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Morphological asymmetry in mammals: genetics and homeostasis reconsidered

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It has been hypothesized that developmental stability is increased at higher levels of genetic variability (heterozygosity) in animals. However, the existence of this relationship is questionable for homeotherms in general and mammals in particular. The difference between the sides of a bilateral character in an individual is a measure of fluctuating asymmetry that can be used as a measure of the developmental stability of mammals. Increased developmental stability should result in a greater degree of similarity between the right and left side of the body even though environmental variability would tend to increase the differences between right and left sides of the body. It is necessary to separate the effects of the three types of asymmetry so that an accurate estimate of the variance attributable to fluctuating asymmetry can be made. In addition, many early studies of asymmetry in poikilotherms used meristic characters (such as scale counts), and these types of characters are not easily studied in mammals. Mammals, because of their precise regulation of body temperature show little phenotypic effect of environmental variability, and thus may exhibit low absolute levels of asymmetry. Mammals may also be able to reduce the level of asymmetry during their prolonged intrauterine development and juvenile growth period. The literature is reviewed relative to relationships between genetic variation and asymmetry in mammals. Hypotheses are reviewed as they relate to the relationship between fluctuating asymmetry and heterozygosity observed in previous studies. Finally, recommendations are put forth regarding the design and interpretation of future research into the relationship between developmental homeostasis and genetic variability.

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Introduction

Developmental homeostasis is the ability of an organism to maintain its developmental trajectory in the face of environmental variability. Small random deviations in the bilateral symmetry of an organism are thought to reflect its degree of developmental homeostasis and have been shown to be environmental effects with little or no heritability. However, an organism's ability to cope with environmental variation is undoubtedly influenced by its overall level of genetic

variability (Teska *et al.* 1991). Increased genomic heterozygosity, whether due to the interactions of genes in the heterozygous state or due to reduced homozygosity for deleterious recessive genes, may contribute to increased developmental stability in a variety of organisms (Allendorf and Leary 1986). Thus, there should be a positive relationship between developmental homeostasis and genetic variability (Lerner 1954). Our ability to test this hypothesis hinges on our ability to estimate both developmental homeostasis and genetic variability.

Van Valen (1962) defined three types of morphological asymmetry. Antisymmetry is the enlargement of one side of a bilateral character, but the side enlarged varies randomly among individuals in the population. An example of this would be the claws of certain species of fiddler crabs. Antisymmetry results in a population distribution of left/right differences that deviate from a normal distribution, usually being platykurtic, or in the extreme, bimodal. Directional asymmetry is the consistent enlargement of one side of a bilateral character with no variation in the side enlarged among individuals. An example of this would be testicular size in humans. This results in a distribution of left/right differences that is normal but the mean is displaced, positively or negatively, from zero. Fluctuating asymmetry (FA) is the occurrence of random deviations among the sides of a bilateral character. Unless a trait exhibits perfect canalization and no morphological variation, all traits will exhibit some degree of fluctuating asymmetry. Fluctuating asymmetry results in a normal distribution of left/right differences with a mean of zero and variance proportional to the amount of fluctuating asymmetry the character exhibits. The proportion of variance in a bilateral set of characters attributable to fluctuating asymmetry is thought to be explained purely by environmental factors, and thus, can be used as an independent measure of developmental homeostasis. A bilateral character may exhibit any combination of the three types of asymmetry. Both antisymmetry and directional asymmetry have a genetic component (Van Valen 1962) and provide no useful measure of developmental homeostasis. However, both are important in that they may confound and inflate estimates of fluctuating asymmetry (Palmer and Strobeck 1986).

The advent of enzyme electrophoresis for population genetic studies in the 1960's allowed direct estimation of genetic variability in natural populations of organisms. Multilocus heterozygosity has been used as an estimator of overall genic variation at the population and individual levels. It has been hypothesized that estimates of overall genomic variation made from small suites of unlinked loci are reliable predictors of the true total genomic variation. However, sampling variance related to the total number of individuals and loci surveyed must be considered in the interpretation of total genomic variance estimates derived from electrophoretic data. The ability to measure fluctuating asymmetry (developmental homeostasis) and heterozygosity (genomic variability) in individual organisms provides the means to test hypotheses involving the relationship between these two variables.

