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Assessing fluctuating asymmetry of white-tailed deer antlers in a three-dimensional context

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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, we 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. We found no association 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. Examination of these data suggests that fluctuating asymmetry of white-tailed deer antlers is not a reliable indicator of quality. DOI: 10.1644/09-MAMM-A-134R.1.

Key words: antlers, fluctuating asymmetry, modeling, *Odocoileus virginianus*, 3-dimensional asymmetry, white-tailed deer

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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 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 the quality or fitness of an individual (Møller 1998). Although it is assumed that fluctuating asymmetry itself is not heritable (Polak 2008), it also is assumed that the ability to overcome developmental stress is at least partially heritable (Palmer 1996).

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 are important factors influencing mate choice and intrasexual

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competition in many species (Andersson 1982; Mateos and Carranza 1997; Møller 1988; Pärt and Qvarnström 1997). Also, several studies have documented that females prefer more symmetrical males (López et al. 2002; Schlüter et al. 1998; Sheridan and Pomiankowski 1997). 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 (Berglund et al. 1996; Zahavi 1975), and several studies have reported cases of ornamental characters signaling honest information about condition (David et al. 2000; Malo et al. 2005; Møller 1991; Velando et al. 2001). 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 indicate a male's heritable ability to cope with stress, so a female should choose to mate with a more symmetrical male 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 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 nonornamental 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 (Bowyer 1986; Lincoln 1972), and possibly mate choice (Bartoš and Bahbouh 2006; Ditchkoff et al. 2001a; Kruuk et al. 2002; 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 might 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 can 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.

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 (Bowyer et al. 2001; Ditchkoff et al. 2001b; Mateos et al. 2008; Putman and Sullivan 2000) have reported support for Møller's (1992) hypothesized negative relationship between fluctuating asymmetry and trait size. Solberg and Sæther (1993) further hypothesized a decrease in fluctuating asymmetry with increasing age because only higher quality males will survive to older ages.

Although 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 2 antler tines of equal length to appear asymmetrical based on the way that they are curved or oriented in space. Two corresponding tines of equal length could appear very different if, for example, 1 tine was oriented 90° from the ground plane and the other 45° from the ground plane. However, traditional linear measures would consider those 2 tines to be symmetrical because they have the same length. Visual asymmetry is the type of asymmetry that most likely would 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-dimensional 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.

Materials and Methods

Data were collected from hunter-harvested deer from Tallapoosa and Bullock counties in Alabama 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 also was calculated for each antler side by omitting

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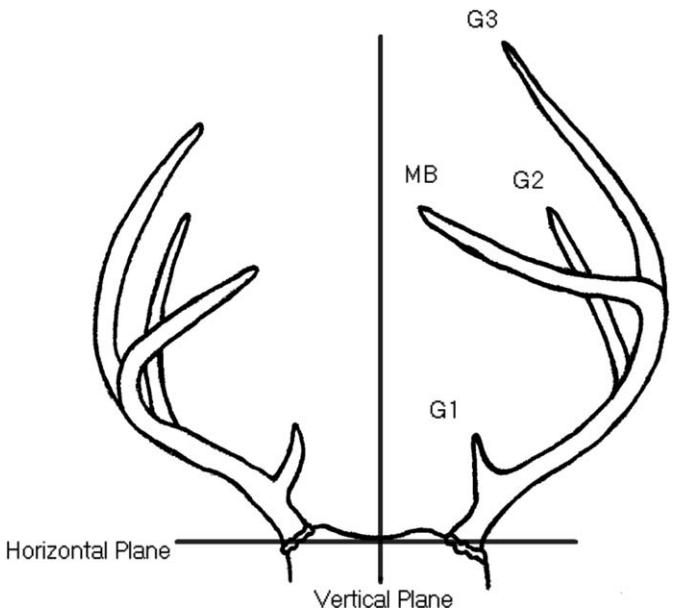

FIG. 1.—Diagram showing vertical and horizontal planes used to measure 3-dimensional asymmetry of white-tailed antler traits. The main beam (MB), brow tine (G1), and G2 and G3 tines are labeled on the left antler.

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 made using a flexible measuring tape and were recorded to the nearest millimeter. In addition, deer were aged using tooth wear and replacement patterns (Severinghaus 1949).

