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Evolution of Morphological Integration: Developmental Accommodation of Stress-Induced Variation

Alexander V. Badyaev,[1,*] Kerry R. Foresman,[2] and Rebecca L. Young[1]

1. Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, Arizona 85721;
2. Division of Biological Sciences, University of Montana, Missoula, Montana 59812-1002

ABSTRACT: Extreme environmental change during growth often results in an increase in developmental abnormalities in the morphology of an organism. The evolutionary significance of such stress-induced variation depends on the recurrence of a stressor and on the degree to which developmental errors can be accommodated by an organism's ontogeny without significant loss of function. We subjected populations of four species of soricid shrews to an extreme environment during growth and measured changes in the patterns of integration and accommodation of stress-induced developmental errors in a complex of mandibular traits. Adults that grew under an extreme environment had lower integration of morphological variation among mandibular traits and highly elevated fluctuating asymmetry in these traits, compared to individuals that grew under the control conditions. However, traits differed strongly in the magnitude of response to a stressor—traits within attachments of the same muscle (functionally integrated traits) had lower response and changed their integration less than other traits. Cohesiveness in functionally integrated complexes of traits under stress was maintained by close covariation of their developmental variation. Such developmental accommodation of stress-induced variation might enable the individual's functioning and persistence under extreme environmental conditions and thus provides a link between individual adaptation to stress and the evolution of stress resistance.

Keywords: developmental plasticity, functional integration, modularity, *Sorex*, stress, variation.

Exposure to environments outside the normal range experienced by a population is commonly associated with

* Corresponding author; e-mail: abadyaev@email.arizona.edu.

an increase in phenotypic and genetic variation in organismal traits (Bijlsma and Loeschcke 1997; Hoffmann and Parsons 1997; Hoffmann and Hercus 2000; Price et al. 2003). Increased stress-induced variation is either a product of the increase in generation of novel genetic and phenotypic variation (Wills 1983; Jablonka and Lamb 1995; Caropale 1999; Imasheva 1999; Hadany and Beker 2003) or, more often, especially in morphological traits, a result of reduction in the strength of regulatory mechanisms that release previously accumulated but unexpressed variation (Bradshaw and Hardwick 1989; Eshel and Matessi 1998; Gibson and Wagner 2000; Lipson et al. 2002; Schlichting and Smith 2002; Rutherford 2003). It is often suggested that increased stress-induced variation is a prerequisite for novel adaptations under changed environments (e.g., Siegal and Bergman 2002). However, for stress-induced modifications to have evolutionary significance, they have to be inherited and to persist in a sufficient number of individuals within a population (West-Eberhard 1989, 2003; Oyama 2000). Thus, stress-induced variation has to be accommodated by an organism without reducing its functionality, so that an organism can survive a stressor and reproduce. Yet it is not clear how such accommodation is accomplished.

Organisms can maintain functionality in stressful environments by channeling stress-induced developmental variation through buffering of some organismal functions while increasing the flexibility of others (Alberch 1980; Lauder 1981; Nijhout 2002). Proximately, greater flexibility of individual systems is produced by lessening their homeostatic integration (West-Eberhard 2003); such a decrease might enhance the range of performance of individual organismal systems and ultimately increase organismal capacity to adapt to changing conditions (reviewed in Rutherford 2003; Badyaev 2005). However, the mechanisms behind differences of organismal systems in their capacity to buffer or accommodate stress-induced variation are poorly understood. On the one hand, buffering of a stressor might be a consequence of developmental complexity rather than an evolved stress resistance mechanism such that developmental or functional complexity can lead directly to

resilience to stressors (Baatz and Wagner 1997; Rice 1998; Waxman and Peck 1998; Meiklejohn and Hartl 2002; Siegal and Bergman 2002). Under this scenario, the complexes of traits that share the greatest number of developmental interactions (i.e., the most developmentally integrated) should be the most able to maintain functionality and to accommodate the effects of stress during ontogeny.

On the other hand, an organism's ability to function in different environments requires the ability to track and respond to environmental change (Waddington 1941; Schmalhausen 1949; Wagner et al. 1997; Eshel and Matessi 1998; Ancel 1999; Schlichting and Smith 2002). For example, in some species different life stages or populations vary in bite force and corresponding muscle attachments in relation to prey characteristics (reviewed in Herring 1993; Herring et al. 2001; Hallgrímsson et al. 2004), and species differ in the ability to accommodate such environment-induced changes (Meyer 1990; Smits et al. 1996a, 1996b; Thompson et al. 2003). An evolved system that completely shields an organism from potential stressors during development will restrict its ability to recognize and capacity to incorporate favorable environmental change (Wagner et al. 1997; Ancel 1999). Critical to the understanding of the evolution of stress response is the knowledge of functional and developmental integration among organismal components as well as the extent and occurrence of extreme environments.

Here we experimentally examine the interaction between functional and developmental integration and organismal response to an environmental stressor. We investigate patterns of integration and accommodation in developmental variability and in stress-induced developmental errors (measured as a fluctuating asymmetry) in bilaterally symmetrical lower mandibles of four closely related species of soricid shrews (*Sorex monticolus*, *Sorex vagrans*, *Sorex cinereus*, and *Sorex hoyi*). Shrews are particularly suited for the study of accommodation of stress-induced variation because most growth and ossification of their foraging apparatus takes place after birth and temporally coincides with the onset of functional use (Foresman 1994). Thus, there is a rare opportunity to examine the interaction between stress-induced variation during development and patterns of integration imposed by functional requirements. We first show that stressful conditions during development lead to a greater magnitude of developmental errors in the components of the foraging apparatus. Second, we show that within functional complexes (here with the muscle attachments), the expressed response to a stressor is lower than among other traits, whereas the coordination of developmental errors among individual characters is higher. We also show that although cohesiveness among traits lessens under stressful conditions, it remains high in the functional complexes because of the compensation for and accommodation of developmental errors among individual components of these complexes. We discuss the importance of developmental accommodation of stress-induced variation for the maintenance of organism functionality in extreme environments.

