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10 **Fluctuating asymmetry in elk antlers is unrelated to**
11 **environmental conditions in the Greater Yellowstone**
12 **Ecosystem**

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16

17 **Abstract**

18 Fluctuating asymmetry (FA) is a measure of the deviation from perfect bilateral symmetry, and
19 has been used across mammals as a reliable indicator of environmental stress during growth and
20 development. Antler size and symmetry can be an indicator of individual fitness and social rank
21 among ungulates such as the North American elk (*Cervus elaphus*). When environmental
22 conditions are favorable, ungulates allocate additional resources to antler development to

1 increase secondary sexual traits and enhance reproduction. We tested whether there was an
2 appreciable change in antler length and the number of points as extreme climatic conditions (e.g.,
3 heavy snow and drought) reduced the nutritional condition of elk using 8690 antler
4 measurements collected at hunter check stations in south-central Montana surrounding the
5 Greater Yellowstone Ecosystem (GYE) from 1982-2006. We also hypothesized that FA in elk
6 antlers would increase at high elk density because of density-dependent competition for food.
7 We developed a-priori general linear models of FA expressed as a function of climate covariates,
8 elk density, and relevant ecological interactions between variables. In contrast to previous
9 studies, especially of European ungulates, our results show little support for strong effects of
10 climate or density on FA in length or the number of points. Thus, North American elk do not
11 appear to respond to environmental variation by varying allocation to antler growth, instead
12 showing stronger age-related effects on fluctuating asymmetry.

13

14 **Introduction**

15 Antler size and symmetry among ungulates such as the North American elk (*Cervus elaphus*) can
16 be an indicator of individual fitness and social rank (Ditchkoff et al. 2001, Bartos & Bahbouh
17 2006). Fluctuating asymmetry (FA), the measure of random deviations from perfect bilateral
18 symmetry (Ditchkoff et al. 2001, Bartos & Bahbouh 2006), is assumed to be a result of
19 developmental instability (Van Valen 1962, Moller 1996,). Developmental instability is the
20 inability of an organism to buffer against genetic or environmental disturbances during
21 development (Lerner 1954, Debat & David 2001). Low levels of heterozygosity in a population
22 may increase developmental instability, as homozygous individuals are less capable at buffering
23 against developmental variation than heterozygous individuals (Lerner 1954).

1 Organisms that express FA in sexually selected traits are assumed to have incurred some
2 form of environmental stress or accident during earlier developmental stages. Sexual selection
3 should favor individuals with symmetric ornamental traits because they advertise genetic quality
4 of that individual to buffer against perturbations during development (Moller 1996, Vanpe et al.
5 2007). As a secondary sexual trait, antler size and symmetry is an honest indicator of social
6 rank, or “good genes” to females (Ditchkoff et al. 2001). When environmental conditions are
7 favorable, elk allocate additional resources to antler development to increase secondary sexual
8 traits (Putman et al. 2000, Mysterud et al. 2005). Reduced size and increased FA of elk antlers
9 under adverse nutritional conditions may be the result of a tradeoff between body size and antler
10 development (Mysterud et al. 2005).

11 All bull elk will assume the cost of maintaining ornamental traits and a reduction in
12 homeostasis for those traits under poor conditions (Markusson & Folstad 1997, Putman et al.
13 2000). However, the cost of maintenance is greater for individuals in poorer condition or quality
14 than that of an individual in higher condition, so we would expect to see greater asymmetry in
15 poorer condition individuals because they would be more sensitive to developmental stress
16 (Markusson & Folstad 1997, Lageson & Folstad 1998). The process of sexual selection insures
17 that only the individuals of higher quality will pass along their genes and not individuals of lower
18 quality (Markusson & Folstad 1997). Thus, asymmetry in ornamental traits would be selected
19 against and not be heritable, and be more of a product of developmental stress.

20 We would also expect high elk densities to increase FA because of density dependent
21 food competition (Taper & Gogan 2002, Mysterud & Ostbye 2006). Stress from reduction of
22 available forage has a high energetic cost such as increasing vulnerability to parasites, predation,
23 and developmental abnormalities (Lagesen & Folstad 1998, Taper & Gogan 2002, Cook et al.

1 2004, Mysterud et al. 2006). As indicated by Cook et al. (2004), ungulate reproduction depends
2 on their nutritional condition as a function of the availability of high quality forage. Thus, for
3 polygynous breeders like many ungulates, higher quality males become sexually dominant and
4 procure the bulk of the breeding opportunities (Bartos & Bahbouh 2006).