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 1st marked with approximately 3-mm dots using paint or stickers or both to provide landmark points for use in modeling. These photographs then were entered into the program PhotoModeler (Eos Systems Inc., Vancouver, British Columbia, Canada). Using between 9 and 12 pictures for each antler set, we marked the landmark points and tips of tines and main beams and cross-referenced them 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 (2nd 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 (Table 1) to allow for comparison among individuals. Coordinate points were exported to SAS (SAS Institute, Inc. 1990) for all analyses.

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 was calculated. 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 2 base points is the origin of the coordinate system:

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

The y-axis runs between the 2 antler bases. The x-axis runs from the origin toward the nose, and the z-axis runs from the origin up between the 2 antlers perpendicular to the x-axis. Therefore, the x–y plane is the horizontal 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:

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

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° based upon a subjective determination by the authors that this approximated the angle that a prospective mate or rival would view the antlers in a normal heads-up display relative to the x-axis as used in these calculations. The unit vector in the uncorrected z-direction ($\hat{z}_{UNC}$) was calculated by the following equation:

$$\hat{z}_{UNC} = \frac{\left(\vec{b} - \vec{a}_R\right) \times \hat{y}}{\left\| \left(\vec{b} - \vec{a}_R\right) \times \hat{y} \right\|}, \quad (3)$$

where b was 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:

$$\hat{x}_{UNC} = \hat{y} \times \hat{z}_{UNC}. \quad (4)$$

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

$$\vec{N}_H = (-\sin\theta)\hat{x}_{UNC} + (\cos\theta)\hat{z}_{UNC}. \quad (5)$$

The vertical plane (N_V) was calculated as follows:

$$\vec{N}_V = \hat{y}. \quad (6)$$

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

$$d_H = \vec{N}_H(\vec{p} - \vec{m}). \quad (7)$$

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

$$d_V = \vec{N}_V(\vec{p} - \vec{m}). \quad (8)$$

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.

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Table 1.—Abbreviations and descriptions of antler variables (features).

Variable	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.
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 (right–left difference) of the distances from the tip of the G(x) tines to the horizontal plane, where x = 1, 2, 3, etc.
absymg(x)h	Absolute asymmetry (right–left difference) of the distances from the tip of the G(x) tines to the horizontal plane, where x = 1, 2, 3, etc.
labsymg(x)v	Natural log of the absolute asymmetry (right–left difference) of the distances from the tip of the G(x) tines to the vertical plane, where x = 1, 2, 3, etc.
absymg(x)v	Absolute asymmetry (right–left difference) of the distances from the tip of the G(x) tines to the vertical plane, where x = 1, 2, 3, etc.
labsymbh	Natural log of the absolute asymmetry (right–left difference) of the distances from the tip of the main beams to the horizontal plane, where x = 1, 2, 3, etc.
absymbh	Absolute asymmetry (right–left difference) of the distances from the tip of the main beams to the horizontal plane, where x = 1, 2, 3, etc.
labsymbv	Natural log of the absolute asymmetry (right–left difference) of the distances from the tip of the main beams to the vertical plane
absymbv	Absolute asymmetry (right–left difference) of the distances from the tip of the main beams to the vertical plane
labsymg2a	Natural log of the absolute asymmetry (right–left difference) of the angles of the G2 tines from the main beams
absymg2a	Absolute asymmetry (right–left difference) of the angles of the G2 tines from the main beams
labsymc1	Natural log of the absolute asymmetry of the manual measurements of antler basal circumferences
absymc1	Absolute asymmetry of the manual measurements of antler basal circumferences
labsymsc	Natural log of the absolute asymmetry (right–left difference) of the antler scores (manual measurements)
absymsc	Absolute asymmetry (right–left difference) of the antler scores (manual measurements)
labsymmb	Natural log of the absolute asymmetry (right–left difference) of the lengths of the main beams (manual measurements)
absymmb	Absolute asymmetry (right–left difference) of the lengths of the main beams (manual measurements)
lg(x)symm	Natural log of the absolute asymmetry (right–left difference) of the lengths of the G(x) tine (manual measurements), where x = 1, 2, 3, etc.
g(x)symm	Absolute asymmetry (right–left difference) of the lengths of the G(x) tine (manual measurements), where x = 1, 2, 3, etc.
avc1	Average size of basal circumference of individual
avscore	Average antler score of individual
avmb	Average length of main beam of individual

We calculated absolute asymmetry 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; and 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.