Material and Methods

Data Collection

The study was carried out on eight experimental plots (6–28 ha) located in the Swan River Valley of western Montana. Each study site contained control plots (untreated at the time of sampling) and plots where forest overstory (250–500 trees per hectare) was removed and debris was burned by Plum Creek Timber Company the summer before sampling. Study sites were surrounded by large, contiguous forested stands. Previous work showed that the vegetation removal treatment strongly modifies site microclimate, alters food resources and foraging efficiency of shrews, and results in both an increase in developmental instability of shrew embryos and a decrease in individual condition of adult shrews (Badyaev et al. 2000). All four coexisting shrew species (*Sorex monticolus*, *Sorex vagrans*, *Sorex cinereus*, and *Sorex hoyi*) were trapped with pitfall traps or Sherman live traps. Sherman live traps were arrayed in 10 × 10 grids, spaced at 10-m intervals with one trap per station, and baited with rolled oats. Trapping grids were run for four consecutive 24-h periods and checked twice each day. In addition, three pitfall arrays containing four unbaited pitfalls each were placed across the core of each plot surrounding live trap grids and were checked once per day. We aged captured shrews on the basis of tooth wear (Dannelid 1994) and restricted our analyses to 2–3-month-old shrews that were born in May–June of the year of sampling.

We obtained data on 726 individuals of four species: *S. monticolus* (control: 52 males and 50 females; vegetation removal [VR]: 45 males and 41 females), *S. vagrans* (control: 53 males and 64 females; VR: 48 males and 59 females), *S. cinereus* (control: 46 males and 43 females; VR: 74 males and 44 females), and *S. hoyi* (control: 28 males and 34 females; VR: 17 males and 28 females). The skulls were cleaned in a dermestid beetle colony, and the left and right sides of the lower mandibles were separated. We photographed images of each side of each mandible under 7.5× magnification, using an Olympic SZH stereo photomicroscope. The analyses of digital images were conducted with Mocha 1.2 and SigmaScan 5.0 Pro software (Jandel Scientific).
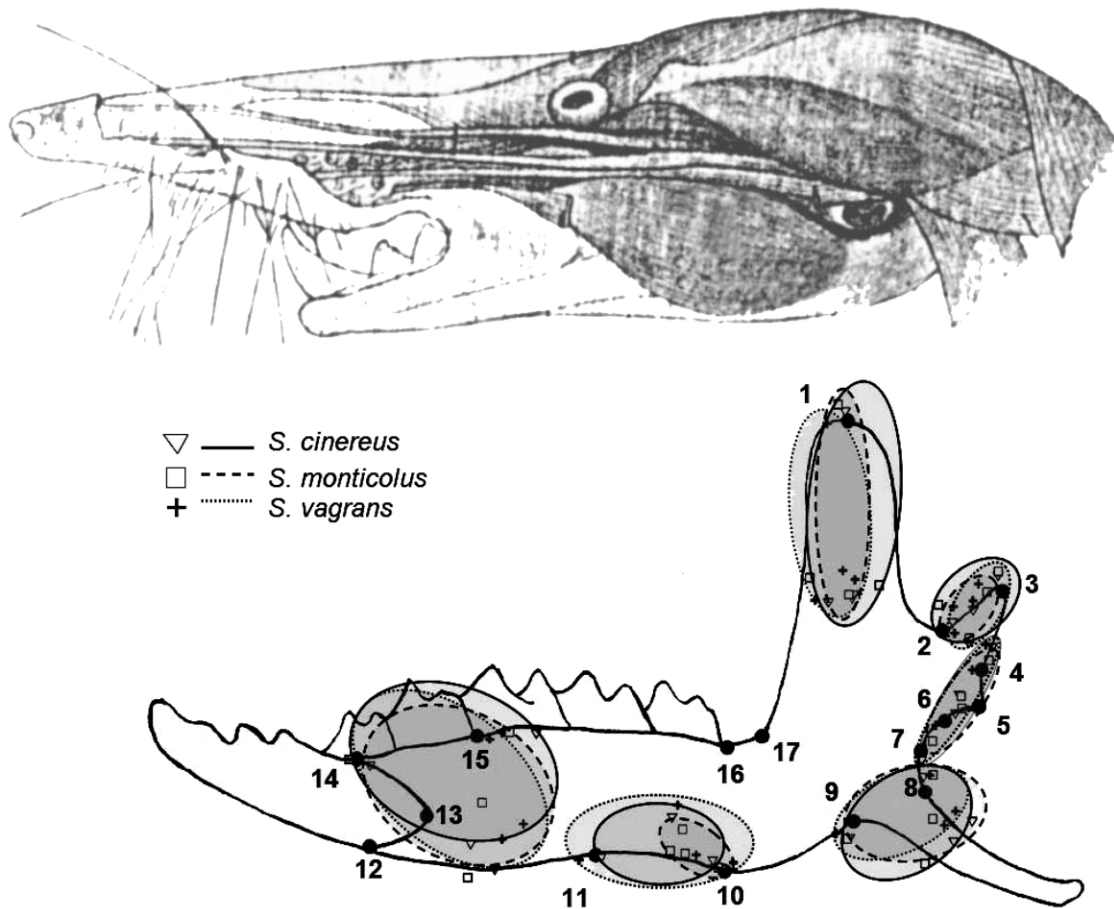
Figure 1: *Sorex* shrew skull and outline of the lower mandible showing 17 homologous landmarks and the six muscle attachment regions for species used in this study. Muscle attachment regions are shown as the within-species (average among individuals of both sexes) highest, lowest, leftmost, and rightmost locations of muscle attachments and ellipsoids of muscle attachment coordinates for each species. Coordinates of the muscle attachment locations, landmarks, and jaw outline are transformed by a single Procrustes superimposition to account for the effect of size on shape among these species. Overlap in ellipsoids indicates shape overlap of muscle attachment regions among species. Mandibular linear measurements (n = nonintegrated, not involved in the attachment of the same muscle; f = functionally integrated, involved in the attachment of the same muscle, see "Material and Methods" for details) were as follows: n1: 1–2, n2: 1–9, n3: 3–4, n4: 8–17, n5: 10–13, n6: 10–16, n7: 11–15, n8: 11–16, n9: 12–13, f1: 2–3, f2: 4–5, f3: 4–6, f4: 5–8, f5: 8–9, f6: 13–14, f7: 14–15, f8: 10–11, and f9: 13–15.