Numerous studies have examined the relationship between fluctuating asymmetry and heterozygosity in fish (Vrijenhoek and Lerman 1982, Leary *et al.* 1983, 1984, 1985a), lizards (Soulé 1979), birds (Handford 1980), and mammals (Smith *et al.* 1982, Wayne *et al.* 1986, Wooten and Smith 1986, Patterson and Patton 1990, Keiser and Groeneveld 1991, J. M. Novak and M. H. Smith, in litt.). The positive relationships between genomic heterozygosity and developmental homeostasis, as indicated by fluctuating asymmetry, have been most readily detectable in poikilotherms and have been less evident in homeotherms. Unfortunately, studies for both poikilotherms and homeotherms vary in the types of characters measured, the exact fluctuating asymmetry statistic used, the types and numbers of enzymes used to estimate H, and the hierarchical level of biological organization at which the relationships were investigated. Thus, overall patterns for both groups of organisms may be obscured by methodological differences.

The objectives of this review are to analyze the relationship between fluctuating asymmetry and heterozygosity with an emphasis on the patterns seen in mammals. In addition the differences in results between mammals and other organisms will be examined and possible explanations for these differences will be explored. Studies not directly examining the relationship between developmental homeostasis and genetic variability are included only when needed to exemplify a particular point. We have not made an attempt to provide a comprehensive review of all papers dealing with fluctuating asymmetry. Methodological suggestions for future studies are provided in the final section of the paper.

Review

Poikilotherms

Associations between fluctuating asymmetry and genetic variability have been detected in numerous poikilotherms, most notably side-blotched lizards *Uta stansburiana sensu lato* and numerous fish species (Table 1). An early study involving 15 populations of the side-blotched lizard discovered strong evidence of association between asymmetry (4 characters) and heterozygosity (Soulé 1979; Table 1). The results of this study suggested that even though populations with high heterozygosity exhibited relatively high frequencies of individuals with extreme phenotypes, intra-individual variability in bilateral characters was reduced. Therefore, the average fitness of individuals within populations having high heterozygosity may be increased relative to the fitness of individuals in populations exhibiting low heterozygosity. Soulé (1979) pointed out that heterozygosity explains less than half of the inter-population variation in asymmetry in lizards used for his research and concluded that the observed heterozygosity effects alone do not eliminate other potential explanations for the observed results. This is an important point for all studies involving inter-population or species comparisons.

Vrijenhoek and Lerman (1982) examined the relationship between heterozygosity and developmental homeostasis in bisexual and unisexual species of

Poeciliopsis (Table 1). In the sexually reproducing form a positive relationship existed between heterozygosity and developmental homeostasis (as measured by FA). However, the unisexual form did not exhibit this relationship. The explanation for this dichotomy was thought to be the differential impact of environmental stress on reproductive success of the two forms.

In a series of articles, Leary *et al.* (1983, 1984, 1985a, c) demonstrated a positive association between heterozygosity and developmental homeostasis in a variety of

Table 1. Vertebrate species studied, references, character types analyzed, number of loci surveyed and level of analysis for studies addressing the relationship between developmental homeostasis and genomic variability. For comparison level, A refers to studies conducted among populations or species and W refers to studies conducted within a single population except as noted. * – study involved hybrids, ** – study used differences in multilocus heterozygosity as a measure of differences in genic variability between species, # – heterosis measured as effect of crossing inbred lines, [1] – loci were used to determine hybrid status, not *H*, [2] – comparison among family groups bred from individuals from a single population, [3] – comparison of parental species and hybrids collected from a single population, [4] – individuals were pooled from 5 sampling locations.