5 Using a long-term and large data set from hunter check stations within the northern portion
6 of the Greater Yellowstone Ecosystem (GYE) in Montana from 1982-2006, we tested for the
7 factors driving fluctuating asymmetry using the relative FA in antler length and the number of
8 points on bull elk. We tested two main hypotheses expected to drive antler characteristics based
9 on previous studies (Ditchkoff et al. 2001, Mysterud et al. 2005). We first tested the hypothesis
10 that the level of asymmetry in elk antlers is a result of seasonal climate affecting the nutritional
11 condition of elk (Mysterud et al. 2005, Bartos & Bahbouh 2006). If this hypothesis was true, we
12 predicted an increased frequency of FA in elk antlers following winters with heavy snow and
13 summers with low precipitation (Putman et al. 2000, Taper & Gogan 2002, Mysterud & Ostbye
14 2006). Second, we hypothesized that the occurrence of FA in elk antlers was associated with
15 high elk density because of food-limitation (Taper & Gogan 2002, Hebblewhite 2005). We
16 predicted increased density would be positively correlated with the amount of FA. Age of
17 ungulates has also been shown to strongly influence the patterns of fluctuating asymmetry
18 because sensitivity to environmental stressors is more pronounced in younger and older age
19 classes (Putman et al. 2000, Mysterud et al. 2005). Therefore, under the assumption that climate
20 and elk density affect nutritional condition we would expect to see a stronger relationship with
21 FA in sub-adult and older senescent bull elk.

22 **Study area**

1 The total study area was approximately 10,861 km², and encompasses four different elk
2 management units (hereafter Elk Units) corresponding to four different subpopulations northwest
3 of Yellowstone National Park (hereafter Yellowstone Park) in south-central Montana (latitude
4 45° 03' N, longitude 110° 60' W, Figure 1). Land ownership is divided between federal, state,
5 and private lands, with 60% designated as public land and the other 40% divided amongst
6 various private land owners (Hamlin 2004). Topography varies widely with elevations ranging
7 between 1200m and 3400m. Low elevation valleys consist mostly of stream networks,
8 sagebrush grasslands, and complex bog and meadow systems as well large grassland complexes
9 associated with elk winter range. Higher elevation montane areas include complex topography
10 with varying aspects, degree of slopes, and canyons providing a variety of different vegetation
11 types. Annual precipitation within the study area ranges between 21cm in Gardiner (Coughenour
12 & Singer 1996) to 32cm in Ennis (NOAA, 2008). The study area experienced a relatively
13 pronounced drought during the last 8-years of the study (Vucetich et al. 2005). Forest types are
14 primarily dominated by Douglas fir (*Pseudotsuga menziesii*), Englemann spruce (*Picea*
15 *engelmannii*), and lodgepole pine (*Pinus contorta*) species. This area is also occupied by whitetail
16 deer (*Odocoileus virginianus*) and mule deer (*O. hemionus*), moose (*Alces alces*), coyotes (*Canis*
17 *latrans*) and gray wolves (*C. lupus*), mountain lion (*Puma concolor*), black bear (*Ursus*
18 *americanus*) and grizzly bears (*U. arctos*). Importantly, gray wolves were reintroduced to the
19 GYE in 1995, and their populations have expanded dramatically both in distribution and number
20 since (Vucetich et al. 2005).

21 Antler data for bull elk were collected during the fall within three Elk Units
22 corresponding to four different subpopulations, the Northern Range Elk Unit, the Gravelly Elk
23 Unit, and the Gallatin-Madison Elk Unit (Fig. 1). This latter Elk Unit was divided into two Elk

1 Units (hunter districts 301, 310 and 311 for Gallatin, 360 and 362 for Madison) representing
2 different mountain ranges and thus elk subpopulations: the Gallatin and Madison (Hamlin 2004).
3 The Gallatin-Madison Elk Unit is 4,837 km² and borders the extreme northwest corner of
4 Yellowstone Park extending down to the Idaho/ Wyoming border. The Gravelly Elk Unit borders
5 the western portion of the Gallatin/Madison Elk Unit and the northern border of east central
6 Idaho. This Elk Unit covers approximately 4,898 km² encompassing the Gravelly, Greenhorn,
7 Snowcrest, Centennial, and Blacktail Mountain ranges. The Northern Yellowstone Elk Unit is
8 located directly north of the Yellowstone Park border between Cooke city and Gardiner and
9 north to the Boulder River divide. This Elk Unit is approximately 1,126 km² with the Absaroka-
10 Beartooth Wilderness comprising 75% of the area.

11 **Materials and Methods**

12 **Elk Data**

13 Montana Fish Wildlife and Parks (hereafter MT Fish and Game) collected measurements of
14 antler size and symmetry from a total of 8,690 hunter harvested bull elk from all four
15 subpopulations between 1982-2006, representing perhaps one of the most extensive datasets of
16 its kind [e.g., see Mysterud et al. (2005) who used data from 5,462 red deer (*Cervus elaphus*)
17 stags]. The Gallatin and Madison Elk Units contained 3,440 and 1,305 antler measurements,
18 respectively, the Gravelly Elk Unit 2,064 records, and the Northern Yellowstone Elk Unit
19 contained 1,892 records. Antler measurements were collected at hunter check stations within
20 each Elk Unit during the Montana firearm (e.g., not including archery hunting) hunting season
21 starting in mid-October and continuing through late November. However, one exception is the
22 Gardiner late hunt that starts between mid-December or early January through mid-February
23 (depending on yearly elk counts) within the Northern Yellowstone Elk Unit. All antler

1 measurements were made by MT Fish and Game biologists and game wardens. Beam length was
2 measured in millimeters along the outside of the main beam and points were counted for each
3 side.

