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FLUCTUATING ASYMMETRY IN ANTLERS OF ALASKAN MOOSE: SIZE MATTERS

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We studied characteristics of paired antlers, including types of asymmetry, from 1,501 Alaskan moose (*Alces alces gigas*). We observed no evidence of antisymmetry in moose antlers, but number of tines was greater on left than right antlers, indicating directional asymmetry. Absolute and relative fluctuating asymmetry (FA) occurred for palm characteristics but not for beam circumference. Relative FA varied inversely with the overall size of antlers for attributes of the palm, which was expected for a secondary sexual characteristic. Smaller-antlered males exhibited greater FA than did larger-antlered moose in palm characteristics. Because large-antlered males, which mate most often among moose and other polygynous cervids, expressed the least relative FA, we hypothesize that this metric indicates quality of individual moose. Whether symmetry of antlers is related to antler breakage or honest advertisement or whether females select mates based on FA is unknown and deserves additional study.

Key words: Alaskan moose, *Alces alces gigas*, antisymmetry, antler size, directional asymmetry, fluctuating asymmetry, honest advertisement, individual quality, mate selection, secondary sexual characteristics

Fluctuating asymmetry (FA) is characterized by random deviations from perfect bilateral symmetry (Van Valen 1962) and has been used widely to measure developmental stability of morphologic characteristics among insects, fishes, amphibians, reptiles, birds, and mammals (Clarke 1998; Cuthill et al. 1993; Møller 1997; Palmer and Strobeck 1986; Parsons 1990; and many others). Organisms that are better buffered against environmental or genetic stresses (such as inbreeding) are thought to exhibit less FA during development of particular morphologic structures; consequently, FA has been proposed as a measure of phenotypic quality for individuals (Emlen et al. 1993; Gangestad and Thornhill 1999; Watson and Thornhill 1994). Absolute FA (i.e., right minus left) in a bilateral structure is characterized by a normal distribution with a mean of zero. Animals also may exhibit directional asymmetry where the size development of a character is more pronounced on 1 side than the other (i.e., $\bar{X} \neq 0$, or a skewed distribution). Antisymmetry is reflected in a bimodal or platykurtotic distribution for a morphologic structure (Van Dongen et al. 1999).

Fluctuating asymmetry has been studied widely in ungulates, in part because of their elaborate hornlike structures (Geist 1966; Goss 1983; Lincoln 1992, 1994), which provide ideal characteristics for evaluating departures from bilateral symmetry. Indeed,

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FA has been investigated for many large herbivores, including bovids (Alados et al. 1995; Arcese 1994; Côté and Festa-Bianchet 2001; Møller et al. 1996), antilocaprids (Min 1997), and cervids (Baccus and Welch 1983; Ditchkoff et al. 2001; Folstad et al. 1996; Goss 1980; Malyon and Healy 1994; Markusson and Folstad 1997; Pélabon and Van Breukelen 1998; Scribner and Smith 1990), but there has not been unanimity as to whether FA occurred or was related to individual quality (Solberg and Sæther 1993). Antlers of male cervids provide prototypical traits for studying FA; these structures are cast and regrown each year, vary with age and size of the animal that possesses them, and are correlated with social rank and reproductive success of males (Bowyer 1986; Chapman 1975; Clutton-Brock et al. 1982; McCullough 1969, 1982; Van Ballenberghe and Miquelle 1993, 1996). Moreover, antlers are a secondary sexual characteristic, and, in consequence, an inverse relation is expected between size of these bony structures and FA as well as a leptokurtotic distribution for relative FA (Gangestad and Thornhill 1999; Thornhill and Møller 1998; Watson and Thornhill 1994).

Moose (*Alces alces*) possess exceptionally large and elaborate antlers (Bubenik 1990; Gasaway et al. 1987; Sæther and Haagenrud 1985; Van Ballenberghe 1983) that are costly to produce (Brown 1990; Solberg and Sæther 1994; Stewart et al. 2000). Moreover, males of various ages invest differentially in development of antlers (Stewart et al. 2000). Males with larger antlers mate more often than smaller-antlered males (Van Ballenberghe and Miquelle 1993, 1996). Thus, we hypothesized that antlers of Alaskan moose (*A. a. gigas*) would exhibit FA and that FA would vary inversely with antler size within and across age classes of males. We also hypothesized that if antlers were involved in sexual selection, particular attributes of antlers used in fighting or display, such as palms or tines, should exhibit FA, whereas others characters might not do so.

