8	0.167	1.269
lengthg1l	0.702	0.177	10	0.145	2.024	0.725	0.120	10	0.176	1.406
lengthg2r	0.835	0.200	10	0.001	2.007	0.535	0.115	10	0.001	1.116
lengthg2l	0.786	0.213	10	0.115	1.980	0.467	0.104	10	0.081	0.986
lengthg3r	1.321	0.272	7	0.611	2.154	1.756	0.537	7	0.550	4.753
lengthg3l	0.913	0.228	6	0.368	1.933	0.961	0.158	6	0.594	1.570
distg1tip	0.676	0.149	8	0.016	1.152	0.618	0.147	8	0.010	1.113
distg2tip	0.112	0.111	10	<0.001	1.110	0.043	0.042	10	<0.001	0.421
distg3tip	1.049	0.561	6	0.116	3.636	0.378	0.184	6	0.051	1.105
distg1base	1.063	0.405	8	0.142	3.190	0.694	0.239	8	0.127	1.98
distg2base	1.062	0.401	10	0.155	3.834	0.301	0.110	10	0.046	1.095
distg3base	1.162	0.510	6	0.077	3.271	0.323	0.125	6	0.018	0.753
rg1h-tip	0.594	0.122	8	0.136	1.003	0.800	0.242	8	0.093	1.827
lg1h-tip	0.880	0.235	10	0.086	2.012	0.723	0.157	10	0.084	1.390
rg1v-tip	0.965	0.251	8	0.268	2.349	1.784	0.447	8	0.610	3.914
lg1v-tip	0.591	0.163	10	0.015	1.420	0.907	0.259	10	0.025	2.622
rg2h-tip	0.946	0.354	10	0.039	3.858	0.362	0.115	10	0.014	1.109

Table 1. Continued.

Measurement	Absolute difference (mm)					Percent difference				
	$\bar{x}$	SE	n	Min	Max	$\bar{x}$	SE	n	Min	Max
lg2h-tip	1.245	0.401	10	0.028	3.190	0.427	0.130	10	0.011	0.961
rg2v-tip	1.630	0.322	10	0.083	3.208	1.355	0.247	10	0.071	2.357
lg2v-tip	1.245	0.401	10	0.028	3.190	1.489	0.406	10	0.035	4.452
distmb	0.950	0.345	10	0.010	3.357	0.486	0.123	10	0.005	1.127
angleg2r	0.472	0.194	7	0.034	1.315	0.609	0.230	7	0.048	1.562
angleg2l	0.417	0.126	9	0.029	1.207	0.633	0.236	9	0.036	2.341

[a] Descriptions of abbreviations are found in Appendix 1.

Table 2. Mean differences (mm) between manual and computer-generated measurements of antler dimensions and corresponding statistical tests for difference from parity.

Measurement	$\bar{x}$	SE	n	t	P
lengthg1r[a]	28.260	0.964	108	29.33	<0.001
lengthg2r	8.277	1.759	121	4.71	<0.001
lengthg3r	13.516	2.444	89	5.53	<0.001
lengthg4r	16.958	1.878	12	9.03	<0.001
lengthg1l	32.402	1.039	104	31.20	<0.001
lengthg2l	9.871	1.083	121	9.11	<0.001
lengthg3l	16.072	3.301	88	4.87	<0.001
lengthg4l	14.169	0.977	14	14.50	<0.001

[a] Descriptions of abbreviations are found in Appendix 1.

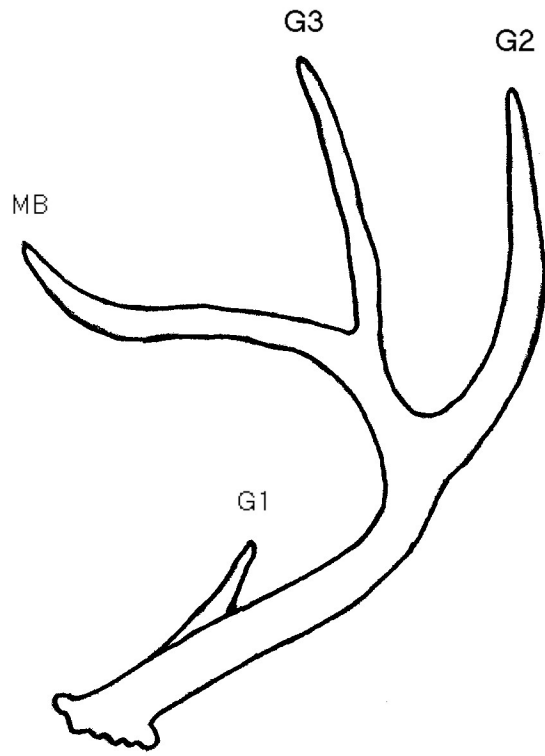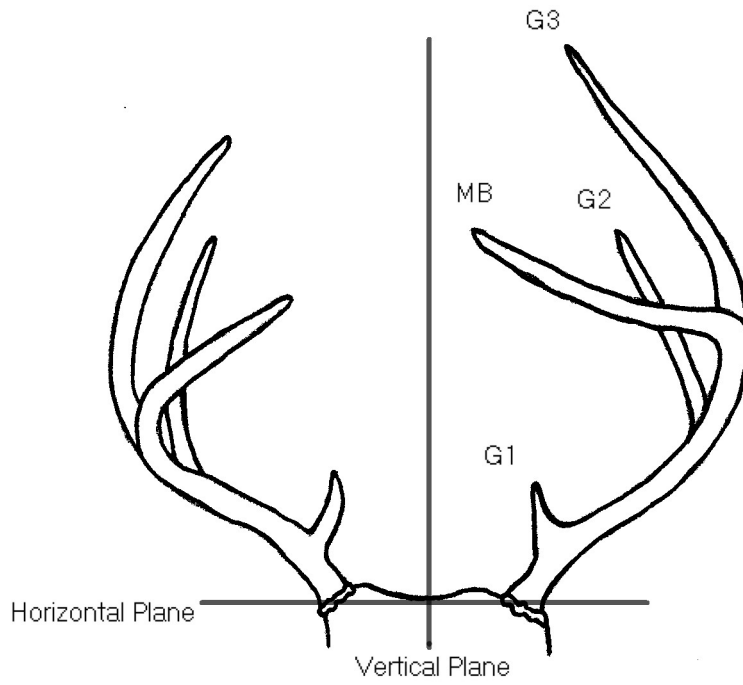Figure 1. Diagram showing the typical anatomical features of a white-tailed deer antler.