4 Measurement error is important to account for in studies of FA, and Palmer and Strobeck
5 (1986) recommend repeated measurements as a method to incorporate measurement error into
6 quantitative tests of FA. Fortunately, measurement error in the number of points can be assumed
7 to be negligible because elk antler points are well defined (Hudson and Haigh 2002). For antler
8 length, however, we only obtained one length measurement in the field from 1982 – 2006,
9 making use of the methods of Palmer and Strobeck (1986) impossible for the entire dataset. To
10 understand the relative magnitude of measurement error in antler length relative to FA, we
11 conducted a field study in 2009 on elk antlers in museum specimens using the same methods as
12 in the field. We compared the magnitude of measurement error to FA using the z-test to
13 determine if there was significant overlap (De Veaux et al. 2006). In addition to measurement
14 error, we tested for directional asymmetry (Van Valen 1962, Palmer and Strobeck 1986) using
15 raw FA measurements and testing whether the confidence interval overlapped zero.

16 For the purpose of this study we examined relative measurements of FA assigned as the
17 absolute difference between each side divided by the largest side (Ditchkoff et al. 2001, Bartos &
18 Bahbouh 2006). We used relative FA instead of other measures used by other authors, such as
19 absolute, or body mass/antler mass ratio (Myserud et al. 2005) because previous authors
20 reported inconsistency between relative and absolute (Bartos & Bahbouh 2006) and because
21 relative FA would standardize for any trends in antler size over the study period. Body mass was
22 also unavailable in our study area. We tested for the degree of correlation between FA in antler
23 length and the number of points using Pearson's correlations to determine the independence of

1 these FA measures because other authors (e.g., Bartos et al. 2007) found strong correlations
2 between FA measurements in red deer.

3 **Environmental Covariates**

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

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

22 As a broad-scale measure of climatic variation, we used the North Pacific Oscillation
23 (NPO) anomaly index for November to March 1980 – 2007, obtained from the Climate Analysis

1 Section of the National Centre for Atmospheric Research (NCAR, USA
2 <http://www.cgd.ucar.edu/cas/jhurrell/indices.data.html#.mon>). The NPO is based on sea-
3 surface temperature anomalies measured over the North Pacific Ocean (Trenberth & Hurrell
4 1994), and has been linked to elk population dynamics (Hebblewhite 2005) like the similar, and
5 more extensively studied, North Atlantic Oscillation (NAO, Stenseth et al. 2002). We tested
6 relationships between the NPO and local winter and summer climate data from North
7 Yellowstone (reported in Vucetich et al. 2005) between 1980 and 2006, to validate the use of
8 NPO. We used a pair-wise correlation in STATA 10 (StataCorp 2008), to test relationships
9 between NPO and winter minimum temperature, snowfall, and summer precipitation from
10 Vucetich et al. (2005) for the Northern Range Elk Unit.

11 **Statistical Analysis**

12 We tested how elk density, winter NPO index, and age classes affected FA for each of the four
13 elk subpopulations over the 25-year time-series separately. We created categorical variables for
14 all age classes, where the yearling age class was treated as the Y-intercept. We also tested for
15 the effect three important biological interactions on FA; (1) elk density and NPO (2) elk density
16 and age classes, and (3) NPO and age classes based on their importance to ungulate population
17 growth rate in previous studies (Taper & Gogan 2002, Hebblewhite 2005, Mysterud & Ostbye
18 2006). We also examined non-linear effects of covariates. We developed an all inclusive set of
19 32 a-priori general linear models (GLMs)(McCullough & Nelder 1989) as a function of the main
20 effects and interactions to test our hypotheses about FA as a function of climate and elk density.
21 We tested for the appropriate distribution to model relative FA in comparison to Poisson,
22 negative binomial, and log-normal using the Vuong likelihood ratio test (Vuong 1989). We
23 found that the log-transformed antler length and number of points were still best fit by a Poisson

1 distribution (unpublished data). Therefore, we used a negative binomial link function to model
2 FA in both antler length and number of points using GLM.

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

15 **Results**

16 The number of antler records for prime age elk in Northern Yellowstone and Gallatin was higher
17 than all other age classes, in contrast the Madison and Gravelly Elk Units had more sub-adult
18 records (see Table 1). For all Elk Units the old age class had the lowest number of measurement
19 records, Gravelly (n=1), Madison (n=13), Gallatin (n=54), and Northern Yellowstone (n= 156).

