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FLUCTUATING ASYMMETRY AND TESTING ISOLATION OF MONTANA GRIZZLY BEAR POPULATIONS

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Abstract: Fluctuating asymmetry of adult skulls was used to test the genetic isolation of the Yellowstone grizzly bear population from its nearest neighbor. An overall summary statistic was used in addition to 16 other parameters. Tests found the males of the Yellowstone population to be more variable than those of the North Continental Divide Ecosystem. Evidence for precipitation effects is also included. This test tends to support the existing management hypothesis that the Yellowstone population is isolated.

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Although mammals are bilaterally symmetrical, differences in growth occur between the 2 sides of the body. Some of this asymmetry is normal or directional. A second type of asymmetry is non-functional and is called fluctuating asymmetry. This developmental "noise" has been observed to be greater in inbred populations (Soulé 1967, Leamy 1984, Wayne et al. 1986) than in populations with normal genetic diversity. It is also considered to be an indicator of environmental stress (Leamy 1984) and represents pressure put upon developmental homeostatic mechanisms by genetic limitations in interaction with the environment. Thus it can be hypothesized that high levels of fluctuating asymmetry may indicate genetic limitations on the ability to accommodate environmental variation. This would then indicate a management need to supplement or expand the population.

Grizzly bear (*Ursus arctos horribilis*) skulls were collected from both the Yellowstone and Northern Continental Divide ecosystems since 1967 and are held in the collections of the Montana Fish, Wildlife and Parks Department. This collection is a unique resource and data from its analysis may have a direct bearing upon the threatened Montana grizzly bear populations. Although the Yellowstone grizzly bear population is regarded as an isolated population, bears have been recently observed in the mountain ranges connecting to the Northern Continental area (Picton 1986). Therefore, this project was undertaken to provide information concerning the extent of the genetic isolation of the Yellowstone population by using fluctuating asymmetry.

METHODS

A total of 64 adult (≥5 years) skulls was measured. The year of death for these animals ranged from 1967 to 1984. Thirty-eight of the skulls were from the Yellowstone ecosystem and 36 were from the North Continental Divide ecosystem. Cementum ages were determined for all of these skulls. Accession information for all specimens is available in the collections of the Montana Fish, Wildlife and Parks Department in Bozeman, Montana.

The measurements taken were adapted from Wayne et al. (1986). Measurements of 16 different parameters were taken for each side of each skull with a micrometer caliper: ^{1}Upper incisor width = midline of the skull to the gum line on upper I^3. ^{2}Lower incisor width = midline of the skull to the gum line on lower I^3. ^{3}Upper midline to canine = midline of the skull to the proximal point on the socket of the upper canine. ^{4}Nasal width = a measurement of the width of the nasal bones from the midline of the skull to the suture in the anterior portion of the eye socket. ^{5}Maximal palatine width = midline of the skull to the distal suture of the palatine. ^{6}Width of the zygomatic arch = posterior end of the center line of palate to the apex of the lateral surface of the zygomatic arch. ^{7}Length of the upper diastema from tooth socket to socket. ^{8}Length of the lower (mandibular) diastema from tooth socket to socket. ^{9}Length of the upper cheek teeth = the length at gum line from the anterior end of upper molar 1 to the posterior end of upper molar 2 as measured on the distal side. ^{10}Length of the lower cheek teeth row = the length at gum line from the anterior end of lower molar 2 to the posterior end of lower molar 3 as measured on the proximal side. ^{11}Length of upper molar 1. ^{12}Length of upper molar 2. ^{13}Length of lower molar 2. ^{14}Length of lower molar 3. ^{15}Length of the mandibular condyle. ^{16}Maximum length of the jugal bone.

Since some skulls had been damaged, it was not always possible to obtain a full set of measurements. This factor is reflected in the *n* values in Table 1. The possible effect of a size scaling in which large skulls might have a proportionately larger asymmetry than small skulls was assessed by correlation, regression and examination of data plots.

The variances of the data were compared following

Table 1. Asymmetry measurements of 64 adult grizzly bear skulls from the Yellowstone and North Continental Divide grizzly bear ecosystems.