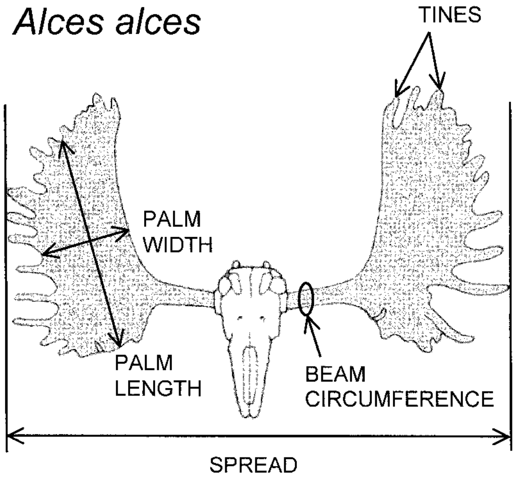

FIG. 1.—Antler characteristics of Alaskan moose (*Alces alces gigas*) measured in our analyses of fluctuating asymmetry (FA). Measurements originally were collected by Gasaway et al. (1987). This figure was modified from Nesbitt and Wright (1981).

MATERIALS AND METHODS

Antlers were obtained originally from 1968 to 1983 across 6 regions that spanned much of the distribution of moose in Alaska; locations sampled were provided by Gasaway et al. (1987). Our retrospective analyses are based on a subset of those data ($n = 1{,}501$ moose) for which both a complete set of antler measurements and age were available. Antler characters included right and left palm width, palm length, beam circumference, number of tines (including abnormal tines), and total spread (Fig. 1). Measurements of antlers were made primarily by employees of the Alaska Department of Fish and Game, who were experienced in recording those data (Gasaway et al. 1987). Data were gathered in accordance with specifications from the Boone and Crockett Club scoring system for moose; palm length was measured parallel to the inside edge of the antler, and palm width was oriented perpendicular to the line describing palm length (Gasaway et al. 1987; Nesbitt and Wright 1981; Fig. 1). Ages of moose were estimated from cementum-line counts of teeth (Gasaway et al. 1978, 1987; Sergeant and Pimlott 1959). Although we present data on age of moose in whole years, many animals used in our analyses were legally killed by hunters in autumn and, consequently, were 4–7 months older than indicated.

We describe antler growth among moose for each age class with multiple regression analyses weighted by sample size (Neter et al. 1985). We obtained the regression of principal component 1 (PC1), which represented antler size against age, from Stewart et al. (2000). PC1 explained 73% of the variation in antler measurements (Fig. 1), and the eigenvector associated with PC1 exhibited similar loadings across antler characters (0.30–0.35), indicating that PC1 provided a reliable index to antler size (Stewart et al. 2000). A curvilinear pattern was expected for each of the antler traits measured because antler size declines in senescent males (Stewart et al. 2000); senescence is common for other life-history characteristics of ungulates (Bérubé et al. 1999; Loison et al. 1999).

Types of asymmetry were assessed by the difference between right and left antlers for an individual moose for each antler character. We determined means, standard errors (*SE*), and coefficients of variation (*CV*) for absolute asymmetry (large minus small) and relative asymmetry (large minus small, divided by large) of antler characteristics. We compared degree of asymmetry among antler characters measured because measurement error had the potential to underestimate FA or be mistaken for FA where none exists. Neither measurement error nor an underestimate of FA would be expected in counts of tines; thus, we compared amounts of asymmetry among antler characters (palm width, palm length, beam circumference) with number of tines using a z-test (Remington and Schork 1970). A Bonferroni correction (Rice 1989) was used because we made multiple comparisons among antler measurements. Likewise, number of tines exhibited a sufficiently large range (>5) that any bias in assessing FA from a meristic character was unlikely (Swain 1987).

We examined distributions for each antler character (Zar 1999) for assumptions related to asymmetry to determine whether those distributions were normal, bimodal, or platykurtotic; bimodal or platykurtotic distributions indicate antisymmetry. To determine directional asymmetry, we used a signed-rank test to assess whether right or left characters were significantly larger or more numerous (Zar 1999).

