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Environmental stress and developmental stability in dentition of the Yellowstone grizzly bears

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Asymmetry in bilateral traits is often used to assess an individual's quality and stress resistance, but stress-induced variation in developmental stability is largely undocumented for free-living populations. Over many years, grizzly bears (*Ursus arctos horribilis*) extensively foraged around garbage dumps in Yellowstone National Park. Abrupt closure of these dumps 26 years ago was a severely stressful event and was followed by excessive mortality and a many-fold increase in grizzly home-range size. I examine how this stress affected developmental stability by comparing dentition of bears born before and after the dump closure. I predicted that (1) asymmetry in dentition should be greater in bears born after dump closure compared to before closure, and asymmetry in sexually selected canines should change more than nonsexually selected premolars following dump closure and (2) the relationship between tooth asymmetry and tooth size should change in the populations following the stressful events as compared with populations before stressful events. I found that developmental stability of canines, which are under directional sexual selection in males, was more responsive to stress compared to that of male premolars or female dentition (both under stabilizing selection), and, because of the increased cost of canine production, fewer animals were able to achieve both large size and symmetrical development of these teeth, and thus the slope of the relationship between fluctuating asymmetry and canine size increased. I conclude that stress appears to act as an honesty-reinforcement mechanism in sexual selection for symmetrical dentition. *Key words:* dentition, developmental stability, environmental stress, grizzly bears, sexual selection, *Ursus arctos horribilis*. *[Behav Ecol 9:339–344 (1998)]*

Periods of rapid environmental change can alter individual energy expenditure during development and thereby increase phenotypic variation in populations (e.g., Parsons, 1993, 1995). Such increased variation may be evident in deviations from optimal development in morphological traits (i.e., ideal concordance between genotype and phenotype), which is expressed as increased asymmetry (Mather, 1953; Palmer and Strobeck, 1986; Swaddle and Witter, 1994, Van Valen, 1962; Zakharov, 1987). Although environmental stress can be the proximate cause of increased fluctuating asymmetry (FA), the ability to cope with stress must have a genetic basis (Thornhill and Sauer, 1992). Several studies found significant, although usually low, heritability for FA (Bailit et al., 1970; Livshits and Kobyliansky, 1989; Møller and Thornhill, 1997; Potter and Nance, 1976; Reeve, 1960). Because of its low heritability, asymmetry is commonly used to assess fitness of an individual (e.g., Bailit et al., 1970; McKenzie and Clarke, 1988; Mitton and Grant, 1984; Møller and Pomiankowski, 1993; Møller and Thornhill, 1997; Watson and Thornhill, 1994).

Although close associations between stress and developmental stability have been documented in numerous laboratory experiments (e.g., Imasheva et al., 1997; Sciulli et al., 1979; Siegel and Doyle, 1975a,b), studies of free-living populations documenting effects of distinct stressful events are rare (e.g., Møller, 1993). For example, temporal increases in skeletal fluctuating asymmetry in free-living populations as a presumed result of pollution have been documented for a number of animal taxa (e.g., Jagoe and Haines, 1985; Pankakoski et al., 1992; Schandorff, 1997; Valentine and Soulé, 1973; Zakharov and Yablokov, 1989). However, several classic studies have relied mostly on examination of FA in museum specimens from different populations (Manning and Chamberlain, 1994; Wayne et al., 1986) and may partially confound interpopulation differences in FA by intrapopulation increases in FA following of stress (e.g., Picton et al., 1992; Swaddle et al., 1994, 1995).

A single stressful event in the Yellowstone National Park population of grizzly bears (*Ursus arctos horribilis*) provided a unique opportunity to examine stress effects on developmental stability of morphological traits. For more than 13 years, Yellowstone grizzlies foraged extensively around open garbage dumps maintained at the ecocenters of the park (Craighead et al., 1995). Before 1970 (hereafter called the "preclosure period"), approximately 125 tons of edible trash were deposited daily at these dumps, and all grizzlies of the Yellowstone population ($n \cong 300$) foraged there during summer (Craighead et al., 1995). Dumps were abruptly closed and fenced off in 1969–70, causing excessive mortality and more than a fivefold increase in annual home ranges of grizzlies (Blanchard, 1987; Craighead et al., 1995). Summarizing data on bear movements and mortality after the summer of 1970–1980 (hereafter called the "postclosure period"), Craighead et al., (1995: 377) concluded that "the grizzly bear population was under immense stress following closure of the dumps."