Delineation of Muscle Attachments and Landmark Data Analysis

The data were coordinates of homologous morphological landmarks, from which 18 linear measurements were selected (see Badyaev and Foresman 2000 and Badyaev et al. 2000 for details of landmark selection). Within- and among-species variation in muscle attachments were determined by dissection of freshly collected shrews of three species (*S. cinereus*, *S. monticolus*, and *S. vagrans*) and by comparison with those previously described in exploratory analysis of all four species under this study and with closely related species (Ärnbäck-Christie-Linde 1907; Gaughran 1954; Fearnhead et al. 1955; Sharma 1958; Dötsch 1985,

1986; Badyaev and Foresman 2000). We described the following associations between muscle attachment areas and landmarks used in this study (fig. 1): *Musculus temporalis* attachment on the coronoid process in all species and all individuals includes landmark 1. *Musculus temporalis* attachment on the condyloid process in all species and all individuals includes landmarks 2 and 3. *Musculus masseter* attachment on condyloid process in *S. cinereus* involves landmarks 4–6 and in some individuals also includes landmark 7; in *S. monticolus* it involves landmarks 4–7; in *S. vagrans*, landmarks 5–7 and, in some individuals, also landmark 4. *Musculus masseter* and *Musculus pterygoideus internus* attachment on the angular process involves land-

marks 8 and 9 in *S. cinereus* and *S. vagrans;* in *S. monticolus* it always involves landmark 9 and, in some individuals, also landmark 8. *Musculus digastricus* attachment on the mandibular body always involves landmark 10 in *S. monticolus;* in *S. cinereus* it involves landmark 10 in some individuals and landmark 11 in other individuals; in *S. vagrans* it always involves landmark 11 and, in some individuals, also landmark 10. *Musculus buccinator* attachment on the mandibular body (mental foramena to incisor) in all species and all individuals involves landmarks 12–15 (fig. 1).

Each cleaned mandible was repositioned and digitized three times to distinguish variance resulting from the positioning of a mandible under the microscope from variance from repeated measures of already scanned images. We used repositioning error for mean squares$_{error}$ (MS$_{error}$) in our analysis (Badyaev and Foresman 2000), except for the effect of treatment on fluctuating asymmetry, where MS$_{individual}$ was used (see below). Repeated measures were separated by several measurement sessions, and mandible photography (by a research technician) and mandible measurements (by A.V.B.) were conducted without knowledge of treatment, sex, or species of a measured animal. To account for size differences among species, the landmarks of muscle attachments (fig. 1) were transformed by Procrustes superimposition (see below), and residual shape coordinates were used in further analyses. Landmarks associated with the attachment of the same muscle were considered functionally integrated. Landmarks either outside of muscle attachment areas or associated with the attachment of different muscles were identified as nonintegrated. Figure 1 shows consensus areas of muscle attachments in three study species. We did not have sufficient data to de novo describe the muscles' attachments in *S. hoyi*; however, because of the similarity in muscle attachment areas among these closely related species (fig. 1), we assigned the landmarks of *S. hoyi* to the functional integration categories based on those confirmed for the other three *Sorex* species in this study and on limited data on muscle attachment in specimens of *S. hoyi* (fig. 1).

To calculate the mandible's centroid size, we applied a single Procrustes superimposition (generalized orthogonal least squares fit; Rohlf and Slice 1990) to align simultaneously the landmark configurations from all species, treatments, individuals, body sides, and replicas (after Klingenberg and McIntyre 1998). Before this superimposition, left mandibles were reflected to their mirror images by assigning a negative sign to their *x*-coordinates. Residual shape coordinates were used in all analyses.

Fluctuating asymmetry (FA) was calculated from between-landmark measurements (fig. 1). Each landmark distance selected for this study showed significant and repeatable FA and was tested for outliers, directional asym-

metry, deviation from normal distribution (Palmer and Strobeck 2003), and shared point dependence (see Badyaev and Foresman 2000). Natural log–transformed values of the left and right sides were used to control for size dependence. We used Levene's test (PROC GLM option, SAS 9.0) to test for significant differences in heterogeneity of FA among traits and between treatments within individuals (fig. 3) and a two-tailed *t*-test or *F* ratio tests (PROC GLM or PROC ANOVA in SAS 9.0) to test for difference in the means of traits between the treatments (fig. 2), percentage increases in FA of integrated and nonintegrated groups of traits (fig. 4), and significance of individual terms (table 1). Mean squares used in the denominator of the *F* ratio in Levene's tests of FA differences between treatments and group of traits are given in Palmer and Strobeck (2003, p. 310; see also SAS Institute 1989). The coefficient of integration for size and fluctuating asymmetry traits was computed as $I = [\sum (\lambda_i - 1)^2/(n^2 - n)]^{1/2}$ (Cheverud et al. 1983), where *n* is the number of traits and λ_i is an eigenvalue of the correlation matrix of the normalized data. Statistical significance of the integration coefficient was obtained by resampling, with replacement, of the within–principal component loadings (1,000 samples; Badyaev and Foresman 2000). For ANCOVA (table 1), sex-related variation was removed from the data in general linear models, and standardized residuals were used.

Table 1: Sources of variation in mandible centroid size in four species of *Sorex* shrews

Species, source	Variance (%)	MS	F	P
Sorex monticolus:				
Treatment	29.13	84,083.49	7.65	**.011**
Individual	39.10	10,990.04	4.25	**.000**
Side	3.89	7,716.27	2.97	.103
Side × individual	27.84	2,598.07	1.22	**.001**
Sorex vagrans:				
Treatment	6.09	30,270.02	4.13	.050
Individual	49.98	7,326.49	4.53	**.000**
Side	5.10	2,750.30	1.72	.198
Side × individual	38.77	1,617.67	2.56	**.000**
Sorex cinereus:				
Treatment	.07	31.42	.02	.892
Individual	59.05	1,700.97	6.25	**.000**
Side	1.85	583.10	2.14	.148
Side × individual	36.52	272.00	1.94	**.001**
Sorex hoyi:				
Treatment	10.12	28,271.12	5.18	**.010**
Individual	48.98	6,906.41	6.03	**.000**
Side	2.10	2,158.70	.98	.198
Side × individual	38.79	1,410.67	3.16	**.000**

Note: Shown are percentage of total variance due to treatment, individual, side, and side × individual interaction and observed mean squares (MS). *F* values are from ANOVA, where effects of sex were removed before analyses. Bold *P* values indicate statistical significance.