20 We calculated mean age for all Elk Units, which revealed a slight contrast – representing

21 differences in hunter selection and harvest regulations: Northern Yellowstone ($\mu=6.79$),

1 Gravelly ($\mu=2.88$), Madison ($\mu=3.85$), and Gallatin ($\mu=4.55$). Raw measurements of antler
2 length and the number of points were correlated in all Elk Units, with Yellowstone the highest (r
3 = 0.86, $p<0.0005$), followed by Gallatin ($r = 0.79$, $p<0.0005$), Madison ($r = 0.71$, $p<0.0005$), and
4 Gravelly ($r = 0.58$, $p<0.0005$).

5 However, this correlation broke down when we considered fluctuating asymmetry.
6 Relative FA in length and points were only weakly correlated in all Elk Units, with the highest in
7 Gallatin ($r = 0.38$, $p<0.0005$), followed by Madison ($r = 0.33$, $p<0.0005$), and Gravelly ($r = 0.30$,
8 $p<0.0005$) and Yellowstone ($r = 0.24$, $p<0.0005$). Relative FA in points for the Yellowstone Elk
9 Unit was lower for subadult and old age classes and much higher for prime aged individuals.
10 The relationship between FA in length and FA in points was the weakest of all Elk Units in
11 Yellowstone, especially for prime aged animals, compared to all other Elk Units (Fig. 2). Other
12 Elk Units showed more variable results, but generally, FA in points and length were not strongly
13 correlated (Fig 2), with the biggest discrepancies occurring in yearlings in Gravelly, old and
14 subadult elk in Gallatin, and subadults in Madison (Fig. 2).

15 We obtained 109 estimates of measurement error from 65 different antler pairs to
16 examine measurement error in antler length. Absolute FA for this subset of antlers was 37.1 mm
17 (SD = 34.99), significantly greater than (Z-test p-value < 0.00005) the measurement error which
18 was 7.9 mm (SD = 13.1) only 21% of absolute FA. Therefore, we did not consider this low level
19 of measurement error in antler length in subsequent analyses. There was no evidence for
20 directional asymmetry as the 95% confidence intervals for raw FA for each Elk Unit overlapped

1 zero (Yellowstone, $\mu = 0.50$, 95% CI -2.9 to 3.9; Gravelly, $\mu = -2.36$, 95% CI -5.58 to 0.85;
2 Madison, $\mu = -0.94$, 95% CI -5.42 to 3.54; and Gallatin, $\mu = 2.73$, 95% CI -0.52 to 5.98).

3 **Climate Relationships**

4 The winter NPO was negatively correlated with winter minimum temperature ($r = -0.7$,
5 $p < 0.001$), summer precipitation ($r = -0.50$, $p < 0.001$), and positively correlated with annual
6 snowfall ($r = 0.42$, $p < 0.001$). High NPO values were related to warm wet winters followed by
7 hot dry summers; conversely cold dry winters were related to wet summers. Therefore, severe
8 winters are related to high NPO values at this latitude and elevation (Trenberth & Hurrell 1994).
9 We found no evidence for non-linear effects, nor any significant interactions.

10 **Fluctuating Asymmetry in Length**

11 Model selection for FA in length was less certain than for FA in points (range ΔAIC in length
12 0.21- 0.34 and ΔAIC points 0.34 – 0.58), respectively. All top models were relatively simple for
13 each subpopulation with 2-3 parameters for each model including ages. Models were relatively
14 consistent both within Elk Units (unpublished data) and between subpopulations. For example, in
15 the Northern Yellowstone subpopulation, variable importance weights (Burnham & Anderson
16 1998) in Table 2 show that amongst the top model set (0-4 ΔAIC), elk density and climate both
17 had an Akaike weight of 0.79, prime age classes were 0.73, and old and subadult age classes
18 were both < 0.30 Akaike weight. Therefore, despite model selection uncertainty in the top set for
19 Yellowstone, all top models showed FA in antler length increased with increasing elk density,
20 climatic severity, and in prime age classes. For all other subpopulation's variable of importance
21 weights displayed a similar pattern, with most of the variable weight retained in elk density (AIC
22 weight, $w_i = 0.69- 0.94$, Table 2). Variable importance weights for age classes in other

1 subpopulations were moderate depending on if the age class was retained in the top model (see
2 Table 2, 3a,b).

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

9 Elk density was positively correlated with length FA in the Gardiner, Gallatin, and
10 Gravelly subpopulations (Table 4, Figure 3a), consistent with our prediction that intraspecific
11 competition would increase nutritional stress. However, in the Madison, elk density was
12 negatively correlated with FA in relative antler length. Despite this support in principle for our
13 predictions, however, the coefficients for elk density effects were weak and not statistically
14 significant in all four subpopulations (Table 4). Figure 3 shows relationships for Northern
15 Yellowstone Elk Unit illustrating the wide confidence intervals – results were similar for the
16 other three Elk Units and are not shown here but coefficients are given in Table 4. The weak
17 statistical effects of climate and elk density were further evidenced in the low explanatory power
18 of all the top models for length relative FA (Table 4) – the best models explained only from 0.5-
19 4 % of the variation in FA.