We investigated the relationship between spread and relative FA of each antler character with Spearman rank correlations (r_s) to test whether FA was related inversely to size. We also tested distributions of antler traits exhibiting relative FA for leptokurtosis (Gangestad and Thornhill 1999)—values >0 indicated that leptokurtosis occurred (Zar 1999). We further compared relative FA in small and large antlers to test whether developmental stability was greater among large-antlered males. We investigated those differences in antler size within age classes of moose by comparing animals with small ($\leq$33rd percentile) and large ($\geq$67th percentile) antlers from each age class. That analysis, which combined males from across age classes, eliminated effects of age on antler size. We used analysis of variance (ANOVA) following multivariate analysis of variance (MANOVA) to test for differences in relative asymmetry of antler characters among small- and large-antlered moose. We met statistical assumptions for those analyses (Neter et al. 1985).

RESULTS

Antlers developed rapidly in Alaskan moose from 1 to 6 years of age, reached a plateau in prime-aged males (7–11 years old), and then regressed in size slightly in senescent individuals (12–17 years old). Weighted regression analyses of antler characteristics on age revealed that this pattern held with respect to an index, PC1, of overall size of antlers as well as antler spread, palm width and length, number of antler tines, and beam circumference (Fig. 2).

We assessed each antler characteristic separately for assumptions related to types of asymmetry. No antler characteristic exhibited a bimodal or platykurtotic distribution indicative of antisymmetry. Indeed, all characteristics had means (e.g., right minus left antlers; Table 1) that were not different from zero, but number of antler tines was marginally not significant. The signed-rank test indicated that neither left nor right antler was significantly larger than the other for palm characteristics or beam circumference (Table 1). Tines, however, were more numerous on left than on right antlers (Ta-