Results

Effects of Stress on Size and Fluctuating Asymmetry in Mandible Traits

Mandible size (centroid) of shrews raised under the stressful conditions was smaller in female *Sorex monticolus* (control: 860.06 ± 40.55 [SD] mm^2; stress: 785.73 ± 41.33, $t = 5.19$, $P < .001$), male *Sorex vagrans* (control: 854.58 ± 53.40; stress: 819.13 ± 32.19, $t = 2.27$, $P = .04$), and male *Sorex hoyi* (control: 560.01 ± 20.55; stress: 440.70 ± 31.33, $t = 6.07$, $P < .001$; fig. 2; table 1). With the exception of female *S. monticolus* (fig. 2*A*), the size of most individual mandible traits did not differ between shrews raised under the two treatments. In all four species, there were strong changes in FA in jaw centroid and in individual traits (table 1; fig. 3; tables A1, A2 in the online edition of the *American Naturalist*); however, traits differed strongly in their reaction to stress, from no change to a more than 200% increase in some traits (e.g., f4 vs. n4 in male *S. hoyi*; fig. 3). For example, in *S. monticolus*, stress-induced change in FA varied from a 50% increase in f3 to a 17.7% decrease in n1 (table 1; fig. 3*A*). Similarly, in *S. hoyi*, the average change in FA in response to stress varied from a 62% increase in f1 to just a 2% increase in n5 (tables A1, A2; fig. 3*D*).

Effects of Muscle Attachments on Stress Response

Functional integration strongly influenced the change in FA in response to stressful treatment (fig. 4; Levene's test: species: $F = 9.51$, $P < .001$; integration category: $F = 6.04$, $P < .01$). As a group, functionally integrated traits had a smaller increase in FA in male *S. monticolus* ($t = -7.68$, $P = .001$; fig. 4*A*), *S. hoyi* ($t = -2.52$, $P = .014$; fig. 4*D*), and female *Sorex cinereus* ($t = -2.92$, $P = .04$; fig. 4*C*). Change in trait sizes did not differ between functionally integrated and nonintegrated groups of traits and was not different from 0 in all species, except female *S. monticolus* (fig. 4).

### Changes in Functional Integration between Treatments

Integration of trait sizes. In all species and under both treatments, the index of integration was greater among traits belonging to the same functional group than among nonintegrated traits (fig. 5; species: $F = 3.79$, $P = .04$; integration category: $F = 5.28$, $P < .001$). Cohesiveness among traits tended to decrease in both integrated and nonintegrated traits in shrews raised under stressful conditions (fig. 5); the decrease in integration under stress reached statistical significance in *S. cinereus* (nonintegrated group only: $t = 2.23$, $P = .03$; fig. 5*C*) and *S. hoyi* (both groups: $t > 3.58$, $P < .01$; fig. 5*D*).

Integration of fluctuating asymmetries. In all species and under both treatments, with the exception of *S. cinereus* (fig. 5*C*), the index of integration of FA of individual traits was greater for traits belonging to a functional group than for nonintegrated traits (species: $F = 2.17$, $P = .05$; integration category: $F = 3.24$, $P = .02$). Integration of FA of individual traits was significantly higher in shrews raised under control conditions than in shrews raised under stress ($t > 2.7$, $P < .05$; fig. 5).

Discussion

Increase in developmental variation in extreme environments can be due to either novel directional selection on individual organismal components (Wagner and Altenberg 1996; Hadany and Beker 2003) or effects of a stressor on organism-wide homeostasis (Bradshaw and Hardwick 1989; Eshel and Matessi 1998; Schlichting and Pigliucci 1998; Gibson and Wagner 2000; Newman and Muller 2000; Nanjundiah 2003; Rutherford 2003; Gibson and Dworkin 2004). The former scenario might produce a more directional response to stress at the population level, because stress-induced variation is channeled and amplified by existing functional complexes, whereas the latter scenario might produce a greater opportunity for the evolution of novel morphological structures (Goldschmidt 1940; Schlichting and Pigliucci 1998; West-Eberhard 2003). Overall, the weakening of organismal integration, specifically of regulatory systems, may provide a mechanism behind the frequently documented association among morphological diversification, evolutionary change, and extreme environments.