Species	References	Character	Number of loci	Comparison level
Poikilotherms				
Poeciliopsis monacha	Vrijenhoek and Lerman 1982	Meristic	25	A
Salmo gairdneri	Leary *et al.* 1983, 1984, 1985b*, c	Meristic	40, 42, 42, 13	W, W, A, A[2]
Salmo clarki lewisi	Leary *et al.* 1984, 1985a, b*	Meristic	42, 35, 42	W, W, A
Salmo clarki bouvieri	Leary *et al.* 1985b*	Meristic	42	A
Salmo clarki clarki	Leary *et al.* 1985b*	Meristic	42	A
Salvelinus conflueneus	Leary *et al.* 1985b*	Meristic	42	A
Salvelinus fontinalis	Leary *et al.* 1984, 1985b*	Meristic	42, 42	W, A
Enneacanthus gloriosus	Graham and Felley 1985*	Both	27	A
Enneacanthus obesus	Graham and Felley 1985*	Both	27	A
Hyla cinerea	Lamb *et al.* 1990*	Metric	51	A[3]
Hyla gratiosa	Lamb *et al.* 1990*	Metric	51	A[3]
Uta stansburiana sensu lato	Soulé 1979	Both	18	A
Homeotherms				
Zonotrichia capensis	Handford 1980	Metric	4	W[4]
Acinonyx jubatus	Wayne *et al.* 1986, Keiser and Groeneveld 1991	Metric	**	A
Felis caracal	Keiser and Groeneveld 1991	Metric	**	A
Felis lybica	Keiser and Groeneveld 1991	Metric	**	A
Leopardus pardalus	Wayne *et al.* 1986	Metric	**	A
Leopardus wiedii	Wayne *et al.* 1986	Metric	**	A
Panthera pardus	Wayne *et al.* 1986	Metric	**	A
Mus musculus	Leamy 1984*, Wooten and Smith 1986	Metric	#, 63	A, W
Thomomys bottae	Patterson and Patton 1990	Metric	23 – 27	A
Odocoileus virginianus	Smith *et al.* 1982, Smith *et al.* 1992	Both	7, 7	W, W

salmonid species (Table 1). Leary *et al.* (1983) showed the most heterozygous individuals in a population of rainbow trout *Salmo gairdneri* had reduced bilateral asymmetry relative to those individuals with low *H*. In that study, the authors pointed out positive relationships between single locus heterozygosity and developmental homeostasis at two loci involved in biochemical pathways used to produce energy for metabolic activities during development. They suggested that the functions of those enzymes may be directly related to the observed relationships. Leary *et al.* (1984, 1985a, c) provided evidence that heterozygosity and developmental homeostasis were positively correlated in several salmonid fish species (Table 1). In addition, the authors documented increased numbers of morphological deformities in populations of salmonid fishes with greater than average levels of fluctuating asymmetry and lower heterozygosity (Leary *et al.* 1984). The authors proposed that these results linked heterozygosity to fitness in individuals of the study species. Leary *et al.* also suggested that there has been selection for increased developmental homeostasis in rainbow trout (1985c) and that fluctuating asymmetry might be of value as a diagnostic tool for detecting the loss of genomic variability in cultured stocks of fish (1985a) .

Graham and Felley (1985) studied asymmetry in banded sunfish *Enneacanthus obesus*, bluespotted sunfish *E. gloriosus*, and their hybrids. They found a positive relationship between fluctuating asymmetry and multilocus heterozygosity for 43% (3 of 7) of their morphological characters and between their estimate of overall asymmetry and heterozygosity. However, heterozygosity was estimated from six loci chosen for their ability to correctly assess species identification. In this case, heterozygosity as a measure of genetic variability was confounded by the degree of genomic coadaptation.

Homeotherms

One of the earliest studies of the relationship between developmental homeostasis and heterozygosity in homeotherms was performed using the rufous-collared sparrow *Zonotrichia capensis* (Handford 1980). No association was found between single or multilocus genetic variation and asymmetry based measures of developmental homeostasis in this species. He concluded that there were fundamental differences between homeotherms and poikilotherms with regard to relationships between heterozygosity and fluctuating asymmetry (or developmental homeostasis). Furthermore, Handford (1980) suggested that differences in the relationship between heterozygosity and developmental homeostasis for poikilotherms and homeotherms should be expected given the documented differences in overall genomic variability of the two groups of organisms.

In a study of asymmetry in the white-tailed deer *Odocoileus virginianus*, Smith *et al.* (1982) found no evidence of a relationship between heterozygosity and asymmetry of bilateral antler characteristics. However, they did detect a trend toward reduced asymmetry in heterozygous genotypes versus homozygous genotypes in 63% (22 of 35) of single locus comparisons. Furthermore, the authors noted a

pattern in which both the magnitude of antler asymmetry and the range of variation of asymmetry decreased with age in white-tailed deer. The amount of asymmetry in main beam length varied from about 13.5 percent for 1.5 year old deer to 1 percent for deer 4.5 years of age or older. A similar age related effect for asymmetry of shape in cotton rat *Sigmodon hispidus* skulls has also been found (Fig. 1). Although the confounding effects of antisymmetry and directional asymmetry were assessed in the study of cotton rats, they were not assessed in the study on white-tailed deer.