Figure 2. Diagram showing vertical and horizontal planes used to measure 3-dimensional

asymmetry of white-tailed antler traits.

G3

MB   G2

G1

Horizontal Plane

Vertical Plane

APPENDIX 1. DESCRIPTION OF ABBREVIATIONS

Abbreviation	Description
lengthg(x)r	length of right G(x) tine taken from computer model, where x = 1, 2, 3, etc…
lengthg(x)l	length of left G(x) tine taken from computer model, where x = 1, 2, 3, etc…
distg(x)tip	distance between the tips of the G(x) tines taken from computer model, where x = 1, 2, 3, etc…
distg(x)base	distance between the bases of the G(x) tines taken from computer model, where x = 1, 2, 3, etc…
distmb	distance between the tips of the main beams taken from computer model
angleg2r	angle of the right G2 tine from the main beam
angleg2l	angle of the left G2 tine from the main beam
rg(x)h_tip	distance from the tip of the right G(x) tine to the horizontal plane, where x = 1, 2, 3, etc…
lg(x)h_tip	distance from the tip of the left G(x) tine to the horizontal plane, where x = 1, 2, 3, etc…

Appendix 1. Continued.

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Abbreviation	Description
rg(x)v_tip	distance from the tip of the right G(x) tine to the vertical plane, where x = 1, 2, 3, etc…
lg(x)v_tip	distance from the tip of the left G(x) tine to the vertical plane, where x = 1, 2, 3, etc…
labsymg(x)h	natural log of the absolute asymmetry (r-l difference) of the distance from the tip of the G(x) tine to the horizontal plane, where x = 1, 2, 3, etc…
absymg(x)h	absolute asymmetry (r-l difference) of the distance from the tip of the G(x) tine to the horizontal plane, where x = 1, 2, 3, etc…
labsymg(x)v	natural log of the absolute asymmetry (r-l difference) of the distance from the tip of the G(x) tine to the vertical plane, where x = 1, 2, 3, etc…
absymg(x)v	absolute asymmetry (r-l difference) of the distance from the tip of the G(x) tine to the vertical plane, where x = 1, 2, 3, etc…
labsymbh	natural log of the absolute asymmetry (r-l difference) of the distance from the tip of the main beam to the horizontal plane, where x = 1, 2, 3, etc…
absymbh	absolute asymmetry (r-l difference) of the distance from the tip of the main beam to the horizontal plane, where x = 1, 2, 3, etc…

Appendix 1. Continued.

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Abbreviation   Description

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labsymbv   natural log of the absolute asymmetry (r-l difference) of the

distance from the tip of the main beam to the vertical plane

absymbv   absolute asymmetry (r-l difference) of the distance from the tip of

the main beam to the vertical plane

labsymg2a   natural log of the absolute asymmetry (r-l difference) of the angle

of the G2 tine from the main beam

absymg2a   absolute asymmetry (r-l difference) of the angle of the G2 tine

from the main beam

labsymc1   natural log of the absolute asymmetry of the manual measurement

of antler basal circumference

absymc1   absolute asymmetry of the manual measurement of antler basal

circumference

labsymsc   natural log of the absolute asymmetry (r-l difference) of the score

(manual measurements)

absymsc   absolute asymmetry (r-l difference) of the score (manual

measurements)

labsymmb   natural log of the absolute asymmetry (r-l difference) of the length

of the main beams (manual measurements)

Appendix 1. Continued.

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Abbreviation	Description
absymmb	absolute asymmetry (r-l difference) of the length of the main beams (manual measurements)
lg(x)symm	natural log of the absolute asymmetry (r-l difference) of the length of the G(x) tine (manual measurements), where x = 1, 2, 3, etc…
g(x)symm	absolute asymmetry (r-l difference) of the length of the G(x) tine (manual measurements), where x = 1, 2, 3, etc…
avc1	average size of basal circumference for individual
avscore	average score of individual
avmb	average length of main beam of individual

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