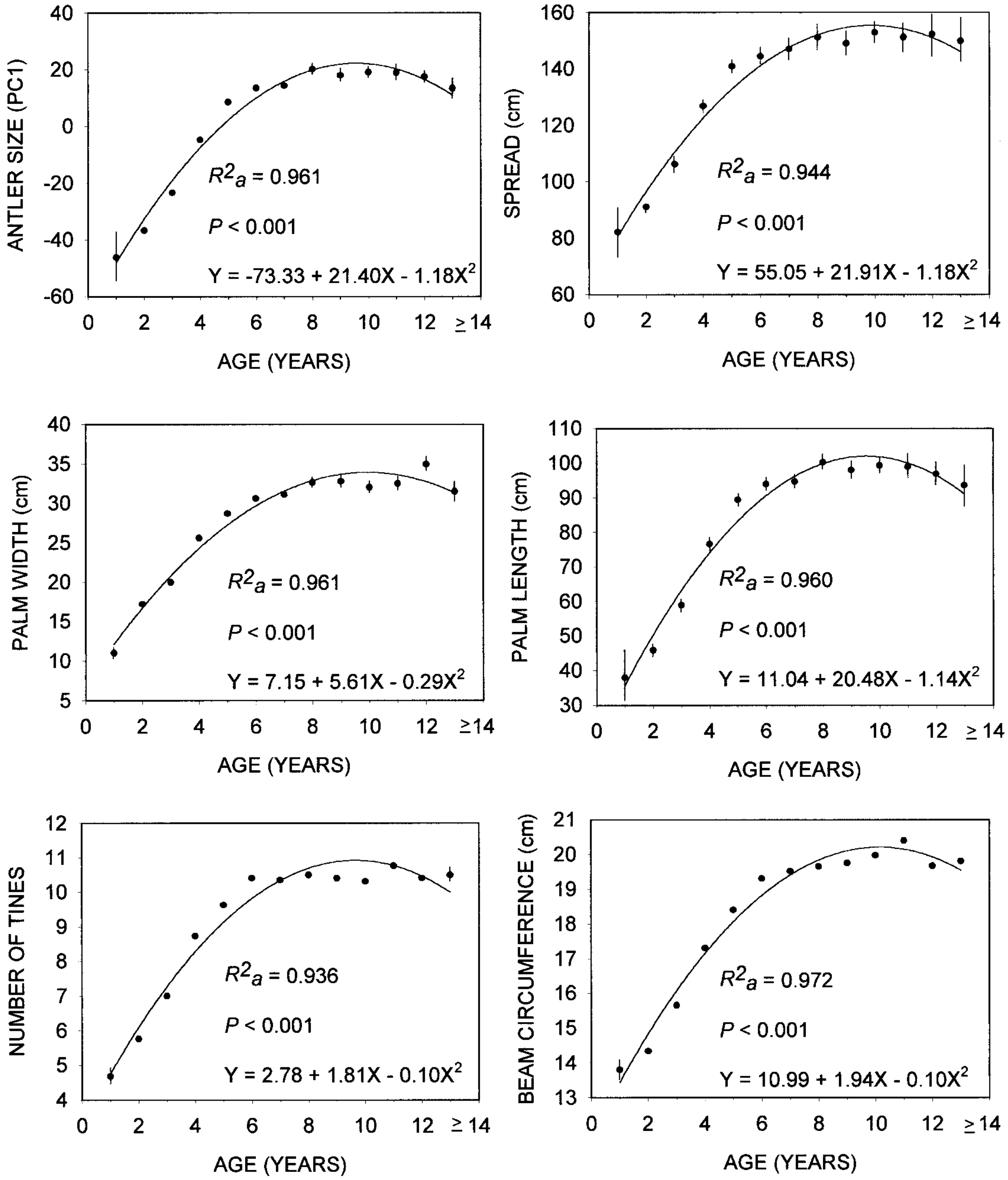

FIG. 2.—Weighted regression analyses of antler characteristics of Alaskan moose (*Alces alces gigas*) against age. Vertical lines are *SE* and, where not visible, are encompassed by data points. Sample sizes for age classes: 1 year, $n = 3$; 2 years, 157; 3 years, 188; 4 years, 283; 5 years, 267; 6 years, 197; 7 years, 136; 8 years, 74; 9 years, 63; 10 years, 51; 11 years, 33; 12 years, 22; 13 years, 16; ≥14 years, 11.

TABLE 1.—Summary statistics for asymmetry (right minus left) of antler characteristics for 1,501 Alaskan moose (*Alces alces gigas*). Data were obtained form Gasaway et al. (1987).

Antler characteristics	Asymmetry $\bar{X}$	Asymmetry *SD*	Asymmetry Range	*P*-value, $\bar{X} = 0$	*P*-value, signed rank[a]
Palm width (cm)	−0.11	3.816	−25.40–18.29	0.26	0.14
Palm length (cm)	0.14	8.280	−40.64–36.83	0.51	0.38
Beam circumference (cm)	−0.02	0.991	−10.16–7.62	0.43	0.77
Number of tines	−0.09	1.930	−11.00–8.00	0.07	0.039

[a] Wilcoxon signed-rank test for differences between right and left.

ble 1). Significantly more left than right tines indicated directional asymmetry in that attribute. Remaining characteristics of moose antlers met assumptions required for tests of FA.

Measurement error can cause an underestimation of FA (i.e., small differences in bilateral symmetry go undetected). Nonetheless, percentage of moose exhibiting asymmetry (differences in structural characteristics between right and left antlers) was great among the 1,501 pairs of moose antlers we sampled: palm length (92%), palm width (86.9%), number of tines (75.3%), and beam circumference (56.5%). Little or no measurement error would be expected in counts of tines, yet asymmetry of all other antler characteristics, except beam circumference, was significantly greater than for tines (*z*-test for proportions, $P < 0.05$ for all comparisons with tines, following Bonferroni correction).

Absolute measurements of asymmetry were most pronounced for palms compared with other measurements of antlers (Table 2). Such measurements, however, may be affected by the overall size of antlers—larger antlers have the potential to be absolutely more asymmetric than smaller ones. When we controlled for the individual size of a particular attribute of an antler (i.e., large minus small, divided by large), relative asymmetry was most prominent for tines and palm characteristics (Table 2). *CV* for absolute and relative asymmetry was high (87–150%) for all antler characters (Table 2).

Antler spread provided the best single index to size of moose antlers. With spread withheld from principal components analysis, we obtained a positive relation between spread and PC1 ($r^2 = 0.74$, $n = 1{,}501$, $P < 0.0001$), which provided a reliable index to overall size of antlers (92% variation explained by PC1 without antler spread). Consequently, we used spread to test whether relative FA was related inversely to overall size, an expectation for a secondary sexual characteristic such as antlers. Spearman rank correlations indicated significant inverse relations between spread and relative FA in palm width ($r_s = -0.10$,

TABLE 2.—Absolute (large minus small) and relative (large minus small, divided by large) asymmetry for antler characters from 1,501 Alaskan moose (*Alces alces gigas*). Data for antler characters were obtained from Gasaway et al. (1987).