Variation in the developmental stability of tooth morphology is particularly suitable for studying consequences of severe stress (e.g., Bailit et al., 1970; DeBennardo and Bailit, 1978; Harris and Nweeia, 1980; Garn et al., 1965; Siegel and Smookler, 1973). Development of bunodont teeth occurs over a short period of time and is strongly influenced by diet, prenatal exposure to stressors, disease, and consanguinity (Bailit et al., 1970; Corruccini and Potter, 1981; DeBennardo and Bailit 1978, Garn et al., 1965; Manville, 1992; Niswander and Chung 1965; Suarez, 1974). These teeth do not change after eruption into the oral cavity (e.g., Garn et al., 1965), and their natural wear is limited to the extremely hard enamel surface,

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with maximum wear commonly smaller than measurement error (see below; Greene, 1984). Upper maxillary canines and the third premolar teeth ("premolars") were the focus of this study because they play a different role in behavioral interactions of grizzlies. Canines are likely to be under sexual selection because they are prominently displayed in intra- and intersexual interactions in grizzlies and are also sexually dimorphic (e.g., Craighead et al., 1995). The sexually monomorphic premolars are not visible during such interactions and therefore are unlikely to be under sexual selection (see also Harvey et al., 1978; Kappeler, 1996; Kay et al., 1988; Manning and Chamberlain, 1993, 1994; Plavcan and van Schaik, 1992, 1994).

First, I show that canines and premolars show FA between right and left sides of the upper jaw. I then tested the following predictions: (1) size of sexually dimorphic canines should be linearly negatively proportional to canine asymmetry, under the assumption that canine size is under directional selection, whereas asymmetry in premolar size should be greater in sizes deviating from the population mean, assuming that (a) premolar size is under stabilizing selection (Møller, 1992; Møller and Pomiankowski, 1993; Parker and Leamy, 1991) and (b) canine size indicates male phenotypic quality and large canines are costly to produce (Evans, 1993; Møller, 1992; Møller and Pomiankowski, 1993; Rowe et al., in press). (2) Asymmetry in dentition should be greater in bears born during the postclosure period compared to bears born during the preclosure period, and asymmetry in sexually dimorphic canines should show greater change than premolars following dump closure. Here I assumed that (a) directional selection on traits favors greater response of such traits to environmental conditions and (b) asymmetry in measured traits results from failures of homeostasis during trait development (Møller, 1992; Møller and Pomiankowski, 1993; Soulé and Cuzin-Roudy, 1982), thereby making directionally selected sexually dimorphic traits more variable between individuals and more responsive to variation in environmental conditions (Hill, 1995; McLain, 1993; Parsons, 1995). (3) Finally, costs of changes in food distribution and quality following dump closure (Craighead et al., 1995) are likely to be unequal among individuals because territorial and hierarchical behaviors during stressful conditions commonly contribute to increased variation in individual quality (Parsons, 1995). Under stressful conditions, the development of symmetrical and large traits might be more difficult to achieve. If development of large and symmetrical traits depends on individual quality, then the slope of the FA-versus-trait–size relationship should increase because relatively fewer individuals would be able to develop large and symmetrical traits.

METHODS

I measured asymmetry in dentition in 52 grizzly skulls without visible nondevelopmental damage of teeth. I measured canine diameter and premolar width along the anteroposterior axis at the alveolar margin. Tooth height was measured from the apex of the crown to the alveolar margin. Skull length (condylobasal length) was measured from posteriormost point on occipital condyles and the anteriormost point on premaxillary bones between the first pair of upper incisor teeth. Only individuals with fully erupted molars (adults > 3 years of age in my sample) were measured. Skulls of grizzly bears from a single population in Yellowstone National Park were from the John and Frank Craighead Collection, located at the Phil H. Wright Zoological Museum at the University of Montana in Missoula, Montana, USA (UM) and from the Montana Department of Fish, Wildlife, and Parks collection in Bozeman, Montana, USA (FW). Data on sex and year of birth were obtained by an independent observer from museum catalogs after asymmetry in dentition was measured.

