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Fluctuating asymmetry in elk *Cervus elaphus* antlers is unrelated to environmental conditions in the Greater Yellowstone Ecosystem

Scott L. Eggeman, Mark Hebblewhite, Julie Cunningham & Ken Hamlin

Fluctuating asymmetry (FA) is a measure of the deviation from perfect bilateral symmetry, and has been used across mammals as a reliable indicator of environmental stress during growth and development. Antler size and symmetry can be an indicator of individual fitness and social rank among ungulates such as the North American elk *Cervus elaphus*. When environmental conditions are favourable, ungulates allocate additional resources to antler development to increase secondary sexual traits and enhance reproduction. We tested whether there was an appreciable change in antler length and the number of points as extreme climatic conditions (e.g. heavy snow and drought) reduced the nutritional condition of elk using 8,690 antler measurements collected at hunter check stations in south-central Montana surrounding the Greater Yellowstone Ecosystem (GYE) during 1982-2006. We also hypothesized that FA in elk antlers would increase at high elk density because of density-dependent competition for food. We developed *a priori* general linear models of FA expressed as a function of climate covariates, elk density and relevant ecological interactions between the variables. In contrast to previous studies, especially of European ungulates, our results show little support for strong effects of climate or density on FA in length or the number of points. Thus, North American elk do not appear to respond to environmental variation by varying allocation to antler growth, instead they show stronger age-related effects on FA.

Key words: antlers, *Cervus elaphus*, climate, density, elk, fluctuating asymmetry, Yellowstone National Park

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Antler size and symmetry among ungulates such as the North American elk *Cervus elaphus* can be an indicator of individual fitness and social rank (Ditchkoff et al. 2001, Bartos & Bahbouh 2006). Fluctuating asymmetry (FA), the measure of random deviations from perfect bilateral symmetry (Ditchkoff et al. 2001, Bartos & Bahbouh 2006), is assumed to be a result of developmental instability (Van Valen 1962, Møller et al. 1996). Developmental instability is the inability of an organism to buffer against genetic or environmental disturbances during development (Lerner 1954, Debat & David

2001). Low levels of heterozygosity in a population may increase developmental instability, as homozygous individuals are less capable at buffering against developmental variation than heterozygous individuals (Lerner 1954).

Organisms that express FA in sexually selected traits are assumed to have incurred some form of environmental stress or accident during earlier developmental stages. Sexual selection should favour individuals with symmetric ornamental traits, because they advertise the genetic quality of that individual to buffer against perturbations during de-

velopment (Møller et al. 1996, Vanpe et al. 2007). As a secondary sexual trait, antler size and symmetry is an honest indicator of social rank, or 'good genes' to females (Ditchkoff et al. 2001). When environmental conditions are favourable, elk allocate additional resources to antler development to increase secondary sexual traits (Putman et al. 2000, Mysterud et al. 2005). Reduced size and increased FA of elk antlers under adverse nutritional conditions may be the result of a trade-off between body size and antler development (Mysterud et al. 2005).

All bull elk will assume the cost of maintaining ornamental traits and a reduction in homeostasis for those traits under poor conditions (Markusson & Folstad 1997, Putman et al. 2000). However, the cost of maintenance is greater for individuals in poorer conditions or quality than it is of an individual in better condition, so we would expect to see greater asymmetry in poorer condition individuals, because they would be more sensitive to developmental stress (Markusson & Folstad 1997, Lagesen & Folstad 1998). The process of sexual selection ensures that only the individuals of higher quality will pass along their genes and that individuals of lower quality will not (Markusson & Folstad 1997). Thus, asymmetry in ornamental traits would be selected against and not be heritable, and be more of a product of developmental stress.

We would also expect high elk densities to increase FA because of density-dependent food competition (Taper & Gogan 2002, Mysterud & Østbye 2006). Stress from reduction of available forage has a high energetic cost such as increasing vulnerability to parasites, predation and developmental abnormalities (Lagesen & Folstad 1998, Taper & Gogan 2002, Cook et al. 2004, Mysterud et al. 2005). As indicated by Cook et al. (2004), ungulate reproduction depends on their nutritional condition as a function of the availability of high quality forage. Thus, for polygynous breeders such as many ungulates, higher-quality males become sexually dominant and procure the bulk of the breeding opportunities (Bartos & Bahbouh 2006).