20 **Fluctuating Asymmetry in the Number of Points**

21 Model selection was relatively more certain for FA in antler points across compared to length
22 (Table 1). All top models were relatively simple for all subpopulations with 2-3 parameters
23 including age classes. Variable importance weights for the set of top models (0-4 Δ AIC) were

1 similar across all subpopulations (Table 2). Elk density accounted for the majority of variable
2 importance weights; in Northern Yellowstone the Akaike weight for density was 0.72, in
3 Gravelly 0.72, Gallatin 0.69, and Madison 0.88 (Table 2). Climate and age class were retained in
4 top models for each subpopulation, though with at least half or less the variable importance
5 weight (Table 4). While there was high model selection uncertainty for our set of top models, all
6 top models included the variables elk density, climate and ages classes for each Elk Unit (Table
7 2, unpublished data).

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

15 Elk density was negatively correlated with the FA in points in the Northern Yellowstone,
16 Gallatin, and Gravelly subpopulations, consistent with predictions, but positively correlated with
17 elk density in the Madison (Table 4). Once again the coefficients for elk density effects were
18 weak and not statistically significant (Table 4). Climate was not retained in any of our top model
19 except for Yellowstone and had little of the AIC variable importance weight, AIC $w_i = 0.12 -$
20 0.25 . Overall, models explaining FA in the number of points explained slightly more variation
21 than FA in length, but top model R^2 values were still low, ranging from $0.1 - 0.11$.

22 **Discussion**

1 We found weak support for our main hypotheses that adverse climatic conditions and increasing
2 elk density increased FA in either length or the number of points of bull elk antlers in the GYE.
3 Although we had a large sample size of 8,690 measurements, our models could not explain more
4 than 11% of the variation, and coefficients of covariates were statistically and biologically weak.
5 Our large sample size provided strong statistical power, but very little explanatory power with
6 the covariates we selected for analyses. Elk density was consistently positively related to FA in
7 length for 3 of 4 subpopulations, but interestingly we found a negative relationship with elk
8 density and FA in points for 3 of 4 analyses. Only the Madison subpopulation had a negative
9 relationship with elk density and FA in length and a positive relationship with FA in points.
10 Increasing winter severity did increase FA in 3 of 4 subpopulations, but the effect was
11 biologically weak although statistically significant, and only manifested in the Northern
12 Yellowstone subpopulation in FA in antler length and the number of points. Therefore we
13 conclude that the biological impacts of climatic and density-induced competition are weak and
14 inconsistent on fluctuating asymmetry in bull elk in the GYE.

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

1 the average FA in length increase whereas the average FA in points in the population would
2 decrease (see Figure 2 Yellowstone).

3 Effects of age were generally consistent with our expectations, but were weak. We found
4 only slight associations with two (Gallatin and Madison) of the four analyses for the relationship
5 between ages and relative FA in points and length (Fig. 2). However, the sample size for the old
6 age class was substantially smaller than all other age classes. The subadult age class followed
7 the predicted pattern with a slightly higher level of FA in 3 of 4 subpopulations in both antler
8 length and points. Analysis of the dynamics of age-classes themselves would be useful to test
9 hypotheses about climate effects, hunting, and even the recent recolonization of wolves in the
10 GYE (Vucetich et al. 2005). Wolves often select for male elk that have been weakened during
11 the rut. It may also be possible that elk in poorer condition would be more susceptible to wolf
12 predation, therefore removing elk with greater FA from the population.

13 Overall, our weak and negative results are in contrast to several recent studies. For
14 example, Mysterud et al. (2005) found antler size of red deer in Norway to be positively
15 correlated with favorable conditions and negatively correlated with severe winters. While
16 Mysterud et al. (2005) used antler size and body size (which we were unable to measure), antler
17 size and the number of points and length are correlated in ungulates. Therefore, it seems unlikely
18 for methodological differences to drive differences between the Norwegian red deer study and
19 our results from the GYE. In another study on antler characteristics in fallow deer (*Dama dama*),
20 Putman et al. (2000) found environmental stress to significantly affect the relationship of FA in
21 young age deer. Putman et al. (2000) emphasized intraspecific competition by using measures of
22 food quality and deer density, the latter similar to our study.

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

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

1 potentially increasing the additive genetic variance in antler traits, despite their generally low
2 heritability (Coltman et al. 2003).

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

18

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3

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Table 1. Number of records of measurements of fluctuating asymmetry (FA) from male elk antler measurements grouped by age class from four elk management units (Elk Units), Greater Yellowstone Ecosystem (GYE), 1982-2006.