We investigated changes in functional integration among the components of the foraging apparatus of shrews raised under control and stressful environments and found that traits differed in response to a stressor: functionally integrated traits accumulated fewer developmental errors than nonintegrated traits. Moreover, functionally integrated complexes of traits retained their high cohesiveness and, presumably, functionality, even when their individual components varied extensively under stressful treatment. In addition, we documented strong covariation of fluctuating asymmetries among components of functionally integrated groups of traits. These findings raise several questions. First, why did more functionally integrated traits express lower stress-induced developmental variation? Is resistance of functionally integrated complexes of traits to stress an outcome of their complexity, or is it a product of specialized stress-buffering systems? Second, what mechanisms maintain the cohesiveness of function-
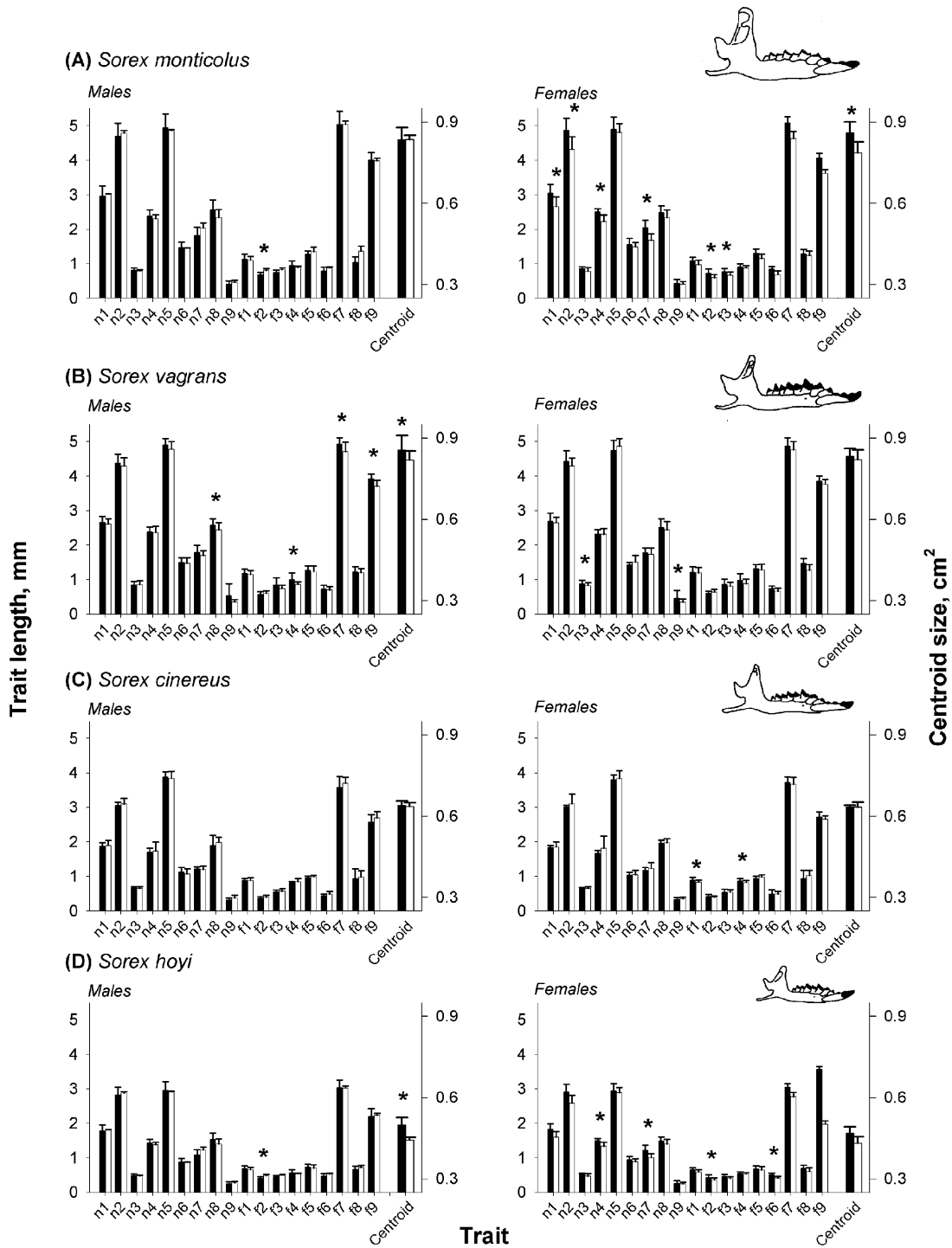
Figure 2: Means ± SE of the two sides of 18 mandibular measurements and jaw size (*centroid*) under control (*black bars*) and vegetation removal (*white bars*) conditions in (*A*) *Sorex monticolus*, (*B*) *Sorex vagrans*, (*C*) *Sorex cinereus*, and (*D*) *Sorex hoyi*. Asterisk indicates significant difference between treatments after sequential within-species Bonferroni correction. Raw values are shown; ln-transformed data are used in analyses.
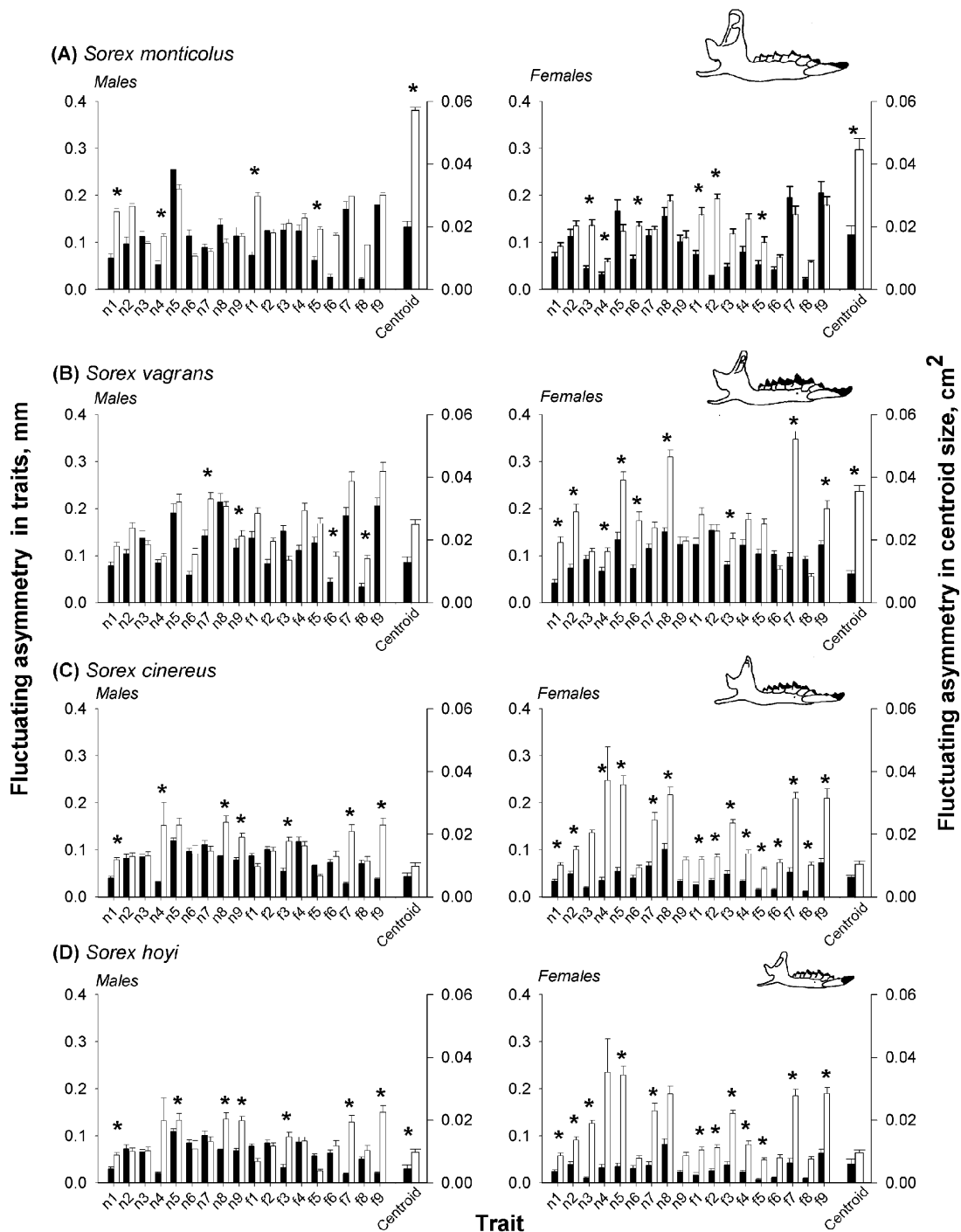