Using a long-term and large data set from hunter check stations within the northern part of the Greater Yellowstone Ecosystem (GYE) in Montana during 1982-2006, we tested for the factors driving FA using the relative FA in antler length and the number of points on bull elk. We tested two main hypotheses expected to drive antler characteristics based on previous studies (Ditchkoff et al. 2001, Mysterud et al. 2005). We first tested the hypothesis

that the level of asymmetry in elk antlers is a result of seasonal climate affecting the nutritional condition of elk (Mysterud et al. 2005, Bartos & Bahbouh 2006). If this hypothesis was true, we predicted an increased frequency of FA in elk antlers following winters with heavy snow and summers with low precipitation (Putman et al. 2000, Taper & Gogan 2002, Mysterud & Østbye 2006). Second, we hypothesized that the occurrence of FA in elk antlers was associated with high elk density because of food-limitation (Taper & Gogan 2002, Hebblewhite 2005). We predicted that increased density would be positively correlated with the amount of FA. Age of ungulates has also been shown to strongly influence the patterns of FA because sensitivity to environmental stressors is more pronounced in younger and older age classes (Putman et al. 2000, Mysterud et al. 2005). Therefore, under the assumption that climate and elk density affect nutritional condition, we would expect to see a stronger relationship with FA in subadult and older senescent bull elk.

Study area

The total study area is approximately 10,861 km², and encompasses four different elk management units (hereafter Elk Units) corresponding to four different subpopulations northwest of Yellowstone National Park (hereafter Yellowstone Park) in south-central Montana (latitude 45°03'N, longitude 110°60'W; Fig. 1). Land ownership is divided be-

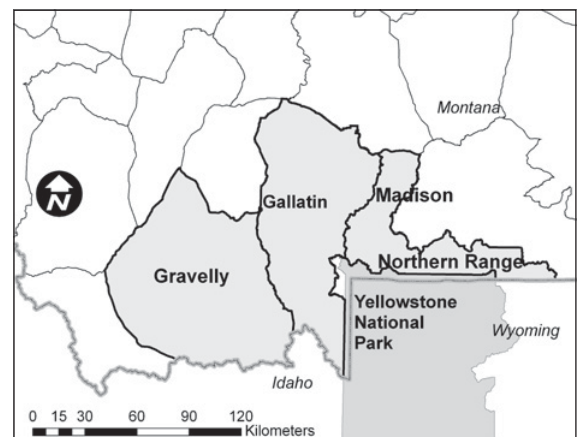


Figure 1. Study area in which the four elk management units (Elk Units) within the Greater Yellowstone Ecosystem (GYE) including the analysis of fluctuating asymmetry (FA) from bull elk was performed during 1982-2006.

tween federal, state and private lands with 60% designated as public land and the other 40% divided amongst various private land owners (Hamlin 2004). The topography varies widely with elevations ranging between 1,200 m and 3,400 m. Low-elevation valleys consist mostly of stream networks, sagebrush grasslands, and complex bog and meadow systems as well large grassland complexes associated with elk winter range. Higher elevation montane areas include complex topography with varying aspects, degree of slopes, and canyons providing a variety of different vegetation types. Annual precipitation within the study area ranges between 21 cm in Gardiner (Coughenour & Singer 1996) and 32 cm in Ennis (National Oceanic and Atmospheric Administration climate data; available at: <http://www.nws.noaa.gov/>). Our study area experienced a relatively pronounced drought during the last eight years of the study (Vucetich et al. 2005). Forest types are primarily dominated by Douglas fir *Pseudotsuga menziesii*, Englemann spruce *Picea engelmannii* and lodgepole pine *Pinus contorta*. The area is also occupied by white-tailed deer *Odocoileus virginianus* and mule deer *O. hemionus*, moose *Alces alces*, coyotes *Canis latrans* and gray wolves *C. lupus*, mountain lion *Puma concolor*, black bear *Ursus americanus* and grizzly bears *U. arctos*. Importantly, gray wolves were reintroduced to the GYE in 1995, and their populations have expanded dramatically both in distribution and number since then (Vucetich et al. 2005).

Antler data for bull elk were collected during the fall within three Elk Units corresponding to four different subpopulations, i.e. the Northern Range Elk Unit, the Gravelly Elk Unit and the Gallatin-Madison Elk Unit (see Fig. 1). This latter Elk Unit was divided into two Elk Units (i.e. hunter districts 301, 310 and 311 for Gallatin, and 360 and 362 for Madison) representing different mountain ranges and thus elk subpopulations: the Gallatin and Madison (Hamlin 2004). The Gallatin-Madison Elk Unit is 4,837 km² and borders the extreme northwest corner of Yellowstone Park extending down to the Idaho-Wyoming border. The Gravelly Elk Unit borders the western part of the Gallatin/Madison Elk Unit and the northern border of east-central Idaho. This Elk Unit covers approximately 4,898 km² encompassing the Gravelly, Greenhorn, Snowcrest, Centennial and Blacktail Mountain ranges. The Northern Yellowstone Elk Unit is located directly north of the Yellowstone Park border between Cooke city and Gardiner and north to the Boulder

River divide. This Elk Unit is approximately 1,126 km² with the Absaroka-Beartooth Wilderness comprising 75% of the area.