Age Class	Elk Management Unit (ELK UNIT)				
	Northern				
	Yellowstone	Gallatin	Madison	Gravelly	Total
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

Table 2. Top general linear models (GLMs) for bull elk fluctuating asymmetry (FA) in each of four elk management units in the Greater Yellowstone Ecosystem (GYE), 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		Log			
	Structure	N	K	Likelihood	Δ 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. Description of variable weights of importance for relative FA in length and points in each ELK UNIT. A sum of weights is given for all variables included within our set of top models (0-4 Δ AIC).

Relative FA								
Length & Points	ELK UNIT							
Variable	Northern Yellowstone		Gravelly		Gallatin		Madison	
	Length	Points	Length	Points	Length	Points	Length	Points
Elk Density	0.78	0.72	0.94	0.72	0.9	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	0.4	0.52	0.58	0.69	0.03	0.28
Old	0.3	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	0.9	0.69	0.98	0.88

Table 4. Top statistical models of Fluctuating asymmetry in bull elk antler length and number of points from the Greater Yellowstone Ecosystem, Montana from 1982 to 2006. Top model structure and coefficients with standard errors (SE) and R² values are reported for relative measures of FA length and points for each ELK UNIT. Symbols are: E = elk density, C = NPO winter, A = ages, S = subadult, P = prime, and O = old.

ELK UNIT		AGES													
LENGTH															
RELATIVE		Elk				Sub-				Prime				Old	R ²
(FA)	Model Structure	B ₍₀₎	SE	density	SE	NPO	SE	adult	SE	Prime	SE	Old	SE	R ²	
	B0 + B(E) +										0.3				
Gardiner	B(C) + B(P)	-3.36	0.729	5.22E-05	4.96E-05	0.026	0.082			-0.67	08			0.04	
											0.2				
Gallatin	B0 + B(E) + B(P)	-3.36	0.308	2.77E-06	1.96E-04					-0.48	87			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)															
	B0 + B(E) +														
Gardiner	B(C) + B(S)	-3.09	0.643	-6E-06	4.61E-05	-0.022	0.069	1.06	0.363					0.04	
	B0 + B(E) +										0.3	1.3	0.6		
Gallatin	B(A)	-3.09	0.643	-1.5E-05	1.60E-04			1.21	0.320	0.83	07	2	21	0.04	
Madison	B0 + B(E) + B(S)	-2.96	0.416	0.000027	1.11E-04			0.44	0.260					0.02	
											0.2				
Gravelly	B0 + B(E) + B(P)	-2.29	0.320	-1.4E-05	5.24E-05					-0.45	08			0.01	