To estimate reliability of measurements, I repeated all measurements twice (FW) or four times (UM). Average values of these measurements were used in the analyses. Repeatability of measurements was sufficiently high (>91%), and the variance of within-tooth measurements was significantly smaller than the variance of between-tooth measurements for all traits [Becker, 1984; e.g., for canine height (UM): 0.12 versus 2.11, $F_{48} = 10.92$, $n_1 = 4$, $n_2 = 24$, $p = .0018$]. The variance of asymmetry expected from measurement error was significantly smaller than the variance of observed tooth asymmetry [Palmer and Strobeck 1986; ANCOVA of model with jaw side (left or right) to control for possible directional asymmetry, individual, and the mean of replicates versus model with jaw side, individual, and replicates as independent factors [e.g., for canine height (UM), $F_{3,24} = 15.32$, $p < .001$].

Mean tooth height (width or diameter) of an individual was the mean of left and right tooth [0.5(L + R)]. Absolute asymmetry was an absolute value of (L − R). Relative asymmetry was $(|L - R|)/0.5(L + R)$. I used the largest of the paired characters in regressions of asymmetry on trait size (Sullivan et al., 1993). I evaluated plots of untransformed data and results of linear and second-order polynomial regressions [PROC RSREG of SAS software (1989)] to examine whether the asymmetry versus tooth size relationship was linear or U-shaped. I examined residual plots and statistics to ensure validity of normality and variance homogeneity assumptions in regressions (Montgomery and Peck, 1992; SAS Institute, 1989).

RESULTS

Males had larger skulls and proportionally longer canines than females (Table 1). Sexes were similar in premolar size and dental asymmetry (Table 1). Results were similar for tooth diameter and width (Table 1). Thus, below I report only analyses of variation in tooth height. Statistically, canine and premolars showed FA, as the population mean of left minus right tooth heights did not differ from zero (canines: both $t < .9$, $p > .40$; premolars: both $t < 1.1$, $p > .30$) and asymmetries were normally distributed (the Shapiro and Wilk's test, both $W < .85$, $p < .001$).

In males, canine asymmetry was negatively linearly related to canine height, but a second-order polynomial regression best fit the relationship between premolar asymmetry and premolar height (canines: linear regression $F = 25.37$, $p < .0001$; second-order polynomial regression: $F = 0.824$, $p = .37$; premolars: linear regression $F = 4.21$, $p = .06$; second-order polynomial regression: $F = 11.89$, $p = .001$; Figure 1). In females, tooth FA versus tooth height relationship was best fitted by second-order polynomial for both canines and premolars (canines: linear regression $F = .075$, $p = .78$; second-order polynomial regression: $F = 7.77$, $p = .003$; premolars: linear regression $F = .167$, $p = .69$; second-order polynomial regression: $F = 3.65$, $p = .057$; Figure 2).

Canines, premolars, and overall skull length were smaller in males born during postclosure than in males born during preclosure periods (Table 1). To account for changes in trait size, relative asymmetry was used to compare changes in dental asymmetry between pre- and postclosure periods. Relative asymmetry in canines, but not in premolars, increased in males born during the postclosure period (Figure 3a). Dental asymmetry of females did not differ between the two periods (Figure 3b). In males, the relationship between asymmetry and tooth height changed in both canines and premolars between pre- and postclosure periods (canines: Figure 1; premolars: preclosure regression coefficient (β) = -0.06 ± 0.02

Table 1

Morphological traits of grizzly bears born before (before 1970) and after (after 1970) dump closure at Yellowstone National Park [untransformed means ± SD (CV)]