Material and methods

Elk data

Montana Fish Wildlife and Parks (hereafter MT Fish and Game) collected measurements of antler size and symmetry from a total of 8,690 hunter harvested bull elk from all four subpopulations during 1982-2006, representing perhaps one of the most extensive data sets of its kind (e.g. see Mysterud et al. (2005) who used data from 5,462 red deer *Cervus elaphus* stags). The Gallatin and Madison Elk Units contained 3,440 and 1,305 antler measurements, respectively, the Gravelly Elk Unit 2,064 records, and the Northern Yellowstone Elk Unit contained 1,892 records. Antler measurements were collected at hunter check stations within each Elk Unit during the Montana firearm (e.g. not including archery hunting) hunting season starting in mid-October and continuing through late November. However, one exception is the Gardiner late hunt that starts between mid-December or early January through mid-February (depending on yearly elk counts) within the Northern Yellowstone Elk Unit. All antler measurements were made by MT Fish and Game biologists and game wardens. Beam length was measured in millimeters along the outside of the main beam and points were counted for each side.

Measurement error is important to account for in studies of FA, and Palmer & Strobeck (1986) recommend repeated measurements as a method to incorporate measurement error into quantitative tests of FA. Fortunately, measurement error in the number of points can be assumed to be negligible because elk antler points are well defined (Hudson & Haigh 2002). For antler length, however, we only obtained one length measurement in the field during 1982-2006, making use of the methods of Palmer & Strobeck (1986) impossible for the entire data set. To understand the relative magnitude of measurement error in antler length relative to FA, we conducted a field study in 2009 on elk antlers in museum specimens using the same methods as in the field. We compared the magnitude of measurement error to FA using the z-test to determine if there was significant overlap (De Veaux et al. 2005). In addition to measurement error, we tested for directional asymmetry (Van Valen 1962, Palmer & Strobeck

1986) using raw FA measurements and testing whether the confidence interval overlapped zero.

For the purpose of our study, we examined relative measurements of FA assigned as the absolute difference between each side divided by the largest side (Ditchkoff et al. 2001, Bartos & Bahbhouh 2006). We used relative FA instead of other measures used by other authors, such as absolute, or body mass* antler mass ratio (Mysterud et al. 2005), both because previous authors reported inconsistency between relative and absolute (Bartos & Bahbhouh 2006), and because relative FA would standardize for any trends in antler size over the study period. Body mass was also unavailable in our study area. We tested for the degree of correlation between FA in antler length and the number of points using Pearson's correlations to determine the independence of these FA measures, because other authors (e.g. Bartos et al. 2007) found strong correlations between FA measurements in red deer.

Environmental covariates

Bull elk age was estimated using cementum-line counts from incisor teeth and tooth eruption wear patterns (e.g. see Hamlin et al. 2000). In instances in which incisor age was not available, we deferred to tooth eruption wear to assign elk to age classes based on elk demography and survival rates (Houston 1982). All records were analyzed using four age classes; yearling elk were 1-2 years of age, subadults (2-3 years), prime-aged (3-10 years) and old ages (>10 years). We chose this age classification based on a previous study by Houston (1982), who found that survival rates for juvenile and senescent age elk were most affected by severe winter. Therefore, we categorized ages into four groups predicting that FA would be highest in the youngest and oldest age classes, reflecting the level of instability and nutritional condition (Putman et al. 2000).

Elk count data were obtained from MT Fish and Game using aerial surveys for most years between 1980 and 2006 (e.g. Hamlin 2004, Singer et al. 1997, Vucetich et al. 2005). Elk counts were typically done during late December and January using both fixed wing aircraft and helicopter following the autumn hunting season (Hamlin 2004). Elk counts were potentially affected by differential sightability in different Elk Units (e.g. Singer et al. 1997), but for our analyses, we were interested in the effects of broad-scale trends on FA. Given that there were large differences between population growth rate in several Elk Units (Gardiner was declining, Madison

and Gallatin increasing; Hamlin 2004, Vucetich et al. 2005), we felt that small differences in sightability could be ignored in our comparative analysis between Elk Units.

As a broad-scale measure of climatic variation, we used the North Pacific Oscillation (NPO) anomaly index for November-March 1980-2007, obtained from the Climate Analysis Section of the National Centre for Atmospheric Research (NCAR, USA; available at: <http://www.cgd.ucar.edu/cas/jhurrell/indices.data.html#.mon>). The NPO is based on sea surface temperature anomalies measured over the North Pacific Ocean (Trenberth & Hurrell 1994), and has been linked to elk population dynamics (Hebblewhite 2005) like the similar, and more extensively studied, North Atlantic Oscillation (NAO; Stenseth et al. 2002). We tested relationships between the NPO and local winter and summer climate data from North Yellowstone (reported in Vucetich et al. 2005) between 1980 and 2006, to validate the use of NPO. We used a pair-wise correlation in STATA 10 (StataCorp 2008) to test relationships between NPO and winter minimum temperature, snowfall and summer precipitation from Vucetich et al. (2005) for the Northern Range Elk Unit.