To assess the precision of the measurement technique that used the computer models we used the same photographs to model a subset of 10 antler sets twice. Differences in lengths of corresponding tines were divided by the average trait size to obtain a percent difference between the 2 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 on nontransformed data (Zar 1984).

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 (Zar 1984). Pearson correlations also were used to test for relationships between levels of asymmetry of the manual measurements and asymmetry measures generated with the computer model. In addition, we compared relationships between asymmetry measures and measures of trait size (basal circumference, antler score, and main beam length) and age using Pearson correlation. To test for differences in level of asymmetry between age classes a 1-way analysis of variance (ANOVA) was conducted (Zar 1984). Because of 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 objectively divided into 3 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.

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 2). Mean

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TABLE 2.—Absolute and percent differences between measures from repeated computer models for selected antler traits.

	Absolute difference (mm)					Percent difference				
Measurement[a]	$\bar{X}$	*SE*	*n*	Minimum	Maximum	$\bar{X}$	*SE*	*n*	Minimum	Maximum
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
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 variable abbreviations are found in Table 1.

percent differences were <1% for all but 4 variables measured and were <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 3). Mean measurements for computer model lengths were greater than manual lengths, and mean differences ranged from 8.28 to 32.40 mm.

Overall, no consistent patterns in correlations among asymmetry measures emerged (Table 4), and correlation coefficients were generally weak, where $r \leq 0.33$. We found no consistent correlations between asymmetry measures and variables used to estimate trait size, that is, 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.

No age affect ($P \geq 0.153$) on any measures of asymmetry (Table 5) was apparent, and also no consistent directional trends in mean measures of asymmetry among ages (Table 6) or antler score classes (Table 7) were found. Between the 3 score classes only 2 asymmetry variables (labsymbv and labsymsc) were different (Table 5). 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.

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 (Kodric-Brown and Brown 1984; Zahavi 1975). 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

TABLE 3.—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 variable abbreviations are found in Table 1.

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Table 4.—Correlation matrix of relationships between measures of fluctuating asymmetry of antler traits, trait size, and age.[a]

	labsymg2h	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												
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	0.247										
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									
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							

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TABLE 4.—Continued.

	labsymg2h	labsymg2v	labsymg1h	labsymg1v	labsymbh	labsymbv	labsymg2a	labsymc1	labsymsc	labsymmb	lg1symm	lg2symm	avc1	avscore	avmb
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						
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			
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 variable abbreviations are found in Table 1.

Table 5.—Results from ANOVA comparing degree of fluctuating asymmetry in selected traits of white-tailed deer antlers among age and score classes.

	Age class			Score class		
Variable[a]	*F*	*P*	*d.f.*	*F*	*P*	*d.f.*
labsymg1h	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 variable abbreviations are found in Table 1.

linear measurements of antler traits. Specific trends exist 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, no consistent relationship between antler asymmetry measures and trait size was apparent. Secondary sexual characters, like antlers, are costly to produce, and the relative cost to produce equal-sized traits is greater for low-quality individuals (Grafen 1990; Zahavi 1977). Thus, only high-quality individuals are expected to produce large antlers, and because fluctuating asymmetry is an indirect measurement of individual quality (Møller 1998), these high-quality individuals are expected to produce symmetrical traits. We also found 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. We found no evidence that 3-dimensional asymmetry of antlers as measured in this study 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. Although many previous studies have found positive relationships between fluctuating asymmetry and antler size (Bowyer et al. 2001; Ditchkoff et al. 2001b; Putman and Sullivan 2000), other studies have failed to find this hypothesized relationship. Kruuk et al. (2003) found no

Table 6.—Absolute asymmetry of selected antler traits among 4 age classes (1.5, 2.5, 3.5, and ≥4.5 years of age).