Antler character	Absolute $\bar{X}$	Absolute *SE*	Absolute *CV* (%)	Relative $\bar{X}$[a]	Relative *SE*	Relative *CV* (%)
Palm width (cm)	2.75	0.068	96.03	0.10	0.002	86.77
Palm length (cm)	5.90	0.150	98.28	0.07	0.002	100.29
Beam circumference (cm)	0.55	0.021	150.46	0.03	0.001	136.70
Number of tines	1.42	0.034	93.03	0.19	0.005	105.18

[a] Values range from 0 to 1.

$n = 1{,}501$, $P = 0.0001$), spread and relative FA in palm length ($r_s = -0.16$, $n = 1{,}501$, $P = 0.0001$) but not spread and relative FA in beam circumference ($r_s = -0.01$, $n = 1{,}501$, $P = 0.57$). Number of antler tines was not considered in those tests because criteria for FA were not met in previous analyses. Inverse correlations indicated that relative FA in palm characteristics declined with an increase in absolute size of antlers (i.e., across all age classes of moose) and supported the hypothesis that developmental stability was more pronounced in large-antlered males. Likewise, all antler traits exhibited strong leptokurtosis: palm width (3.03), palm length (7.23), and beam circumference (18.19).

We also investigated whether negative correlations between antler size and relative FA would be maintained within age classes of moose. We subdivided each age class into individuals with small, medium, and large antlers. We retained only those individuals with small (≤33rd percentile for spread) and large (≥67th percentile for spread) antlers in our analysis. When we combined age classes, significant differences in relative FA occurred between small- and large-antlered males for palm length and width but not for beam circumference (Fig. 3). That palm characteristics exhibited greater FA for small antlers than for large ones (Fig. 3) also supported the hypothesis of greater developmental stability for large-antlered individuals, at least for attributes of the palm.

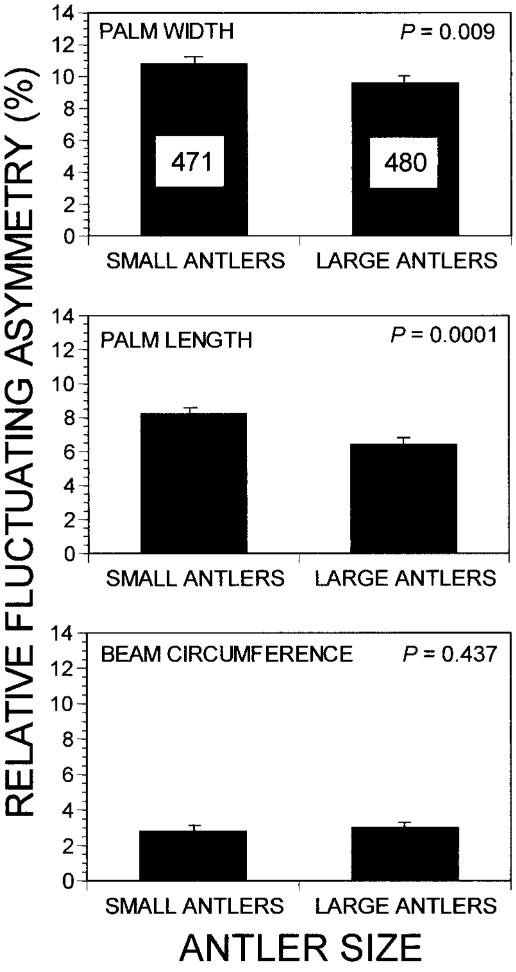

FIG. 3.—Mean (+*SE*) relative fluctuating asymmetry in antlers of Alaskan moose (*Alces alces gigas*) with small (≤33rd percentile) and large (≥67th percentile) antlers. The analysis combines males with the smallest and largest antlers from each age cohort. Sample sizes are shown for palm width within bars and are identical for other antler characteristics. *P*-values comparing small and large antlers are from ANOVA following significant ($P < 0.0001$) MANOVA.