	Preclosure period		Postclosure period		
Morphological trait	Males (n = 19)	Females (n = 12)	Males (n = 15)	Females (n = 8)	p_{sex}
Canine height (mm)	40.25 ± 4.83 (12.00)	33.20 ± 2.91 (8.78)	36.48 ± 4.05 (11.09)	31.86 ± 3.89 (12.22)	.0001[b]
Canine diameter (mm)	21.39 ± 3.06 (14.29)	16.33 ± 1.80 (11.05)	18.72 ± 2.15 (11.47)	14.42 ± 2.40 (16.67)	.0001[b]
Premolar height (mm)	10.70 ± 1.22 (11.36)	10.14 ± 0.72 (7.13)	10.57 ± 0.82 (7.72)	9.26 ± 0.98 (10.57)	.02
Premolar width (mm)	14.65 ± 1.70 (11.58)	13.37 ± 1.69 (12.62)	16.27 ± 1.28 (7.89)[a]	14.84 ± 0.32 (2.15)	.04
Condylo-basal length (cm)	32.64 ± 2.53 (7.76)	28.71 ± 2.16 (7.52)	30.13 ± 2.43 (8.07)[a]	27.87 ± 3.28 (11.75)	.0004
FA in canine length (mm)	1.13 ± 0.97 (85.64)	1.15 ± 0.70 (61.28)	2.44 ± 1.96 (80.24)[a]	1.14 ± 0.58 (51.39)	.16
FA in canine diameter (mm)	0.99 ± 1.13 (113.95)	1.03 ± 1.40 (135.81)	1.46 ± 1.97 (135.03)	0.43 ± 0.64 (148.94)	.17
FA in premolar height (mm)	0.69 ± 0.50 (72.98)	0.80 ± 0.66 (82.18)	0.40 ± 0.42 (105.85)	0.23 ± 0.15 (65.17)	.89
FA in premolar width (mm)	0.44 ± 0.37 (83.24)	0.40 ± 0.26 (64.40)	1.13 ± 1.61 (143.34)	0.29 ± 0.36 (120.69)	.75

[a] Significantly different from preclosure period at $\alpha < 0.05$ in sequential within-sex Bonferroni tests.

[b] Significantly different between sexes (pre- and postclosure combined) at $\alpha < 0.05$ in sequential Bonferroni tests.

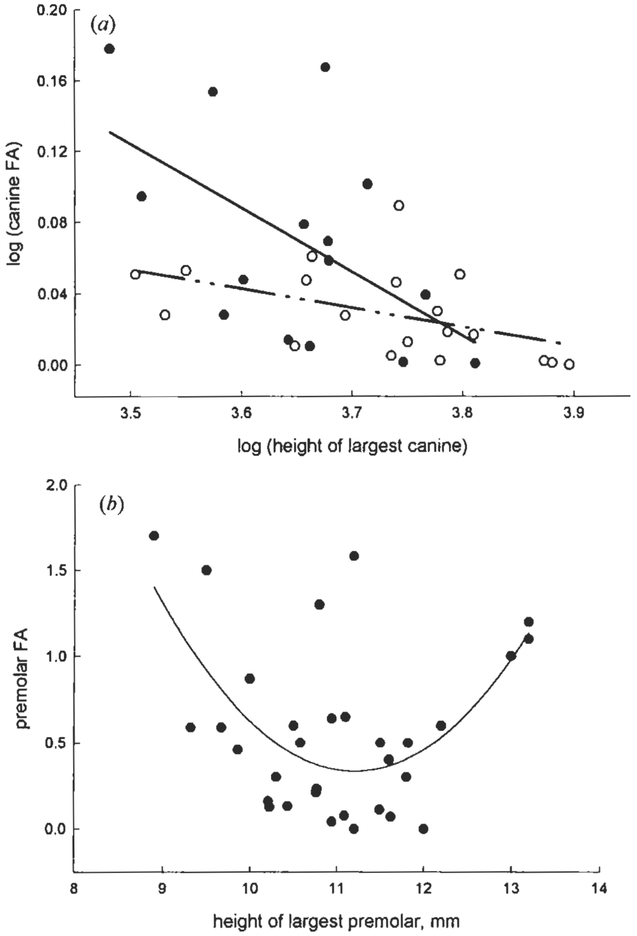

Figure 1
(a) The relationship between absolute fluctuating asymmetry (FA) and largest canine [overall linear regression (combining pre- and postclosure periods) coefficient $\beta = -0.23\pm0.06$ (SE), $t = -3.60$, $p = .001$]. Graphs show changes in relationship between absolute FA and canine height between male grizzly bears born during preclosure (dashed line) and postclosure (solid line) periods. Preclosure $\beta = -0.11\pm0.05$ (SE), $t = -2.50$, $p = .026$; postclosure $\beta = -0.38\pm0.15$, $t = -2.37$, $p = .03$). Slope is steeper in postclosure regression (ANCOVA, $F = 4.25$, $p = .056$). Log scale is used to accomodate changes in canine size between two periods.
(b) The relationship between absolute FA and the largest premolar (second-order polynomial $\beta = -0.05\pm0.02$, $t = -3.35$ $p = .002$) in male grizzly bears in the Yellowstone population.