	1.5 years			2.5 years			3.5 years			≥4.5 years		
Variable[a]	$\bar{X}$	*SE*	*n*	$\bar{X}$	*SE*	*n*	$\bar{X}$	*SE*	*n*	$\bar{X}$	*SE*	*n*
absymg1h	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
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	1,058.380	114.285	8	1,329.560	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 variable abbreviations are found in Table 1.

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TABLE 7.—Absolute asymmetry measures of selected antler traits of white-tailed deer among 3 antler score classes (low, medium, and high).

	Low			Medium			High		
Variable[a]	$\bar{X}$	*SE*	*n*	$\bar{X}$	*SE*	*n*	$\bar{X}$	*SE*	*n*
absymg1h	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 variable abbreviations are found in Table 1.

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 1 of the expected patterns of fluctuating asymmetry as an indicator of quality.

Manual measures of asymmetry were not correlated consistently 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 makes it difficult to draw conclusions about the efficacy of our measurements at quantifying visual asymmetry. Our measures of visual asymmetry may document different components of spatial asymmetry than the linear asymmetry measures. Additionally, it is possible that our measures did not address 3-dimensional asymmetry adequately, 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 3-dimensional fluctuating asymmetry can be used to assess individual quality reliably, as has been predicted for traditional measures of fluctuating asymmetry.

Asymmetry measures of the different antler components were not correlated consistently with each other using either measurement method. This is contrary to expected findings, because fluctuating asymmetry researchers have predicted 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; Palmer and Strobeck 2003; Whitlock 1996); 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 can 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 <1 mm (ranging from 0.11 mm to 1.74 mm); these values are generally below 1% difference between replicates. Therefore, we applied no correction for measurement error in this study. These are similar or lower than levels of measurement error that have been found acceptable in other studies of fluctuating asymmetry of antlers (Bartoš and Bahbouh 2006; Ditchkoff et al. 2001b; Kruuk et al. 2003).

Differences between the manually measured and computer-measured tine lengths can be explained by the disparity in measurement landmarks for the 2 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 one-half the width of the main beam. 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, but manual measurements followed the outside curve of tines. The purpose of comparing corresponding measurements from the 2 techniques was to determine if measurements were similar and differed by approximately one-half the width of the main beam. Measurements differed by approximately 10–20 mm, which is consistent with one-half the width of the main beam. Therefore, computer models were scaled and representative of actual size and proportion of antler sets.

Antler sets that were very simple, such as spikes or forked antlers, were unable to be modeled using PhotoModeler because not enough data points for the computer program were available 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, to provide enough data to model, simpler traits, such as horns, could be marked with numerous landmark points, more than necessary to depict the shape of a trait.

Although analysis of 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

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measures of asymmetry is warranted as this type of visual asymmetry is likely to be assessed by potential mates or rivals. Several authors (Jennions and Møller 2003; Palmer 1999, 2000) have suggested that bias exists 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. 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 scans, and magnetic resonance imaging have been used to measure asymmetry, although these methods are very costly and generally not applicable for fieldwork.

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Literature Cited

Andersson, M. 1982. Female choice selects for extreme tail length in a widowbird. Nature 299:818–820.

Bartoš, L., and R. Bahbouh. 2006. Antler size and fluctuating asymmetry in red deer (*Cervus elaphus*) stags and probability of becoming a harem holder in rut. Biological Journal of the Linnean Society 87:59–68.

Berglund, A., A. Bisazza, and A. Pilastro. 1996. Armaments and ornaments: an evolutionary explanation of traits of dual utility. Biological Journal of the Linnean Society 58:385–399.

Bowyer, R. T. 1986. Antler characteristics as related to social status of male southern mule deer. Southwestern Naturalist 31:289–298.

Bowyer, R. T., K. M. Stewart, J. G. Kie, and W. C. Gasaway. 2001. Fluctuating asymmetry in antlers of Alaskan moose: size matters. Journal of Mammalogy 82:814–824.

Clutton-Brock, T. H. 1982. The functions of antlers. Behaviour 79:108–125.

David, P., T. A. Bjorksten, K. Fowler, and A. Pomiankowski. 2000. Condition-dependent signalling of genetic variation in stalk-eyed flies. Nature 406:186–188.