Leamy (1984) detected an association between heterosis, due to intentional outcrossing, and asymmetry in the house mouse *Mus musculus*. However, this result was detected by manipulation of inbred strains of mice, making the significance of these findings for wild populations questionable. Alternatively, Wooten and Smith (1986) used data from a wild population of house mice to determine if there was a detectable relationship between H, estimated from enzyme electrophoresis, and asymmetry of individuals as well as to address the existence of this relationship for homeotherms in general. They found no evidence for a relationship between heterozygosity and asymmetry in this species. Furthermore, Wooten and Smith (1986) argued that poikilotherms generally exhibit a higher degree of asymmetry than do homeotherms and stated that the dichotomy between the two groups of organisms might depend upon statistical bias, variability in character types, and/or alternative mechanisms for maintenance of developmental stability. The authors also suggested that the extended developmental period of homeotherms might allow them the opportunity to increase developmental stability and reduce FA.

Patterson and Patton (1990) examined the relationship of fluctuating asymmetry between 18 populations of pocket gophers *Thomomys bottae*, that differed in levels of heterozygosity. One of 12 characters showed a negative relationship between fluctuating asymmetry and H. This was not considered significant in light of Type I error considerations. No relationship was found between an estimate of fluctuating asymmetry over characters and heterozygosity.

Wayne *et al.* (1986) compared the relationship between asymmetry of cranial characteristics and genetic variability of the cheetah *Acinonyx jubatus* to those relationships observed for three other representative cat species (leopard *Panthera pardus*, ocelot *Leopardus pardalus*, and margay *Leopardus wiedii*). The results of this study indicated that cheetahs, which are thought to have little or no genetic variation, had the highest levels of cranial asymmetry of the four species studied. The authors concluded that their results corresponded to those exhibited by poikilotherms with regard to the expected relationship between heterozygosity and developmental homeostasis and that the cheetah exhibited reduced developmental stability compared to the other species.

Willig and Owen (1987) pointed out some methodological and conceptual problems with the study by Wayne *et al.* (1986) that may have mitigated their conclusions. Keiser and Groeneveld (1991) sought to analyze the question of reduced

developmental stability in the cheetah in such a way as to alleviate the concerns of Willig and Owen. They compared levels of odontometric asymmetry in the cheetah with levels of asymmetry in the more genetically variable species, the African wildcat *Felis lybica* and the caracal *F. caracal*, all from the South African subregion. No differences in levels of fluctuating asymmetry were found between the cheetah and the other two felid species. They concluded that the cheetah did not exhibit a markedly decreased level of developmental stability.

Alternate hypotheses

The previous review suggests that the relationship of fluctuating asymmetry and heterozygosity differs between poikilotherms and homeotherms. Handford (1980) studying the rufous-crowned sparrow *Zonotrichia capensis* suggested that a relationship between fluctuating asymmetry and heterozygosity exists in poikilotherms but not in homeotherms and this reflects a basic difference in developmental regulation between poikilotherms and homeotherms. This argument was taken up and expanded by Wooten and Smith (1986) in their study of fluctuating asymmetry and heterozygosity in *Mus musculus*. Although the results of both these studies were consistent with the idea that there is a fundamental difference in developmental regulation between poikilotherms and homeotherms, they do not really test the underlying causality. Thus, there are alternate hypotheses to explain the results. The results may be explained by fundamental biological differences between organisms or by differences between studies in methodology.

Biological hypothesis

Most mammals go through a prolonged developmental period in a relatively constant intrauterine environment. Because of the relatively low environmental variance encountered during development, mammals may not generate high levels of fluctuating asymmetry during early development. Asymmetry could be due to a lack of precise control over development during the early rapidly developing embryological stages but because of the length of the developmental period, the asymmetry may be reduced as they develop. In white-tailed deer, fetuses with higher heterozygosity develop faster than those with lower heterozygosity (Cothran *et al.* 1983), thereby complicating potential age and heterozygosity related effects on asymmetry. It is also possible that animals with high levels of fluctuating asymmetry may not survive as well, and the individuals in a population of survivors may exhibit lower levels of fluctuating asymmetry. These three processes would all produce age related differences in FA.