Area[a]	Sex	Number	Difference (Right-Left) Mean (mm)	SD	P (F-test)[b] Area vs Area	F vs M
Overall Summary Asymmetry Value						
Y	F	19	0.035	0.018	0.278	
	M	14	0.044	0.029	0.011*	0.026*
NC	F	18	0.037	0.016		
	M	18	0.034	0.017		0.395
1. Upper Incisor Width						
Y	F	15	-0.307	0.616	0.1379	
	M	10	-0.023	0.767	0.3341	0.2144
NC	F	16	0.045	0.820		
	M	16	-0.070	0.882		0.3873
2. Lower Incisor Width						
Y	F	13	-0.200	0.588	0.4180	
	M	8	-0.095	0.373	0.1369	0.1005
NC	F	13	-0.065	0.553		
	M	15	-0.090	0.548		0.4779
3. Upper Midline to Canine						
Y	F	16	-0.116	0.980	0.4653	
	M	11	-0.303	0.526	0.3431	0.0209*
NC	F	18	-0.092	1.003		
	M	18	-0.285	0.597		0.0164*
4. Width of Nasals						
Y	F	14	0.370	0.703	0.2100	
	M	12	-0.521	0.700	0.2373	0.4992
NC	F	18	0.011	0.871		
	M	19	0.003	0.858		0.4722
5. Width of Palatine						
Y	F	14	0.340	1.016	0.1837	
	M	11	-0.335	1.261	0.1345	0.2209
NC	F	16	0.768	1.295		
	M	18	0.610	0.958		0.0999
6. Width of Zygomatic Arch						
Y	F	13	1.686	1.561	0.3164	
	M	10	0.051	0.063	0.0001**	0.2393
NC	F	16	1.337	1.785		
	M	16	1.934	4.403		0.0004**
7. Length of Upper Diastema						
Y	F	16	-0.270	1.926	0.0099**	
	M	10	0.516	1.304	0.3087	0.1066
NC	F	18	-0.119	1.120		
	M	18	0.253	1.530		0.0729
8. Length of Mandibular Diastema						
Y	F	15	-0.149	1.195	0.4565	
	M	9	-0.754	1.701	0.2053	0.1088
NC	F	16	0.338	1.231		
	M	19	-0.524	1.372		0.3335
9. Length of Upper Molar Row						
Y	F	16	-0.221	1.121	0.0940	
	M	11	-1.083	4.538	0.0001**	0.0001**
NC	F	18	-0.298	0.812		
	M	17	-0.662	0.919		0.3030
10. Length of Lower Molar Row						
Y	F	15	-0.200	0.842	0.2609	
	M	8	-0.133	1.273	0.0605	0.0798
NC	F	16	-0.114	0.715		
	M	14	0.143	0.798		0.3334
11. Length of Upper Molar 2						
Y	F	16	-0.133	0.834	0.4962	
	M	11	0.125	0.930	0.0062**	0.3357
NC	F	17	-0.302	0.833		
	M	18	-0.501	0.479		0.0124*
12. Length of Upper Molar 1						
Y	F	16	0.005	0.536	0.4574	
	M	11	-2.021	5.393	0.0001**	0.0001**
NC	F	18	0.169	0.523		
	M	17	-0.264	0.481		0.3655
13. Length of Lower Molar 3						
Y	F	16	0.006	0.784	0.2182	
	M	11	0.356	0.590	0.3414	0.1703
NC	F	17	0.403	0.646		
	M	18	0.010	0.253		0.2140
14. Length of Lower Molar 2						
Y	F	16	0.029	0.683	0.4541	
	M	11	-0.162	0.809	0.1692	0.2604
NC	F	18	0.495	0.704		
	M	18	0.384	0.632		0.3250
15. Length of Mandibular Condyle						
Y	F	15	0.322	0.891	0.0920	
	M	11	-0.060	1.286	0.0484*	0.0930
NC	F	16	0.700	1.263		
	M	18	0.246	0.831		0.0449*
16. Length of Jugal						
Y	F	13	0.811	1.814	0.1141	
	M	11	1.750	3.205	0.0014**	0.0273*
NC	F	17	0.218	2.530		
	M	16	0.718	3.205		0.0104*

[a] Y = Yellowstone ecosystem; NC = North Continental Divide ecosystem.

[b] *statistically significant, $P < 0.05$ **highly significant, $P < 0.01$

procedures previously used on carnivores (Wayne et al. 1986) and the recommendations of Palmer and Strobeck (1986). Since sample sizes were relatively small, the probability of detection of true differences is <75% (Snedecor and Cochran 1980). This is not unique to studies of fluctuating asymmetry but a simple reflection of sample sizes. The number of skulls measured in this study is greater than the sample sizes used in the felid study of Wayne et al. (1986). STATA (1988) was used for the data analysis.

Following Wayne et al. (1986), a single overall summary assessment of asymmetry was calculated for each adult skull. The non-signed asymmetry values for each skull were summed and divided by the number of measurements for that skull. This provided an asymmetry mean over all measurements for each skull. This value was then tested for differences. Pearson's correlation coefficient was used to test the factors for independence (Wayne et al. 1986) because highly correlated factors would indicate that they separately would not be good measures of fluctuating asymmetry.

Precipitation data were obtained from Climatological Data - Wyoming, for the Yellowstone National Park (Mammoth) weather station.