Statistical analysis

We tested how elk density, winter NPO index and age classes affected FA for each of the four elk subpopulations over the 25-year time series separately. We created categorical variables for all age classes, where the yearling age class was treated as the Y-intercept. We also tested for the effect of three important biological interactions on FA: 1) elk density and NPO, 2) elk density and age classes, and 3) NPO and age classes based on their importance to ungulate population growth rate in previous studies (Taper & Gogan 2002, Hebblewhite 2005, Mysterud & Østbye 2006). We also examined non-linear effects of covariates. We developed an all inclusive set of 32 *a priori* general linear models (GLMs; McCullough & Nelder 1989) as a function of the main effects and interactions to test our hypotheses about FA as a function of climate and elk density. We tested for the appropriate distribution to model relative FA in comparison to Poisson, negative binomial and log-normal using the Vuong likelihood ratio test (Vuong 1989). We found that the log-transformed antler length and number of points were still best fit by a Poisson distribution (M. Hebblewhite, unpubl. data). Therefore, we used a negative binomial link

function to model FA in both antler length and number of points using GLM.

We selected the top model for each subpopulation and dependent variable (length and points) using Akaike Information Criterion (AIC; Burnham & Anderson 1998). We did not use the small sample size correction, AIC_c, because of the large number of FA measurements. We ranked models using Δ AIC, and determined the AIC weights (w_i) for each model as a measure of model uncertainty (Burnham & Anderson 1998). In the interest of brevity, and because there was only moderate model selection uncertainty, we report only the top models for each subpopulation. However, we also report variable importance weight for each variable in the top model set (0-4 AIC) by summing up the Akaike weights for each variable in the top model set (Burnham & Anderson 1998). Variable importance weights give a relative measure of the rank or importance of a variable on the dependent variable, conditional on the specific model set (Burnham & Anderson 1998). We also report the pseudo- R^2 for each top model as a measure of model predictive power. All statistical analyses were done in STATA 10.0 (StataCorp. 2008).

Results

The number of antler records for prime age elk in Northern Yellowstone and Gallatin was higher than all other age classes; in contrast, the Madison and Gravelly Elk Units had more subadult records (Table 1). For all Elk Units, the old-age class had the lowest number of measurement records (Gravelly (N=1), Madison (N=13), Gallatin (N=54) and Northern Yellowstone (N=156)). We calculated mean age for all Elk Units, which revealed a slight contrast, representing differences in hunter selec-

Table 1. Number of records of measurements of fluctuating asymmetry (FA) from male elk antler measurements grouped by age class (yearling, subadult, prime and old) from the four elk management units (northern Yellowstone, Gallatin, Madison and Gravelly) in the Greater Yellowstone Ecosystem (GYE) during 1982-2006.

Age class	Elk management unit				Total
	Northern Yellowstone	Gallatin	Madison	Gravelly	
Yearling	351	650	144	107	1252
Subadult	186	1065	648	1452	3351
Prime	1188	1671	500	504	3863
Old	156	54	13	1	224
Total	1881	3440	1305	2064	8690

tion and harvest regulations: Northern Yellowstone ($\mu=6.79$), Gravelly ($\mu=2.88$), Madison ($\mu=3.85$) and Gallatin ($\mu=4.55$). Raw measurements of antler length and the number of points were correlated in all Elk Units, with Yellowstone being the highest ($r=0.86$, $P<0.0005$) followed by Gallatin ($r=0.79$, $P<0.0005$), Madison ($r=0.71$, $P<0.0005$) and Gravelly ($r=0.58$, $P<0.0005$), respectively.

However, this correlation broke down when we considered FA. Relative FA in length and points were only weakly correlated in all Elk Units, with the highest in Gallatin ($r=0.38$, $P<0.0005$) followed by Madison ($r=0.33$, $P<0.0005$), Gravelly ($r=0.30$, $P<0.0005$) and Yellowstone ($r=0.24$, $P<0.0005$). Relative FA in points for the Yellowstone Elk Unit was lower for subadult and old-age classes and much higher for prime-aged individuals. The relationship between FA in length and FA in points was the weakest of all Elk Units in Yellowstone, especially for prime-aged animals, compared to all other Elk Units (Fig. 2). Other Elk Units showed more variable results, but generally, FA in points and length were not strongly correlated (see Fig. 2), with the biggest discrepancies occurring in yearlings in Gravelly, old and subadult elk in Gallatin, and subadults in Madison (see Fig. 2).