There are no observations for fluctuating asymmetry of mammalian fetuses. Therefore, it is not possible to test hypotheses concerning the degree of fluctuating asymmetry generated during early embryonic development or the reduction of fluctuating asymmetry during intrauterine development. However the previously

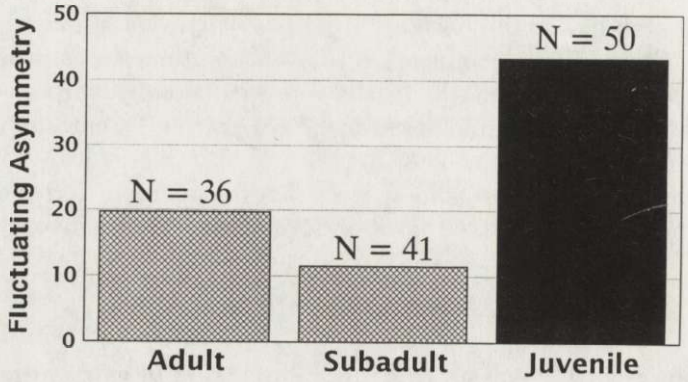

Fig. 1. Fluctuating asymmetry of shape for cotton rat skulls of three different age classes. The amount of fluctuating asymmetry is significantly greater for the juvenile age class compared to the adult and subadult age classes ($F = 2.83$, $p < 0.001$). Sample sizes appear above the bars.

mentioned studies on white-tailed deer and cotton rats (Fig. 1) show an age dependence of fluctuating asymmetry. In the case of deer antlers, they are replaced each year, and the probability of the asymmetries being corrected over time is enhanced. However, it is not known in either case whether the asymmetry is corrected within an individual organism over time or whether there is differential survival of animals with different levels of asymmetry.

Methodological hypotheses

The types of characters used to assess asymmetry vary between studies. Meristic characters predominate for poikilotherms and metric characters predominate for homeotherms. Meristic characters are likely to be threshold characters. Fluctuating asymmetry estimates based upon meristic characters may not accurately estimate the asymmetry of the underlying continuous distribution, the genetic liability thus, not providing an accurate estimate of developmental stability (Falconer 1981, Swain 1987). If the meristic characters are not threshold characters, the estimation of fluctuating asymmetry, because it is a variance, from continuous (metric) and discrete (meristic) characters may not be comparable because of underlying distributional differences between character types.

Because morphological characters vary in their fitness value, heritability, and degree of canalization, the absolute level of fluctuating asymmetry will vary among characters (Palmer and Strobeck 1986). The amount of intercharacter variation will depend on the covariance among characters, itself a function of the distribution of measured characters within and between underlying developmental growth fields. Even when characters are somewhat comparable among studies, intercharacter variation necessitates an overall estimate of fluctuating asymmetry across characters. Summarizing fluctuating asymmetry is not a trivial problem, and numerous methodologies have been suggested to estimate population level fluctuating asymmetry over a suite of characters (Palmer and Strobeck 1986).

J. M. Novak and M. H. Smith (in litt.) have shown that the method of summarization can affect both analytical results and conclusions drawn from them. Unfortunately, there has been little consistency among studies in how fluctuating asymmetry was summarized over characters, making comparisons among studies difficult.

The methodologies used to assess genetic variability also varied among studies. In most cases protein electrophoresis was used, but other measures such as expectations from the crossing of inbred lines (Leamy 1984) have been used to assess genetic variability. Groups of random loci are poor predictors of overall genomic heterozygosity unless there is linkage disequilibrium, inbreeding, or nonrandom mating due to small population size (Chakraborty 1981). The existence or intensity of one or more of the above conditions will necessarily vary between populations or species. Studies employing enzyme electrophoresis used neither the same number nor suite of proteins to estimate heterozygosity, thus increasing variation among studies . Heterozygosity is not the only, nor necessarily the best, estimator of genetic variability and in general underestimates genetic variability (Crow and Kimura 1970). If heterozygosity does not underestimate genetic variability consistently within studies, then it will decrease the reliability of conclusions drawn among studies. Additionally, the variance of heterozygosity estimates is affected by both the number of loci and individuals sampled (Weir 1990). Thus, comparative analyses using data from disparate studies contain a large error component (Palmer and Strobeck 1986).