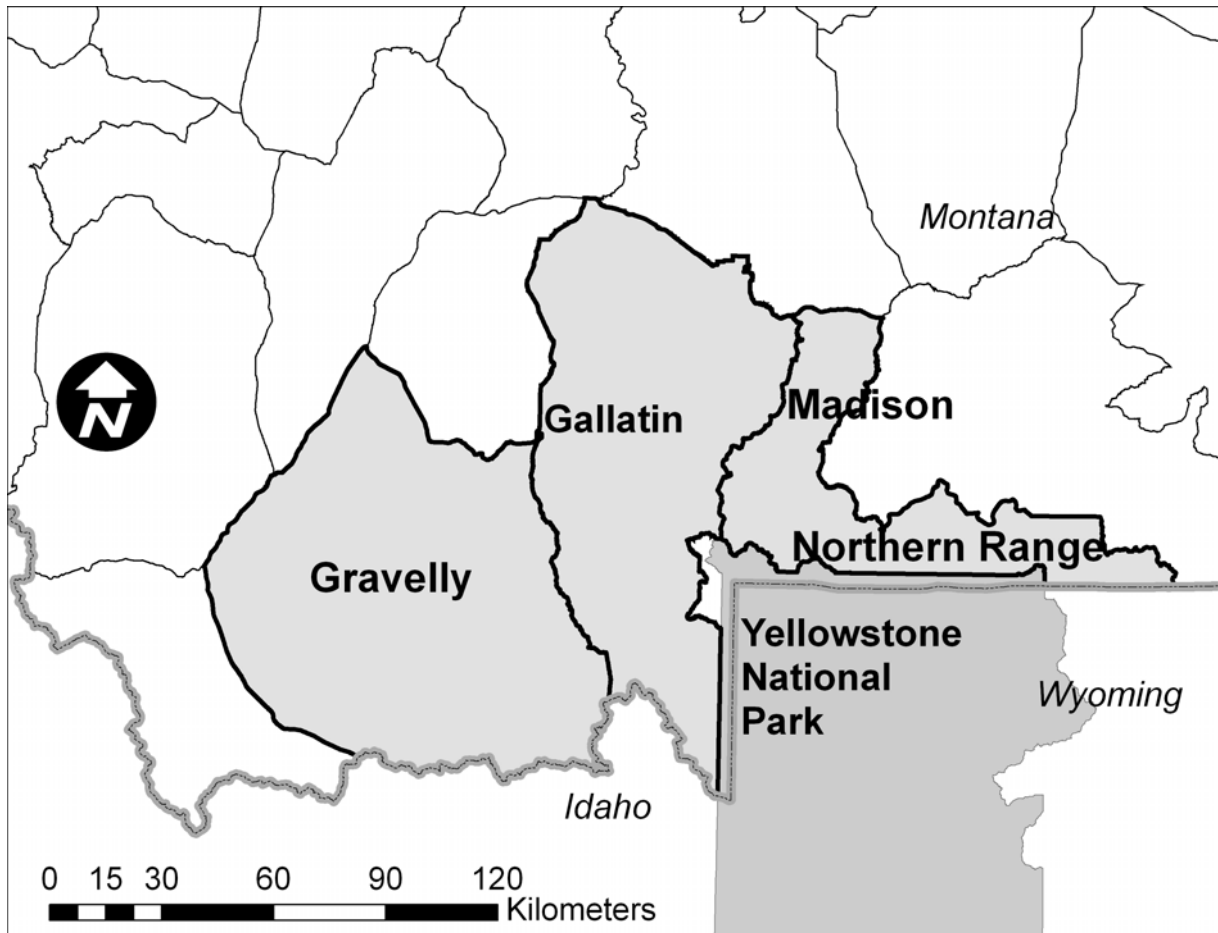


Figure 1: Study area for the analysis of fluctuating asymmetry from bull elk within four elk management units (Elk Units) within the Greater Yellowstone Ecosystem (GYE) from 1982-2006.