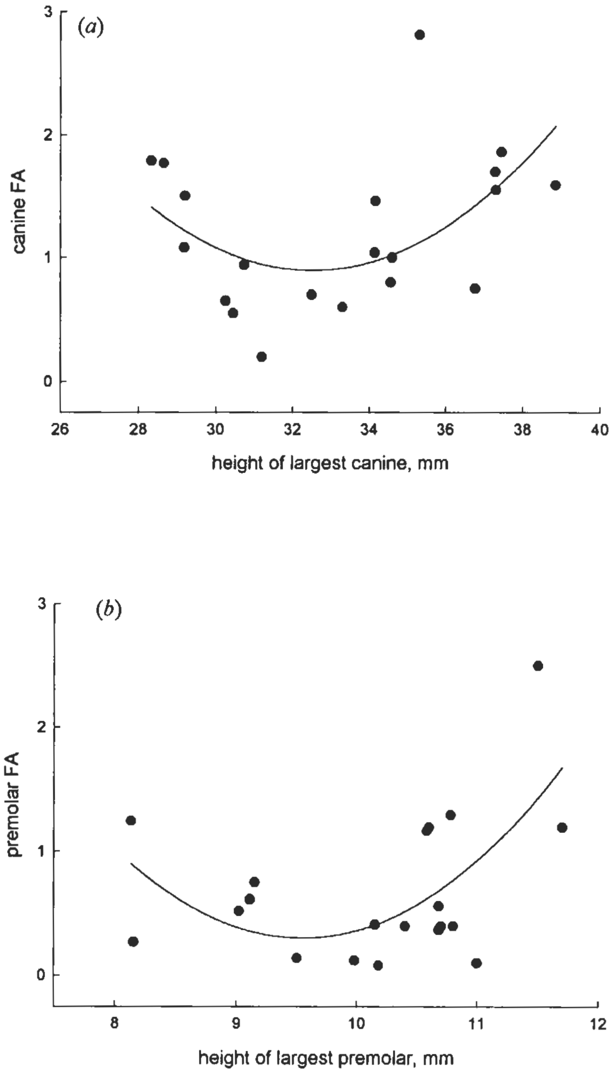

Figure 2
The relationship between absolute fluctuating asymmetry (FA) and largest (a) canine (second-order polynomial $\beta = 0.09\pm0.05$ (SE), $t = 2.25$, $p = .035$) and (b) premolar (second-order polynomial $b = 0.06\pm0.03$, t = 2.39, $p = .04$) in female grizzly bears in the Yellowstone population.