We obtained 109 estimates of measurement error from 65 different antler pairs to examine measurement error in antler length. Absolute FA for this subset of antlers was 37.1 mm (SD=34.99), significantly greater than (Z-test: P-value <0.00005) the measurement error which was 7.9 mm (SD=13.1), and only 21% of absolute FA. Therefore, we did not consider this low level of measurement error in antler length in subsequent analyses. There was no evidence for directional asymmetry as the 95% confidence intervals for raw FA for each Elk Unit overlapped zero (Yellowstone: $\mu=0.50$, 95% CI: -2.9 - 3.9; Gravelly: $\mu=-2.36$, 95% CI: -5.58 - 0.85; Madison: $\mu=-0.94$, 95% CI: -5.42 - 3.54; and Gallatin: $\mu=2.73$, 95% CI: -0.52 - 5.98).

Climate relationships

The winter NPO was negatively correlated with winter minimum temperature ($r=-0.7$, $P<0.001$) and summer precipitation ($r=-0.50$, $P<0.001$), and positively correlated with annual snowfall ($r=0.42$, $P<0.001$). High NPO values were related to warm, wet winters followed by hot, dry summers; conversely, cold, dry winters were related to wet summers. Therefore, severe winters are related to high NPO values at this latitude and elevation (Trenberth

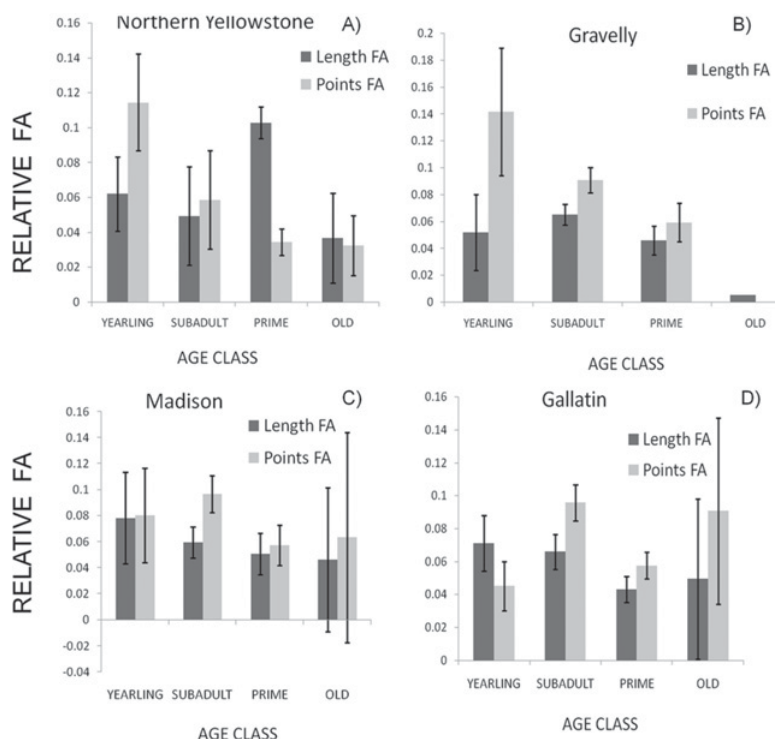


Figure 2. Relationships between the age classes yearling, subadult, prime and old and relative fluctuating asymmetry (FA) in length and points for each of the four elk management units (Elk Unit) in the Greater Yellowstone Ecosystem (GYE) during 1986-2006, with standard error bars shown. Numbers along the y-axis are values of relative (absolute difference between antlers/largest side) FA.

& Hurrell 1994). We found no evidence for non-linear effects, nor any significant interactions.

Fluctuating asymmetry in length

Model selection for FA in length was less certain than for FA in points (range ΔAIC in length 0.21-0.34 and ΔAIC in points 0.34-0.58, respectively). All top models were relatively simple for each subpopulation with 2-3 parameters for each model including ages. Models were relatively consistent both within Elk Units (M. Hebblewhite, unpubl. data) and between subpopulations. For example, in

the Northern Yellowstone subpopulation, variable importance weights (Burnham & Anderson 1998) in Table 2 show that amongst the top model set (0-4 AIC), elk density and climate both had an Akaike weight of 0.79, prime age classes were 0.73, and old and subadult age classes were both <0.30 Akaike weight. Therefore, despite model selection uncertainty in the top set for Yellowstone, all top models showed that FA in antler length increased with increasing elk density, climatic severity and in prime age classes. For all other subpopulations' variable importance weights displayed a similar pattern, with

Table 2. Top general linear models (GLMs) for bull elk fluctuating asymmetry (FA) in each of the four elk management units in the Greater Yellowstone Ecosystem (GYE) during 1982-2006 for two measures of FA, antler length and the number of points. Symbols are: E=elk density, C=NPO, S=subadult, P=prime and A=all age classes. N=number of records, K=number of parameters, AIC_w =Akaike weight. Log-likelihood is the maximum log-likelihood.