Figure 3: Fluctuating asymmetry (unsigned left- minus right-side values, mean ± SE) for 18 mandibular traits and jaw size (*centroid*) under control (*black bars*) and vegetation removal (*white bars*) conditions in (*A*) *Sorex monticolus*, (*B*) *Sorex vagrans*, (*C*) *Sorex cinereus*, and (*D*) *Sorex hoyi*. Asterisk indicates significant difference between habitat treatments in Levene's test of variance heterogeneity (treatment is entered as a fixed effect; mean squares due to individual are used in *F* ratio denominator). The *P* values are sequentially adjusted for multiple comparisons. Raw values are shown; ln-transformed data are used in analyses.
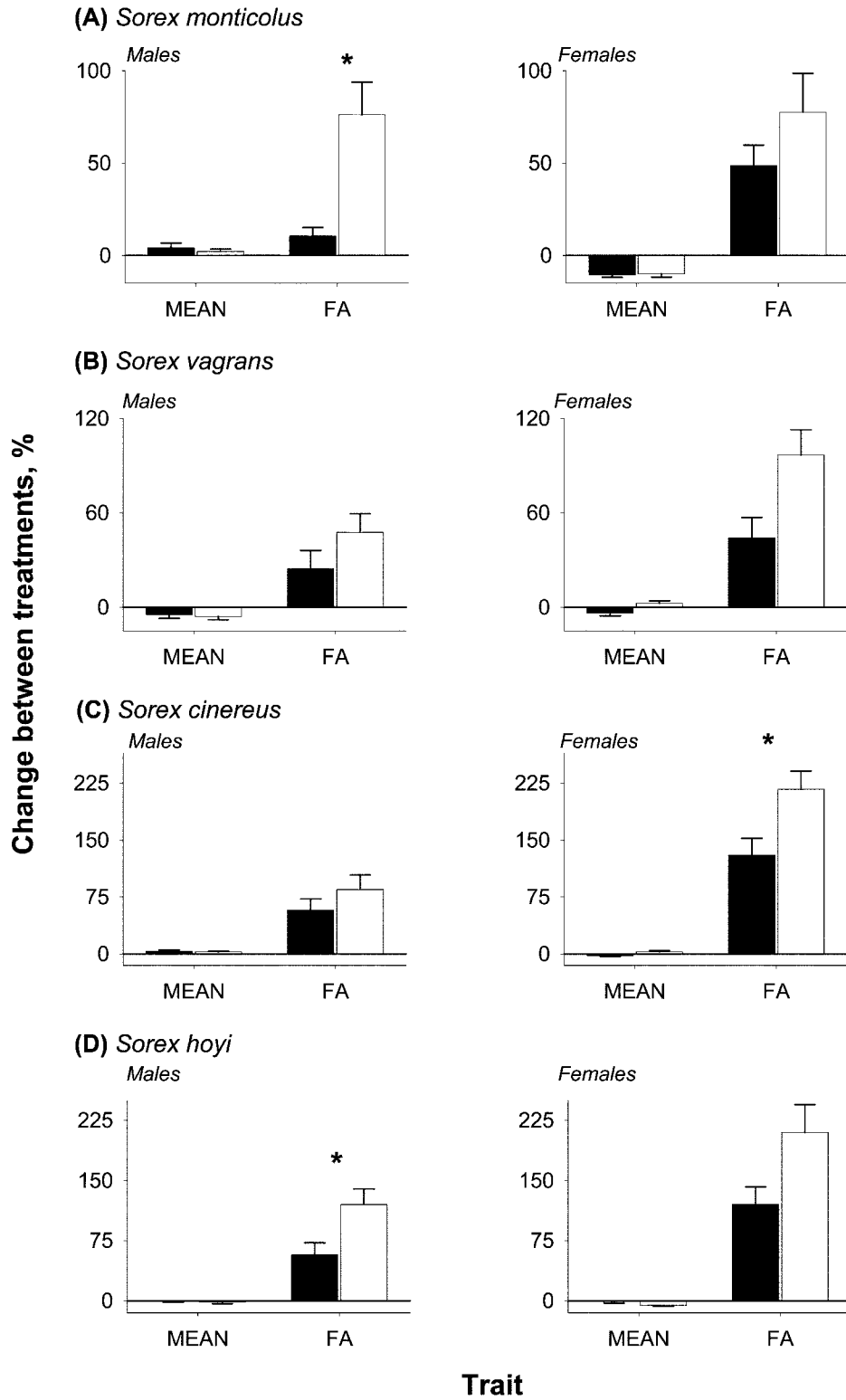
Figure 4: Percent change between control and vegetation removal treatments (VR minus control) in average size (*MEAN*) and average fluctuating asymmetry (*FA*) for a group of functionally related (*black bars*) and nonintegrated (*white bars*) mandibular traits in (*A*) *Sorex monticolus*, (*B*) *Sorex vagrans*, (*C*) *Sorex cinereus*, and (*D*) *Sorex hoyi*. Asterisk indicates significant difference between treatments.
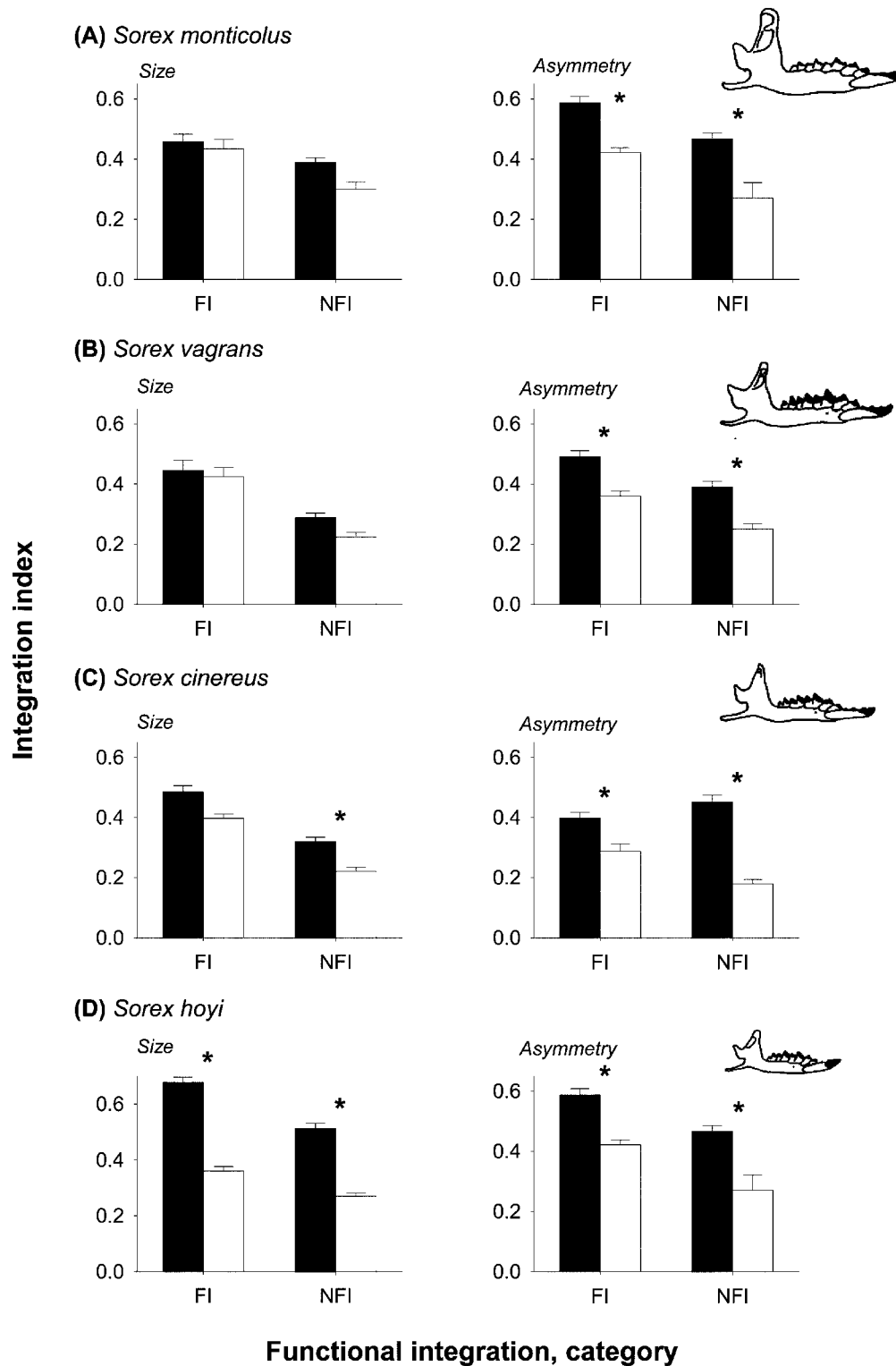
Figure 5: Index of integration among trait sizes (*left*) and traits' fluctuating asymmetries (*right*) in a group of functionally integrated (*FI*) and nonintegrated (*NFI*) mandibular traits under control (*black bars*) and vegetation removal (*white bars*) treatments in (*A*) *Sorex monticolus*, (*B*) *Sorex vagrans*, (*C*) *Sorex cinereus*, and (*D*) *Sorex hoyi*. Asterisk indicates significant difference between treatments (size: $t > 3.49$, $P < .03$; asymmetry: $t > 2.2$, $P < .05$).