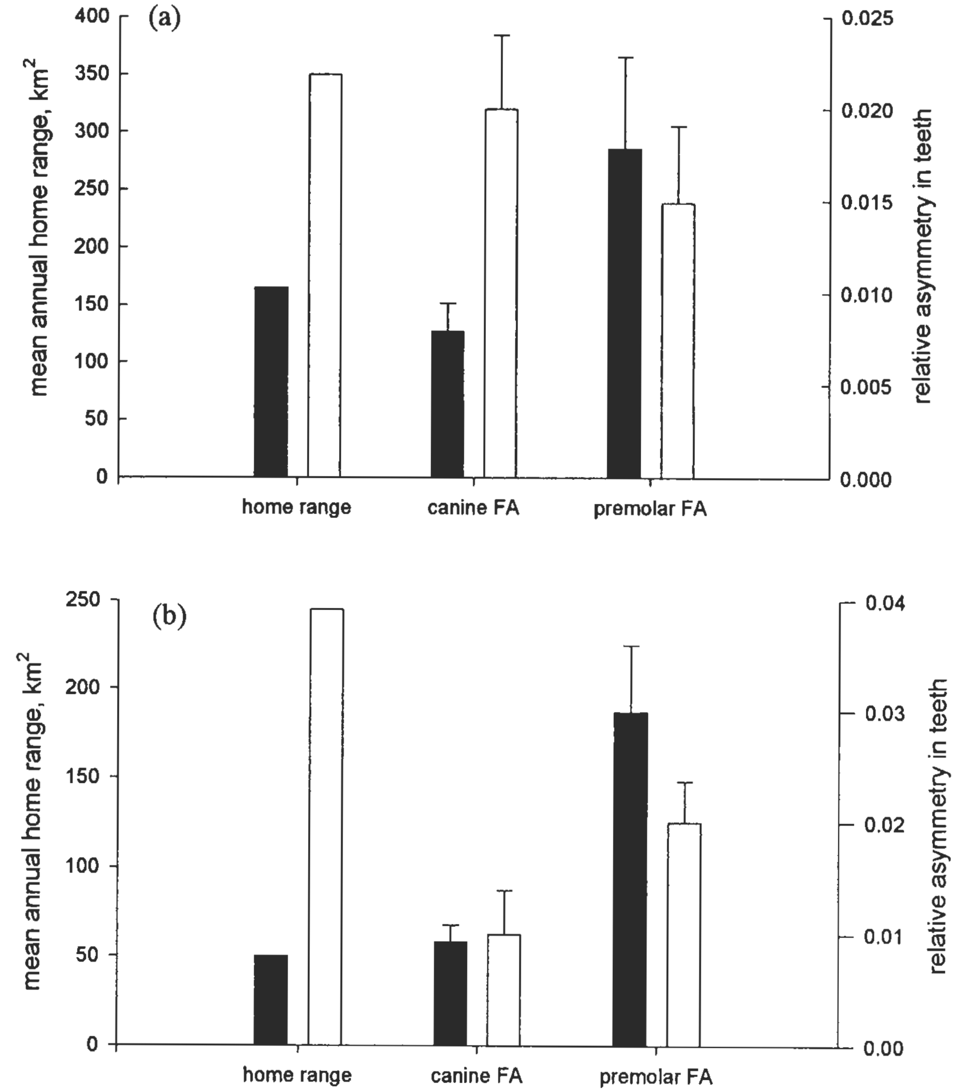

Figure 3
Changes in annual home ranges and relative asymmetry in teeth between the preclosure (solid bars) and postclosure (open bars) periods for (a) males and (b) females. Mean home ranges are for 5 years during preclosure (1963–68) and 5 years during postclosure (1975–80) periods, data from Craighead et al. (1995).

(SE), $t = -2.98$, $p = .008$; postclosure $\beta = -0.05 \pm 0.03$, $t = -1.79$, $p = .09$; ANCOVA for difference, $F = 4.24$, $p = .048$]. In females, the relationship between asymmetry and tooth height did not change (both $F < 2.0$, $p > .20$) between the two periods for either canines of premolars (canines: preclosure $\beta = 0.03 \pm 0.02$, $t = 1.96$, $p = 0.09$; postclosure $\beta = -0.03 \pm 0.03$, $t = -0.96$, $p = .44$; premolars: preclosure $\beta = -0.01 \pm 0.006$, $t = -1.98$, $p = .08$; postclosure $\beta = -0.005 \pm 0.02$, $t = -1.633$, $p = .24$).

DISCUSSION

Phenotypic expression of any component of an organism, including sexual traits, is ultimately controlled by developmental pathways that allocate an organism's resources between the competing demands of maintenance, growth, and reproduction (Badyaev, 1997; Emlen, 1996; Kodric-Brown and Brown, 1984; McLain, 1993; Nur and Hasson, 1984; Parsons, 1995; Sibly and Calow, 1986; Williams, 1966; Zahavi, 1975). Periods of rapid environmental change may cause reallocation of resources away from less important developmental processes toward more essential traits (Graham et al., 1993; Kieser, 1993), leading to unequal effects of stress on different kinds of traits (Parsons, 1995). For example, short-term environmental stress resulting from inadequate nutrition (e.g., Harris and Nweeia, 1980; Swaddle and Witter, 1994), increased parasite infestation (e.g., Potti and Merino, 1996), decreased habitat suitability (Manning and Chamberlain, 1994), pollution (Hurst et al., 1991; Møller, 1993; Schandorff, 1997; Zakharov and Yablokov, 1989), or climatic extremes (e.g., Badyaev and Ghalambor, in press; Parsons, 1995) can directly influence allocation trade-offs and the expression of condition-dependent secondary sexual traits (Hill, 1995). Similarly, I found support for an a priori prediction that different tooth groups respond differently to environmental stress. Developmental stability of canines, which are under directional sexual selection for increased size in males (Figure 1), was more responsive to environmental stress compared to developmental stability of male premolars or female dentition, which are under stabilizing selection (Figures 2, 3). These results correspond with previous findings of increased FA following environmental stress in sexually selected canines, but not in sexually monomorphic, premolars in the western lowland gorilla (*Gorilla gorilla gorilla*) (Manning and Chamberlain, 1994). Similarly, Møller (1993) documented strong increases in FA of sexually selected traits, but not in nonsexually selected traits, in Chernobyl area barn swallows (*Hirundo rustica*) following radioactive contamination caused by the 1986 accident at the Chernobyl Nuclear Power Station.