Elk unit	Model structure	N	K	Log-likelihood	AIC	AIC_w
Length relative (FA)						
Northern Yellowstone	E+C+P	928	4	-153.11	0	0.28
Gallatin	E+P	972	3	-183.784	0	0.34
Madison	E+S	716	3	-140.097	0	0.21
Gravelly	E+S	1734	3	-346.03	0	0.26
Points relative (FA)						
Northern Yellowstone	E+C+S	1050	4	-189.725	0	0.47
Gallatin	E+A	1819	5	-344.959	0	0.58
Madison	E+S	853	3	-196.871	0	0.34
Gravelly	E+P	1948	3	-511.2424	0	0.38

Table 3. Variable weights of importance for relative FA in length and points in each of the four Elk Units. A sum of weights is given for all variables included within our set of top models (0-4 AIC).

Variable	Elk Unit							
	Northern Yellowstone		Gravelly		Gallatin		Madison	
	Length	Points	Length	Points	Length	Points	Length	Points
Elk Density	0.78	0.72	0.94	0.72	0.90	0.69	0.98	0.88
Climate	0.78	0.72	0.31	0.14	0.23	0.12	0.34	0.25
Subadult	0.16	0.72	0.43	0.19	0.29	0.69	0.35	0.51
Prime	0.73	0.08	0.40	0.52	0.58	0.69	0.03	0.28
Old	0.30	0.08	0.17	0.12	0.16	0.69	0.35	0.08
Sum of AIC w_i	0.78	0.72	0.94	0.72	0.90	0.69	0.98	0.88

most of the variable weight retained in elk density (AIC weight: $w_i = 0.69-0.94$; see Table 2). Variable importance weights for age classes in other subpopulations were moderate depending on whether the age class was retained in the top model or not (see Tables 2 and 3).

The effects of age on length FA were consistent with univariate analyses (see Fig. 2), although no subpopulation retained all age classes in all top models. In Gardiner and Gallatin, prime-age elk had lower FA than yearlings (Table 4) while old and subadult age classes were not retained in top models (see Tables 3 and 4). In Madison, subadults had lower FA than yearlings, but prime age and older age classes did not have different FA from yearlings (see Table 4). In contrast, in Gravelly, subadults had higher FA than yearlings, which were the same as all other age classes.

Elk density was positively correlated with length FA in the Gardiner, Gallatin and Gravelly subpopulations (see Table 4 and Fig. 3A), consistent with our prediction that intraspecific competition would increase nutritional stress. However, in the Madison subpopulation, elk density was negatively

correlated with FA in relative antler length. Despite this support in principle for our predictions, however, the coefficients for elk density effects were weak and not statistically significant in all four subpopulations (see Table 4). Figure 3 shows the relationships for Northern Yellowstone Elk Unit and illustrates the wide confidence intervals; results were similar for the other three Elk Units and are not shown here, but the coefficients are given in Table 4. The weak statistical effects of climate and elk density were further evidenced in the low explanatory power of all the top models for length relative FA (see Table 4); the best models explained only 0.5-4% of the variation in FA.

Fluctuating asymmetry in the number of points

Model selection was relatively more certain for FA in antler points compared to length (see Table 1). All top models were relatively simple for all subpopulations with 2-3 parameters including age classes. Variable importance weights for the set of top models (0-4 ΔAIC) were similar for all subpopulations (see Table 2). Elk density accounted for the majority of variable importance weights; in North-

Table 4. Top statistical models of FA in bull elk antler length and number of points from the Greater Yellowstone Ecosystem, Montana, during 1982-2006. Top model structure and coefficients with standard errors (SE) and R^2 values are reported for relative measures of FA length and points for each of the four Elk Units. Symbols are: E=elk density, C=NPO winter, A=ages, S=subadult, P=prime and 0=old.

Elk Unit	Model structure	B ₍₀₎	SE	Elk density	SE	NPO	SE	AGES						R ²
								Subadult	SE	Prime	SE	Old	SE	
Length relative (FA)														
Gardiner	B0 + B(E) + B(C) + B(P)	-3.36	0.729	5.22E-05	4.96E-05	0.026	0.082			-0.67	0.308			0.04
Gallatin	B0 + B(E) + B(P)	-3.36	0.308	2.77E-06	1.96E-04					-0.48	0.287			0.02
Madison	B0 + B(E) + B(S)	-2.70	0.534	-6.6E-05	1.43E-04			-0.05	0.313					0
Gravelly	B0 + B(E) + B(S)	-3.10	0.452	6.05E-06	6.82E-05			0.33	0.237					0.01
Points relative (FA)														
Gardiner	B0 + B(E) + B(C) + B(S)	-3.09	0.643	-6E-06	4.61E-05	-0.022	0.069	1.06	0.363					0.04
Gallatin	B0 + B(E) + B(A)	-3.09	0.643	-1.5E-05	1.60E-04			1.21	0.320	0.83	0.307	1.32	0.621	0.04
Madison	B0 + B(E) + B(S)	-2.96	0.416	0.000027	1.11E-04			0.44	0.260					0.02
Gravelly	B0 + B(E) + B(P)	-2.29	0.320	-1.4E-05	5.24E-05					-0.45	0.208			0.01