Ditchkoff, S. S., R. L. Lochmiller, R. E. Masters, S. R. Hoofer, and R. A. Van Den bussche. 2001a. Major-histocompatibility-complex–associated variation in secondary sexual traits of white-tailed deer (*Odocoileus virginianus*): evidence for good-genes advertisement. Evolution 55:616–625.

Ditchkoff, S. S., R. L. Lochmiller, R. E. Masters, W. R. Starry, and D. M. Leslie, Jr. 2001b. Does fluctuating asymmetry of antlers in white-tailed deer (*Odocoileus virginianus*) follow patterns predicted for sexually selected traits? Proceedings of the Royal Society of London, B. Biological Sciences 268:891–898.

Folstad, I., P. Arneberg, and A. J. Karter. 1996. Antlers and parasites. Oecologia 105:556–558.

Goss, R. J. 1983. Deer antlers: regeneration, function, and evolution. Academic Press, New York.

Grafen, A. 1990. Biological signals as handicaps. Journal of Theoretical Biology 144:517–546.

Houle, D. 1998. High enthusiasm and low R-squared. Evolution 52:1872–1876.

Jennions, M. D., and A. P. Møller. 2003. A survey of the statistical power of research in behavioral ecology and animal behavior. Behavioral Ecology 14:438–445.

Kodric-Brown, A., and J. H. Brown. 1984. Truth in advertising: the kinds of traits favored by sexual selection. American Naturalist 124:309–323.

Kruuk, L. E. B., J. Slate, J. M. Pemberton, S. Brotherstone, F. Guinness, and T. Clutton-Brock. 2002. Antler size in red deer: heritability and selection but no evolution. Evolution 56:1683–1695.

Kruuk, L. E. B., J. Slate, J. M. Pemberton, and T. H. Clutton-Brock. 2003. Fluctuating asymmetry in a secondary sexual trait: no associations with individual fitness, environmental stress or inbreeding, and no heritability. Journal of Evolutionary Biology 16:101–113.

Lagesen, K., and I. Folstad. 1998. Antler asymmetry and immunity in reindeer. Behavioral Ecology and Sociobiology 44:135–142.

Leamy, L. J. 1993. Morphological integration of fluctuating asymmetry in the mouse mandible. Genetica 89:139–153.

Lincoln, G. A. 1972. The role of antlers in the behaviour of red deer. Journal of Experimental Zoology 182:233–250.

Lincoln, G. A. 1992. Biology of antlers. Journal of Zoology (London) 226:517–528.

López, P., A. Muñoz, and J. Martín. 2002. Symmetry, male dominance and female mate preferences in the Iberian rock lizard, *Lacerta monticola*. Behavioral Ecology and Sociobiology 52:342–347.

Malo, A. F., E. R. S. Roldan, J. Garde, A. J. Soler, and M. Gomendio. 2005. Antlers honestly advertise sperm production and quality. Proceedings of the Royal Society of London, B. Biological Sciences 272:149–157.

Mateos, C., S. Alarcos, J. Carranza, C. B. Sánchez-Prieto, and J. Valencia. 2008. Fluctuating asymmetry of red deer antlers negatively relates to individual condition and proximity to prime age. Animal Behaviour 75:1629–1640.

Mateos, C., and J. Carranza. 1997. Signals in intra-sexual competition between ring-necked pheasant males. Animal Behaviour 53:471–485.

Møller, A. P. 1988. Female choice selects for male sexual tail ornaments in the monogamous swallow. Nature 332:640–642.

Møller, A. P. 1991. Viability is positively related to degree of ornamentation in male swallows. Proceedings of the Royal Society of London, B. Biological Sciences 243:145–148.

Møller, A. P. 1992. Patterns of fluctuating asymmetry in weapons: evidence for reliable signalling of quality in beetle horns and bird spurs. Proceedings of the Royal Society of London, B. Biological Sciences 248:199–206.

Møller, A. P. 1996. Parasitism and developmental instability of hosts: a review. Oikos 77:189–196.

Møller, A. P. 1998. Developmental instability as a general measure of stress. Pp. 181–213 in Stress and behavior. Advances in the study of behavior 27 (A. P. Møller, M. Milinski, and P. J. B. Slater, eds.). Academic Press, San Diego, California.