DISCUSSION

Fluctuating asymmetry occurred in antlers of Alaskan moose (Table 2; Fig. 3), an outcome contrary to previous research on moose based only on counts of antler tines (Nygrén 2000; Solberg and Sæther 1993). Indeed, we observed variability in the occurrence of FA among the structural components of antlers, with palm characteristics exhibiting marked FA but beam circumferences lacking that attribute (Table 2). Length and width of palms likely offer structural support for tines that emerge from the forward, top, and bottom edges of moose antlers (Fig. 1), increase overall size and mass of antlers, and provide a shield against tines of opponents during male–male combat (Van Ballenberghe and Miquelle 1993, 1996). Large males also display their antlers prior to and during aggressive encounters (Van Ballenberghe and Miquelle 1993, 1996), and increased palm dimensions likely play a role in intimidating rivals during those interactions. Palm size also may play a role in courtship of females, especially if female choice is involved in selection of mates. Whatever the selective mechanisms, the largest-antlered males mate most often among moose and other polygynous cervids (Bowyer 1986; Clutton-Brock et al. 1982; Hirth 1977; Van Ballenberghe and Miquelle 1993, 1996; Weckerly 1998). This correlation between size and mating success makes antlers an ideal structure for studying FA.

Our results indicate that various structural components of antlers (Fig. 2) might have differential costs during development; FA was documented only for palm characteristics (Table 2; Fig. 3). Prime-aged moose (7–11 years old) invested proportionally more in antler development relative to their body mass than younger or senescent individuals (Stewart et al. 2000), and palms were most enlarged in those prime-aged males (Fig. 2). If the function of antlers is primarily male–male combat (Geist 1966; Lincoln 1992, 1994), perhaps palms could be enlarged substantially only after a sufficient beam circumference had been achieved to support palms and permit effective fighting. If so, costs of producing palms might be added to the expense of increasing beam circumferences and might explain why we observed FA in palm characteristics (where costs of developmental stability would be further increased) but not in beam circumferences. This interpretation does not rule out displaying of antlers by males for inter- or intrasexual purposes, but it does indicate that such displays reflect size and perhaps fighting ability and, thereby, quality of males.

We also documented directional asymmetry in number of tines for moose, which were more numerous on left than right antlers (Table 1). The adaptive significance of that pattern, however, is undetermined. Caribou and reindeer (*Rangifer tarandus*), likewise, have more enlarged brow tines (i.e., shovels) on left than right antlers (Davis 1973, 1974; Goss 1980). Surprisingly, that arrangement is not consistent across years for individuals, which may vary the side that produces the enlarged brow tine (Davis 1973, 1974; Goss 1980). Whether more tines on left than right antlers of individual moose remains consistent over time and, hence, constitutes true ‘‘handedness’’ is unknown and warrants further study.

Directional asymmetry also has been described in fallow deer (*Dama dama*), with right antlers exhibiting greater size and more elaborate development than left antlers; asymmetry was thought to relate to more intense use of right antlers in fighting (Alvarez 1995). The adaptive significance of having 1 antler larger than another, and why that morphologic anomaly would benefit individuals in aggressive encounters, however, is unresolved. Likewise, we cannot imagine that a small difference between number of left and right tines (Table 1) would provide notable benefits to individuals during male–male combat.

We observed a leptokurtotic distribution in relative FA and an inverse relation between antler size and relative FA. Such outcomes were expected for a secondary sexual characteristic, such as antlers (Gangestad and Thornhill 1999; Thornhill and Møller 1998; Watson and Thornhill 1994). Relative FA also occurred for palm characteristics across age classes of moose, where older animals typically have larger antlers (Fig. 2), as well as within age classes (Fig. 3). Cervids possess adult sex ratios strongly biased toward females (Berger and Gompper 1999; Bowyer 1991; Loison et al. 1999), ostensibly a result of strenuous rutting activities that predispose males to increased mortality during the following winter (Bowyer 1981; Miquelle 1990). Thus, older males with larger antlers that exhibit comparatively little FA probably represent high-quality individuals that have survived arduous environmental conditions and energetically costly and dangerous encounters with rivals for mating opportunities. Moreover, males with larger antlers showed greater relative symmetry than small-antlered individuals within age cohorts (Fig. 3). This outcome indicates that greater bilateral symmetry resulting from developmental stability during growth of antlers likely serves as an index to individual quality. Body mass and antler size are correlated positively in moose and other cervids (Bowyer 1986; McCullough 1982; Prieditis 1979; Stewart et al. 2000).