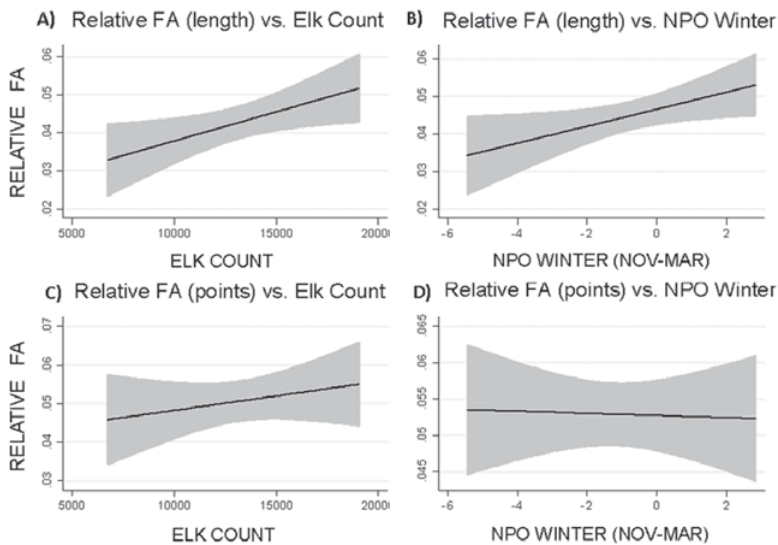


Figure 3. Relative FA vs elk count (A and C) and NPO winter index (B and D) for length (A and B) and points in the Northern Yellowstone elk unit for the years 1982-2006. Positive NPO values relate to warm, wet winters and negative values relate to cold, dry winters. Y-axis relates to the percentage of relative FA.

ern Yellowstone, the Akaike weight for density was 0.72, in Gravelly 0.72, Gallatin 0.69 and Madison 0.88 (see Table 2). Climate and age class were retained in top models for each subpopulation, though with at least half or less the variable importance weight (see Table 4). While there was high model selection uncertainty for our set of top models, all top models included the variables elk density, climate and ages classes for each Elk Unit (see Table 2; M. Hebblewhite, unpubl. data).

The effects of age on points were generally consistent with the univariate analysis presented in Figure 2 and the prediction of higher FA in older and younger animals. In Northern Yellowstone and Madison Elk Units, subadult age classes had higher FA (see Table 4) while prime and old age classes were not retained in our top model. The Gallatin Elk Unit contained all age classes (see Table 4), with each accounting for 0.69 of the AIC variable importance weight. For the Gravelly Elk Unit, prime age class had greater FA (see Table 4) while subadult and old age classes were not retained, opposite to predictions.

Elk density was negatively correlated with the FA in points in the Northern Yellowstone, Gallatin and Gravelly subpopulations, consistent with predictions, but positively correlated with elk density in the Madison subpopulation (see Table 4). Once again, the coefficients for elk density effects were weak and not statistically significant (see Table 4). Climate was not retained in any of our top model except for Yellowstone and had little of the AIC variable

importance weight, $AICw_i = 0.12-0.25$. Overall, models explaining FA in the number of points explained slightly more variation than FA in length, but top model R^2 values were still low, ranging from 0.1 to 0.11.

Discussion

We found weak support for our main hypotheses that adverse climatic conditions and increasing elk density increased FA in either length or the number of points of bull elk antlers in the GYE. Although we had a large sample size of 8,690 measurements, our models could not explain more than 11% of the variation, and coefficients of covariates were statistically and biologically weak. Our large sample size provided strong statistical power, but very little explanatory power with the covariates we selected for analyses. Elk density was consistently positively related to FA in length for three of four subpopulations, but interestingly, we found a negative relationship with elk density and FA in points for three of four analyses. Only the Madison subpopulation had a negative relationship with elk density and FA in length and a positive relationship with FA in points. Increasing winter severity did increase FA in three of four subpopulations, but the effect was biologically weak although statistically significant, and only manifested in the Northern Yellowstone subpopulation in FA in antler length and the number of points. Therefore we conclude that the

biological impacts of climatic and density-induced competition are weak and inconsistent on FA in bull elk in the GYE.