Fluctuating asymmetry has also been estimated in numerous ways as outlined by Palmer and Strobeck (1986). Methods vary in how asymmetry is assessed (signed differences, absolute differences, or ratios), in how or if size scaling is performed, and in their sensitivity to confounding factors (size scaling, measurement error, directional asymmetry and antisymmetry). In addition fluctuating asymmetry estimates are not independent of character type (meristic or metric). Some fluctuating asymmetry estimates are not suitable for the discrete distributions of meristic characters. The disparity between poikilotherms and homeotherms, in terms of character types analyzed, adds a nonlinear component to the between group variability.

As stated previously, homeotherms are buffered from their external environment to a greater degree than are poikilotherms. Most mammals, because of their extended intrauterine development, have a more constant developmental environment than the majority of poikilotherms and egg-laying organisms. Considerations such as these, combined with increased integration of growth fields in homeotherms and the precision of suture boundaries, lead to the expectation of lower absolute levels of fluctuating asymmetry for characters measured in homeotherms compared to homologous characters measured in poikilotherms. Lower absolute values of fluctuating asymmetry necessitate more precise measurements to detect fluctuating asymmetry differences among groups. Confounding fluctuating asymmetry by measurement error, directional asymmetry and antisymmetry becomes

more serious as absolute levels of fluctuating asymmetry decrease. Therefore, it becomes more critical to perform replicate measurements of all characters for all individuals used in a given study. Additionally, metric and meristic characters may be differentially affected by the stability of extended internal development because of differences in underlying character distributions and ranges.

The hierarchical level of the study is crucial in comparing results. The studies that measure fluctuating asymmetry differences among individuals of varying heterozygosity level within a population may not be comparable to those that address differences between levels of heterozygosity among populations or species. For example, it is known that fluctuating asymmetry varies with population size or density in common shrews *Sorex araneus* (Hanski *et al.* 1991, Zakharov *et al.* 1991) and cotton rats (J. M. Novak and M. H. Smith, in litt.). Differences in fluctuating asymmetry among populations may be due to differences in population size and not differences in heterozygosity . In addition, species will exhibit even greater population and life history differences thus confounding fluctuating asymmetry differences between them.

Suggestions for future studies

Repeated measurements over time are needed on individual mammals to determine whether the level of asymmetry changes within an individual as it ages. Secondly, measures of asymmetry during the early stages of life in the uterus are needed to determine whether lower levels of asymmetry in adult mammals are characteristic of all life history stages. Studies of homeotherms and poikilotherms that examine evolutionarily homologous morphological and genetic characters are necessary to determine if fundamental differences exist between the groups relative to the relationship between developmental homeostasis and genetic variability. Methodological differences make studies performed by separate researchers non-comparable. We make the following suggestions for future analyses in order to reduce confounding variation among studies.

Metric characters are more desirable for estimating fluctuating asymmetry because of their distributional characteristics. Meristic characters fail to provide reliable estimates of fluctuating asymmetry based upon the underlying genetic liability of the character. Whenever possible, replicate measurements need to be taken to allow maximum precision in estimates of FA. A powerful analysis method, such as the ANOVA method outlined by Palmer and Strobeck (1986) and expanded by Lamb *et al.* (1990) needs to be used to identify and remove as many confounding factors from the analysis as possible. In addition, the covariance among characters need to be considered in estimating overall FA. A composite method based upon a truss network, or an integrated measure based upon the fractal dimension of a large growth field, such as the cranium, may provide a good index of population level fluctuating asymmetry (J. M. Novak and M. H. Smith, in litt.). Estimates of genetic variability that maximize the number of loci or employ other methodologies

such as mitochondrial or nuclear RFLP analysis, DNA fingerprinting or nuclear DNA sequencing should be used to reduce measurement error. Studies among populations and among species must address possible confounding factors such as population size, body size allometry, etc. If the ANOVA method is used to estimate fluctuating asymmetry, the effects of known confounding variables can be removed by adding them as either covariates or treatment effects in the model and modifying the interaction terms appropriately (Lamb *et al.* 1990, J. M. Novak and M. H. Smith, in litt.). Because of the inherent buffering and integration of mammalian development, it is imperative that errors associated with both the estimation of fluctuating asymmetry and genetic variability be reduced to as low a level as possible if relationships between fluctuating asymmetry and genetic variability can be realistically determined in mammals.

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