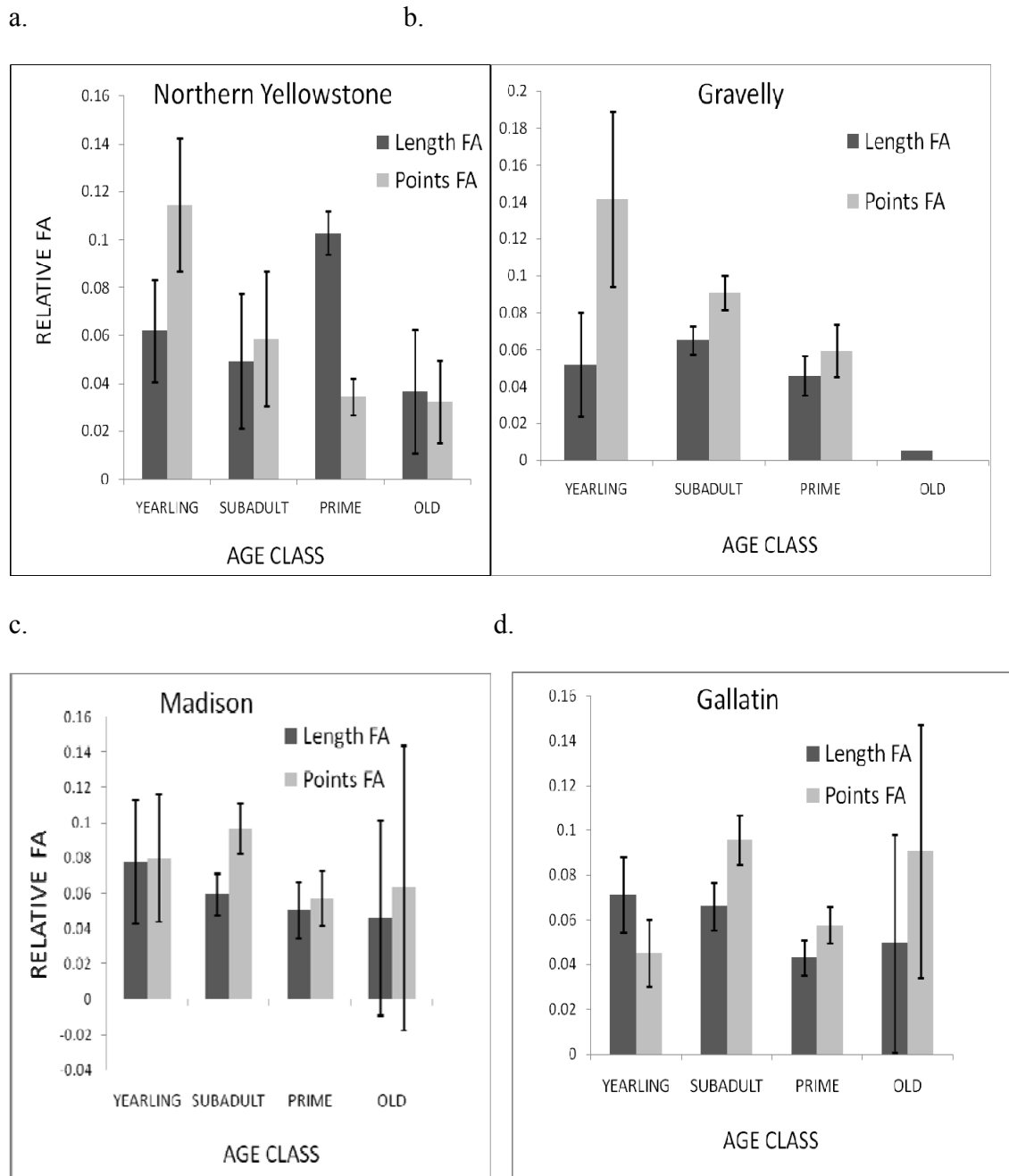


Figure 2. Relationships between age class and relative fluctuating asymmetry (FA) in length and points for each elk management unit (Elk Unit) in the Greater Yellowstone Ecosystem (GYE) from 1986-2006, shown with standard error bars. Numbers along the y-axis is value of relative (abs/ largest side) FA.

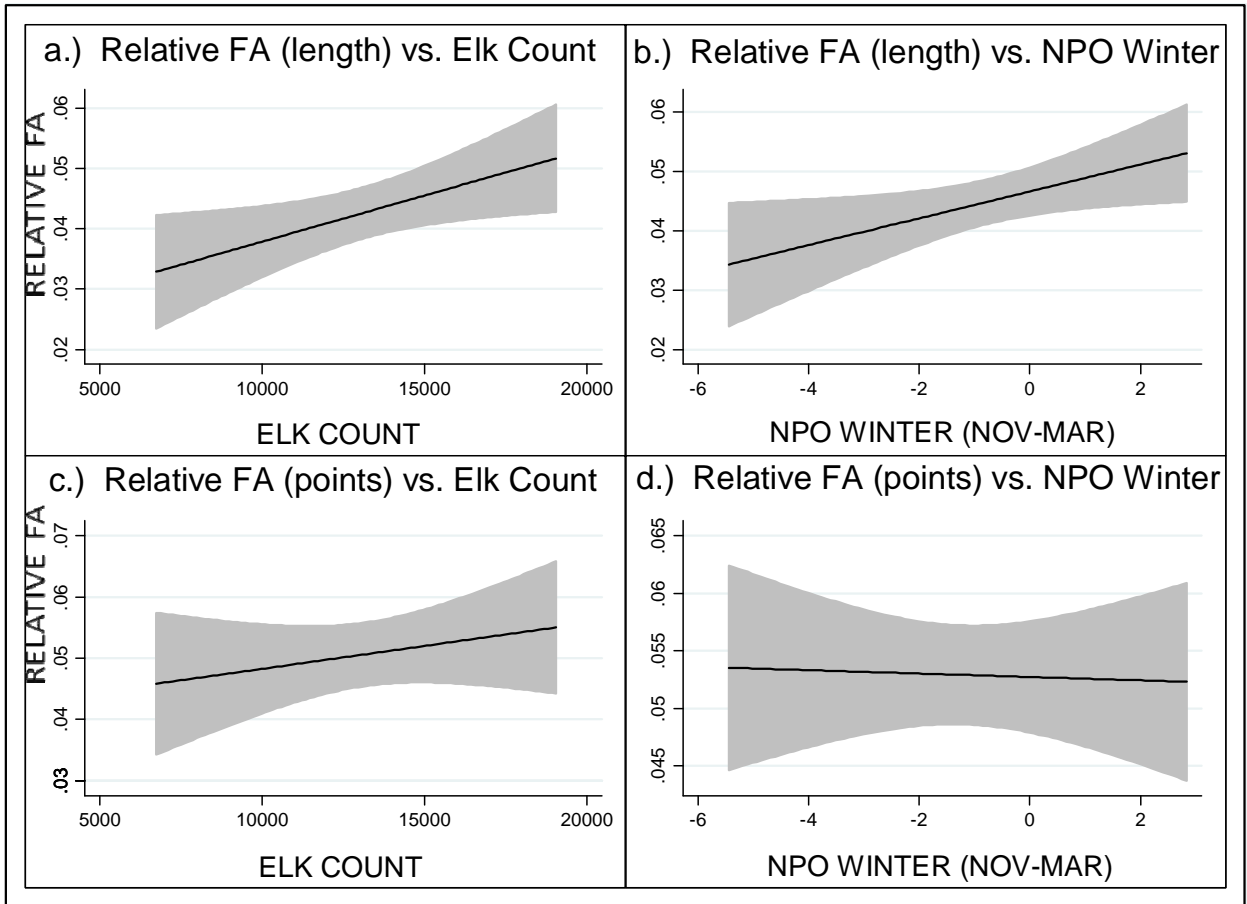


Figure 3. Relative FA vs. elk count and NPO winter index for length and points in the Northern Yellowstone elk unit for the years 1982- 2006. Positive NPO values relate to warm wet winters and negative values relate to cold dry winters. Y-axis relates to the percentage of relative FA.