The mechanisms behind higher sensitivity of sexual traits to environmental conditions are not well understood (e.g., Graham et al., 1993; Hill, 1995). My results support the idea that directional selection on secondary sexual traits may select against strict developmental control (Møller, 1992; Møller and Pomiankowski, 1993) thereby making sexual traits more responsive to resource availability and allocation during growth compared to nonsexually selected traits (Badyaev et al., in press; McLain, 1993; Parsons, 1995; Watson and Thornhill, 1994). I found that developmental stability of canines and premolars is associated with the mode of selection; sexually dimorphic canines and sexually monomorphic premolars showed different patterns of relationship between tooth FA and tooth sizes (Figures 1, 2). For sexually selected canines under directional selection, developmental stability increased with development of the trait (Figure 1). These results therefore support other studies that show that FA decreases with increasing trait size when a trait serves as an indicator of individual quality (Evans, 1993; Møller, 1990, 1992; Møller and Pomiankowski, 1993; Rowe et al., in press).

If large sexual traits are more costly to produce and maintain under stressful conditions compared to more favorable conditions, and symmetry itself is a selected trait, then fewer individuals should be able to achieve both larger and symmetrical traits under stressful conditions. Differences in food distribution and corresponding changes in territorial behavior are likely to result in greater variation in individual quality during stressful periods than during more favorable conditions (e.g., Low, 1990; Møller, 1995; Tomkins and Simmons, 1996). Because the Yellowstone National Park garbage dump sites were small, they could have been successfully defended by a few dominant individuals against intruders. However, it is likely that considerable and renewable amounts of food available at dump sites (Craighead et al., 1995) allowed subdominant bears to acquire more and higher quality food compared to what they would have been able to obtain under natural conditions. Changes in the relationship between canine FA and canine size from pre- to postclosure periods (Figure 1a) clearly demonstrate an increased relative cost of canine tooth production after this stressful event. As a result of the increased cost, fewer animals were able to achieve both large size and symmetrical development of canines, and thus the slope of the relationship between FA and canine size increases (Figure 1a). Therefore, stress appears to act as an honesty-reinforcement mechanism in selection for condition-dependent large and symmetrical canines (Figure 1a). Increased relative cost of canine growth during the postclosure period indicates that foraging at open dump sites allowed more individuals to maintain good body condition, thus decreasing variation in quality among individuals. Furthermore, following the dump closure, the Yellowstone bears' home ranges increased more than fivefold (Figure 3; Craighead et al., 1995). Increase in home ranges could be the result of competition with conspecifics, or it could reflect a shortage of resources such as food (e.g., Badyaev et al., 1996). In either case, stressful conditions resulted from garbage dump closures, and stress appears to act as an honesty-reinforcing mechanism (Grafen, 1990; Kodric-Brown and Brown, 1984; Zahavi, 1975) because only individuals who could successfully withstand stress during growth developed the most symmetrical dentition.

It is interesting that although the garbage dump closure clearly represented a stressful event in the Yellowstone grizzly population (Craighead et al., 1995), stress induced by this event appears to be comparable in range to periodic nutritional stresses suffered by bears. For example, periodic multiyear mast and berry crop failures (e.g., Rogers, 1976), irregular or unusually low salmon runs (Davis et al., 1986), as well as diet change following natural fires (Craighead et al., 1995) have been shown to influence growth, mortality, and fecundity in bears. Field studies of natural populations are needed to further our understanding of how selection for developmental stability is influenced by stressful events and what role periodic stressful events may play in forming preferences for ability to buffer such stresses.

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