ally integrated groups of traits under a stressful environment, and how do such mechanisms evolve?

Integration of fluctuating asymmetries among individual mandibular traits is expected when these traits share common developmental pathways, partition the same resource during growth, or have coordinated development maintained by organism-wide signaling (Riska 1986, 1989; Hall 2003; Hallgrímsson et al. 2003). In soricid shrews, development of integrated muscle attachment complexes and ossification of the lower jaw coincide with the onset of functional use (Foresman 1994; Foresman and Badyaev 2005), and thus integration of fluctuating asymmetries could be due to three main sources. First, integration of asymmetries can be due to shared early development (e.g., Wagner 1990; Polak et al. 2003). This mechanism would result in coordination of asymmetries among traits within functional complexes but would not produce a lower response to stress by these complexes (Hallgrímsson 1999; Hallgrímsson et al. 2004; Sun et al. 2004). Second, the integration of fluctuating asymmetries can be accomplished by compensatory functional interactions of the left and right sides of the homologous muscle attachment complexes (DuBrul and Laskin 1961; Hallgrímsson 1999; Legrell and Isberg 1999). Indeed, shrews have an unfused mandibular symphysis that enables coordination of left and right jaws during prey handling (Dötsch 1985). Thus, traits can grow and accumulate developmental errors separately, and close coordination between left and right jaws during use can provide a source of integration of fluctuating asymmetries between the sides. This mechanism would also result in coordination of asymmetries within functional units but would not predict lower expression of stress-induced variance by functionally integrated traits in the absence of changes in patterns of integration or in trait sizes (Huang et al. 1994; Herring et al. 2001). Finally, the integration of fluctuating asymmetries can be accomplished by channeling of stress-induced variation by functional systems during development (e.g., Moss and Salentijn 1969; Roth and Wake 1985; Hallgrímsson et al. 2004). As a functional group of traits develops, its integration of developmental noise will increase because of the compensatory and constraining interactions among a greater number of linked components (Swaddle and Witter 1997; Badyaev 1998; Hallgrímsson 1999; Aparicio and Bonal 2002; Foresman and Badyaev 2005; Hallgrímsson et al. 2004), which then can accommodate the effects of stressful perturbations without the loss of function. For functionally linked groups of traits, this mechanism would predict both coordinated expression of fluctuating asymmetries within groups of traits and lower accumulation of developmental errors (Baatz and Wagner 1997; Rice 1998; Waxman and Peck 1998; Meiklejohn and Hartl 2002; Siegal and Bergman 2002), as indeed found in this study (fig.