Møller, A. P., and A. Pomiankowski. 1993. Fluctuating asymmetry and sexual selection. Genetica 89:267–279.

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NESBITT, W. H., AND J. RENEAU. 1988. Records of North American big game. Boone and Crockett Club, Dumfries, Virginia.

PALMER, A. R. 1996. Waltzing with asymmetry. BioScience 46:518–532.

PALMER, A. R. 1999. Detecting publication bias in meta-analysis: a case study of fluctuating asymmetry and sexual selection. American Naturalist 154:220–233.

PALMER, A. R. 2000. Quasireplication and the contract of error: lessons from sex ratios, heritabilities and fluctuating asymmetry. Annual Review of Ecology and Systematics 31:441–480.

PALMER, A. R., AND C. STROBECK. 2003. Fluctuating asymmetry analyses revisited. Pp. 279–319 in Developmental instability (DI): causes and consequences (M. Polak, ed.). Oxford University Press, Oxford, United Kingdom.

PARSONS, P. A. 1992. Fluctuating asymmetry: a biological monitor of environmental and genomic stress. Heredity 68:361–364.

PÄRT, T., AND A. QVARNSTRÖM. 1997. Badge size in collared flycatchers predicts outcome of male competition over territories. Animal Behaviour 54:893–899.

POLAK, M. 1993. Parasites increase fluctuating asymmetry of male *Drosophila nigrospiracula*: implications for sexual selection. Genetica 89:255–265.

POLAK, M. 2008. The developmental instability-sexual selection hypothesis: a general evaluation and case study. Evolutionary Biology 35:208–230.

POLAK, M., AND R. TRIVERS. 1994. The science of symmetry in biology. Trends in Ecology & Evolution 9:123–125.

PUTMAN, R. J., AND M. S. SULLIVAN. 2000. Fluctuating asymmetry in antlers of fallow deer (*Dama dama*): the relative roles of environmental stress and sexual selection. Biological Journal of the Linnean Society 70:27–36.

SCHLÜTER, A., J. PARZEFALL, AND I. SCHLUPP. 1998. Female preference for symmetrical vertical bars in male sailfin mollies. Animal Behaviour 56:147–153.

SEVERINGHAUS, C. W. 1949. Tooth development and wear as criteria of age in white-tailed deer. Journal of Wildlife Management 13:195–216.

SHERIDAN, L., AND A. POMIANKOWSKI. 1997. Female choice for spot asymmetry in the Trinidad guppy. Animal Behaviour 54:1523–1529.

SIMMONS, L. W., J. L. TOMKINS, J. S. KOTIAHO, AND J. HUNT. 1999. Fluctuating paradigm. Proceedings of the Royal Society of London, B. Biological Sciences 266:593–595.

SOLBERG, E. J., AND B.-E. SÆTHER. 1993. Fluctuating asymmetry in the antlers of moose (*Alces alces*): does it signal male quality? Proceedings of the Royal Society of London, B. Biological Sciences 254:251–255.

SAS INSTITUTE, INC. 1990. SAS/STAT user's guide. SAS Institute, Inc., Cary, North Carolina.

SWADDLE, J. P., AND M. S. WITTER. 1997. On the ontogeny of developmental stability in a stabilized trait. Proceedings of the Royal Society of London, B. Biological Sciences 264:329–334.

VELANDO, A., C. M. LESSELLS, AND J. C. MÁRQUEZ. 2001. The function of female and male ornaments in the Inca tern: evidence for links between ornament expression and both adult condition and reproductive performance. Journal of Avian Biology 32:311–318.

WATSON, P. J., AND R. THORNHILL. 1994. Fluctuating asymmetry and sexual selection. Trends in Ecology & Evolution 9:21–25.

WHITLOCK, M. 1996. The heritability of fluctuating asymmetry and the genetic control of developmental stability. Proceedings of the Royal Society of London, B. Biological Sciences 263:849–854.

ZAHAVI, A. 1975. Mate selection—a selection for a handicap. Journal of Theoretical Biology 53:205–214.

ZAHAVI, A. 1977. The cost of honesty. Journal of Theoretical Biology 67:603–605.

ZAR, J. H. 1984. Biostatistical analysis. 2nd ed. Prentice Hall, Englewood Cliffs, New Jersey.

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