RESULTS

The assessment of size effects upon asymmetry indicated minimal effects. The highest Pearson's correlation coefficient obtained in comparisons of asymmetry in adult skulls, size and age was $r = 0.43$. Six size-asymmetry regressions of the 16 characters had significant F values ($P < 0.05$) but had very poor explanatory powers with a maximum $R^2 < 0.19$. Examination of data plots indicated that these occasional results were based upon the effects of 1 to 2 extreme values. It was concluded that size scaling was not an important factor in the asymmetries considered in this study of adults.

F-test comparisons of the overall summary asymmetry data found significant differences between the total Yellowstone and North Continental skulls ($P < 0.0017$) with the Yellowstone area showing the greatest variability. Additional tests suggest that this was due to greater variability in Yellowstone males ($P < 0.0114$) (Table 1). No significant differences were found between the females of the 2 areas or between the males and females of the North Continental area. The overall asymmetry values for Yellowstone females differed from Yellowstone males ($P < 0.0257$) with the males showing the greatest variability.

Three of the 16 overall F-test comparisons ($P < 0.01$) indicated differences between skulls from the 2 areas. When females from the North Continental area were compared with those from Yellowstone, 1 test result ($P < 0.01$) suggested differences. When male data from the 2 areas were compared, 6 of 16 tests ($P < 0.05$) indicated differences. The Yellowstone specimens showed the greatest variability.

Sex differences (Table 1) were apparent in the data from both areas. In the North Continental area, 5 tests ($P < 0.05$) indicated differences between sexes with the female having the most variable asymmetry. Four tests of the Yellowstone specimens ($P < 0.05$) indicated that the males showed the greatest variability.

Because both stress and inbreeding (Leamy 1984, Palmer and Strobeck 1986) are believed to produce asymmetry, the data from the Yellowstone specimens were tested for the effect of precipitation-related stress incurred their birth year. In 7 Yellowstone females, a significant weighted regression (Snedecor and Cochran 1980, Palmer and Strobeck 1986) ($P = 0.0028$; $R^2 = 0.83$) was obtained between the summary asymmetry values and precipitation during January, February, March, June and July of their birth years. The birth years of these bears ranged from 1957 to 1972. Strong correlations could not be demonstrated for precipitation and the summary male skull values.

Four individual asymmetry measurements gave significant values when compared to birth year precipitation for various periods: male lower incisor width ($P = 0.036$, $R^2 = 0.47$, $n = 8$); male upper midline to canine ($P = 0.003$, $R^2 = 0.77$, $n = 8$); male length of upper molar row ($P = 0.029$, $R^2 = 0.57$, $n = 8$); female length of lower molar row ($P = 0.007$, $R^2 = 0.62$, $n = 9$).

Pearson's correlation coefficients obtained for all of the skull parameters contributing to near significant differences (Table 1) (Wayne et al. 1986) indicated a fairly high degree of independence of the parameters. Only 19 of the 112 (16%) coefficients in the correlation matrices approached significance.

DISCUSSION

The summary asymmetry differences for males between the North Continental Divide and Yellowstone populations support a hypothesis of impaired movement with resultant genetic separation between them.

The study of the highly inbred cheetah population (Wayne et al. 1986) reported statistical differences in 6 of 16 parameters. The figure most comparable to this from this study would be 8 statistically significant values of 32 individual factor comparisons of the North Continental skulls versus the Yellowstone skulls.

Asymmetry differences between the 2 sexes were noted. Because genome and stress interactions are involved in fluctuating asymmetry (Palmer and Strobeck 1986), the differences in the variability between the sexes in the 2 areas could be biologically significant.

The analysis indicating an influence of precipitation upon skull structure is consistent with precipitation and temperature conditions that favor food plant growth and thus daily weight gain (Picton et al. 1985). The timing of tooth eruption in grizzly bears (Palmisciano 1988) and skull growth in the maturing cub is such that fluctuating asymmetry values may reflect nutritional stress produced by variation in precipitation. These correlations suggest that environmental factors should be evaluated in studies using fluctuating asymmetry.

Only 2 of the females used in the precipitation correlation were born during or after the period of garbage dump closure in Yellowstone. While the dumps were open, the precipitation impact occurred before the peak human travel (dump activity) in the summer. Blanchard (1987) indicates that the bears were physically large during this period when the dumps were open and had large litter sizes (Craighead and Mitchell 1982). She notes that sexual dimorphism became significant by 1 year of age when the male skull measurements exceeded the females by 5.7%. She also indicated that grizzly bear body weights showed a high correlation with annual habitat productivity indices during her study, which began in 1975. The high growth rates of this period may have tended to amplify any tendencies toward asymmetry and decreased developmental homeostasis (Leamy 1984) even if environmental factors were benign.

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