5). Alternatively, greater survival of individuals with greater integration among components of their functional units can result in their overrepresentation in the poststress sample. Below we review these explanations.

The effect of stress depends closely on its timing in the organism's ontogeny (Bradshaw and Hardwick 1989; Huether 1996; Badyaev 2005). Stress exposure during late growth typically affects only a small group of weakly integrated and late-maturing traits (Hallgrímsson 1998; Reichling and German 2000). In contrast, early exposure to stress not only makes the ontogeny of morphological structures more amenable to subsequent modification (Wimberger 1991; Neyfakh and Hartl 1993; Hanken et al. 1997) but also can direct morphological variation. For example, if morphological traits differ in sequence of ossification, then morphological variation in later-ossified components can be directed by stress-induced modifications of earlier-ossified components (Helm and German 1996; Mabee et al. 2000; Reichling and German 2000; Badyaev and Foresman 2004). Moreover, when individuals in a population are synchronous in their development, accommodation and channeling of stress-induced variation during ontogeny by existing morphological structures lead to similar and simultaneous reorganization in many individuals (Chapin et al. 1993; Jablonka and Lamb 1995), thereby creating a cohort of individuals with similar phenotypic patterns (Goldschmidt 1940; Oyama 2000; West-Eberhard 2003; Badyaev 2005). Shrew species in this study have a relatively short life span (10–12 months) and highly synchronized breeding cycles—in the study populations, most individuals were born within a month of each other (Foresman and Long 1998; Gillihan and Foresman 2004). Thus, a large cohort of individuals develops under similar environmental conditions. Similarity among individuals in the patterns of response to stress documented in this and other studies of shrews (Badyaev and Foresman 2000, 2004; Badyaev et al. 2000; Foresman and Badyaev 2005; R. L. Young and A. V. Badyaev, unpublished manuscript), as well as other animals (Leamy 1993; Sowry and Badyaev 1999; Juste et al. 2001; Klingenberg et al. 2001), could be due to the similar effects of temporal changes in developmental integration on expression of stress-induced developmental variation (Cheverud 1982; Debat and David 2001; Meiklejohn and Hartl 2002; Hallgrímsson et al. 2004).

What is the ecological and evolutionary importance of accommodation of stress-induced variation during development in shrews? Short generation time and limited dispersal of shrews might favor the evolution of mechanisms that enable the environment during growth to guide development of the adult form (Badyaev and Foresman 2004; Badyaev 2005; R. L. Young and A. V. Badyaev, unpublished manuscript). Indeed, the overlap between the ossification

sequence and functional use should facilitate production of locally favored mandibular structures (Herring 1993). Morphological structures and integration patterns in shrew mandibles vary with environmental conditions (Pankakoski et al. 1992; Badyaev et al. 2000), population density (Zakharov et al. 1991), and coexistence with similarly sized species (Foresman and Badyaev 2005). Remarkably, however, such environmentally induced structures have similar patterns of functional integration not only among individuals within the same population (fig. 5) but also across shrew species (Badyaev and Foresman 2000, 2004; R. L. Young and A. V. Badyaev, unpublished manuscript). Species were most distinct in variation in traits that were not integrated functionally within each species. This suggests that the retention of integration among functionally related traits under stress has a heritable basis. Interestingly, several traits in this study showed an increase in directional asymmetry under stress (table 1), suggesting that growth-related variation and developmental noise can be expressed by the same developmental mechanisms and that response to stress can involve directional change in developmental mechanisms (e.g., Lens and Van Dongen 2000). Alternatively, similarity in integration patterns among species can reflect recurrence of similar selection pressures among species and environments. Indeed, populations of *Sorex cinereus* and *Sorex vagrans*, which compete for prey of similar size, showed concordant and reversible displacement of integration patterns when they co-occurred in the same area (Foresman and Badyaev 2005).

Retention and inheritance of stress-induced variation by an organism can be facilitated either by recurrent and similar developmental stressors or by the complexity of developmental systems. Here we showed that whereas shrews growing in extreme environments had reduced integration among mandibular traits, groups of functionally related traits remained highly integrated under stress primarily because of the compensatory and accommodating effects of their developmental interactions. Alternatively, this pattern can be produced by differential mortality of individuals with varying degree of integration. To address this explanation, we will examine the ontogeny of integration under two selective regimes, specifically addressing the effects of the ossification sequence on the channeling of stress-induced phenotypic variation. In general, accommodation and channeling of stress-induced variation during development might facilitate phenotypic and genetic assimilation of response to a stressor (Schmalhausen 1949; Waddington 1952; West-Eberhard 2003; Palmer 2004). Together with stress-induced changes in population dynamics, such as fluctuations in developmental synchrony and population sizes, such accommodation, if induced in a large cohort of individuals simultaneously, can significantly facilitate the rate of adaptive evolution.

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