Antlers of moose may have been under artificial selection from hunting, and, hence, the sample of old males may be biased by differential mortality. Hunter effort and success in low-density populations of moose in Alaska, however, are low (Gasaway et al. 1992), and harvest is thought to have a limited effect on antler morphology in these populations (Hundertmark et al. 1998). Moreover, most natural mortality in Alaskan moose occurs prior to development of antlers (Bowyer et al. 1998; Keech et al. 2000). Although old moose likely represent a subset of males that have been subjected to selective pressures, hunting probably has not played a major role in structuring size or conformation of moose antlers in Alaska.

We cannot assess effects of measurement error directly in our retrospective analysis of FA in Alaskan moose because Gasaway et al. (1987) did not repeatedly sample the same antler. Nonetheless, several lines of reasoning indicate that our results are not biased markedly by measurement error and that they represent a biological pattern rather than a statistical artifact. First, differences were documented in counts of tines on left and right antlers, where measurement error likely was nil. Second, some antler characteristics exhibited FA (palm length and width), whereas others did not (beam circumference), indicating that measurement error was not the sole cause of asymmetry. Third, we observed absolute FA in palm characteristics that remained when we corrected for overall size of the antler (i.e., relative FA). Likewise, a constant measurement error across various sizes of antlers did not result in the inverse relation between relative FA and antler size because we failed to detect relative FA in beam circumference. Although we do not know the degree of measurement error in our samples, we do not believe that such error biased our interpretation of antler asymmetry.

To assess FA, we sampled an unusually large number of individuals ($n = 1,501$) compared with other studies on this controversial topic (Palmer 1999). Therefore, our analysis is not beset with the problem of weak size effects associated with reporting FA, as noted by Palmer (1999). Conversely, our large sample size may have revealed significant differences in relative FA with antler size because of size effects alone; our correlations were not strong ($r_s = -0.10$ to -0.16). Nonetheless, we believe that those correlations represent a biological phenomenon because we detected them for palm characters but not beam circumference ($r_s = -0.01$), and sample size was identical for both tests.

Bowyer (1983) reported that large-antlered elk (*Cervus elpahus*) were less prone to break antlers than small-antlered individuals, even though large males engaged in more serious fights (McCullough 1969) where antlers were more apt to be broken. Unfortunately, no measurements of FA were made in that study. If breakage and antler size also were associated in moose, the propensity to break antlers might be related to FA. We demonstrated that large-antlered moose exhibited greater symmetry than males with small antlers (Fig. 3). Consequently, we hypothesize that antler symmetry is related to antler strength and size and thereby to the ability to resist breakage. A male with a broken antler would be at a disadvantage in fierce fights over estrous females (Van Ballenberghe and Miquelle 1993, 1996). Antlers tend to break by developing microcracks in localized areas that ultimately accumulate and interact with the structure of antlers to cause a severe fracture (Currey 1989; Zioupos et al. 1994). How asymmetry, structure, size, and antler breakage are related is unknown. Nonetheless, developmental stability during antlerogensis might relate to a propensity for some antlers to resist breakage during combat; this hypothesis offers a selective advantage for FA that does not require female choice.

We hypothesize that FA serves as an index to quality of individual Alaskan moose. Whittle et al. (2000) suggested that scent marking by moose might constitute a form of honest advertisement (Zahavi 1975; Zahavi and Zahavi 1997), whereby males that become hypophagic during rut (Miquelle 1990) and produce odoriferous urine that is attractive to females (Miquelle 1991) are signaling their quality. Whether developmental stability resulting in symmetry of antlers in moose is a form of honest advertising has not been established. Similarly, whether females respond to FA of antlers in the selection of mates is unknown. Because the largest antlers are most symmetrical, females may use male size as a criterion to assess quality rather than small differences in symmetry of antlers.

We are uncertain whether FA in antlers of Alaskan moose is related to antler breakage, female choice, or some other factor. That males with large antlers mate most often provides compelling evidence that relative FA, which is related inversely to antler size, reflects quality. Clearly, size matters.

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