Our results are suggestive, however, of a climatic effect at higher elevations in our study area. The strongest climatic impact in our study was observed at the highest elevation on the most severe winter range in the Yellowstone subpopulation, while we did not see any climate impact on FA in the lower elevations and milder Gallatin, Madison and Gravelly areas. Also suggestive of this interpretation was the higher FA in antler length than the number of points in the Yellowstone subpopulation. It is possible that during severe winters prime-age adults might suffer higher mortality (perhaps because of the more severe climate) after the mating season, which can be particularly energetically expensive to prime-age bulls (Hudson & Haigh 2002). If prime-age bulls suffer higher mortality in the Yellowstone Elk Unit, then we would expect to see the average FA in length increase whereas the average FA in points in the population would decrease (see Fig. 2 Yellowstone).

Effects of age were generally consistent with our expectations, but were weak. We found only slight associations with two (Gallatin and Madison) of the four analyses for the relationship between ages and relative FA in points and length (see Fig. 2). However, the sample size for the old age class was substantially smaller than all other age classes. The subadult age class followed the predicted pattern with a slightly higher level of FA in three of four subpopulations in both antler length and points. Analysis of the dynamics of age classes themselves would be useful to test hypotheses about climate effects, hunting and even the recent recolonization of wolves in the GYE (Vucetich et al. 2005). Wolves often select male elk that have been weakened during the rut. It may also be possible that elk in poorer condition would be more susceptible to wolf predation, therefore removing elk with greater FA from the population.

Overall, our weak and negative results are in contrast to several recent studies. For example, Mysterud et al. (2005) found antler size of red deer in Norway to be positively correlated with favourable conditions and negatively correlated with severe winters. While Mysterud et al. (2005) used antler size and body size (which we were unable to measure), antler size and the number of points and length are correlated in ungulates. Therefore, it seems unlikely for methodological differences to drive differences

between the Norwegian red deer study and our results from the GYE. In another study on antler characteristics in fallow deer *Dama dama*, Putman et al. (2000) found environmental stress to significantly affect the relationship of FA in young age deer. Putman et al. (2000) emphasized intraspecific competition by using measures of food quality and deer density, of which the latter is similar to our study.

Despite support for influences of climate and density on FA in elk antlers, our results add to a growing number of studies casting doubt on the utility of FA as a indicator of developmental stress. Kruuk et al. (2003) found similar inconsistencies to ours in a red deer study on Rhum Island, Scotland. They concluded that FA in antler length was positively correlated with breeding success and fighting ability rather than individual condition (Kruuk et al. 2003). A recent study on FA in ibex *Capra ibex* horns also found no relationship to senescence (Hardenberg et al. 2004). In a review on FA studies, Palmer (2000) criticized the validity of FA studies for selective reporting and limited statistical power of FA as a measure of developmental instability. Our study, however, had ample statistical power to conduct tests of FA, and used multiple parallel traits that were statistically independent. The differences we observed in our study between subpopulations, and these inconsistencies in the literature suggest that FA may perhaps be less important in North American ungulates than in European ungulates.

Despite criticisms of FA studies, there seems to be a general lack of information about ecological differences between study areas, for example, in history of selective hunting, predation and climatic severity. The GYE is perhaps one of the most heavily studied yet complex ecosystems in the world. The populations in our study area are all under selective pressure from predation by humans, wolves and grizzly bears amongst the major predators. This level of predation could potentially reduce the overall magnitude of density dependence, weakening the signature of climatic variation. In most European studies of FA in ungulates, where FA was found to vary as a function of environmental covariates (e.g. Mysterud et al. 2005, Ditchkoff et al. 2001) predators have been exterminated for centuries, and human hunting systems are often designed selectively to increase antler size, for example, in red deer (Thomas & Toweill 2003), potentially increasing the additive genetic variance in antler traits, despite their generally low heritability (Coltman et al. 2003).

It is also possible that the effects of increased predation by recolonizing wolves could reduce FA in the GYE so that predation reduced the strength of density dependence and thus climatic effects on FA (Hebblewhite 2005, Vucetich et al. 2005). Small sample sizes are more likely to be affected by sample variation than large sample sizes (Palmer 2000), although this was clearly not a problem in our study, nor was measurement error significant. Our negative results are even more convincing if one considers that previous studies showed a direct environmental effect of many of the same covariates (e.g. climate and density) on elk population growth rate, and thus size itself (Hebblewhite et al. 2002, Taper & Gogan 2002, Hebblewhite 2005, Vucetich et al. 2005). Using the same data for elk density in the Northern Yellowstone Elk Unit, for example, Taper & Gogan (2002) and Vucetich et al. (2005) found strong density dependence on elk population growth rate, and Vucetich et al. (2005) showed strong negative effects of winter severity on elk population size and growth. Thus, the biotic processes driving population growth were unreliably captured at the individual level by antler growth and development, supporting our interpretation that FA is unreliable in this system as an index of environmental variation.

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