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On Adaptive Accuracy and Precision in Natural Populations

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ABSTRACT: Adaptation is usually conceived as the fit of a population mean to a fitness optimum. Natural selection, however, does not act only to optimize the population mean. Rather, selection normally acts on the fitness of individual organisms in the population. Furthermore, individual genotypes do not produce invariant phenotypes, and their fitness depends on how precisely they are able to realize their target phenotypes. For these reasons we suggest that it is better to conceptualize adaptation as accuracy rather than as optimality. The adaptive inaccuracy of a genotype can be measured as a function of the expected distance of its associated phenotype from a fitness optimum. The less the distance, the more accurate is the adaptation. Adaptive accuracy has two components: the deviance of the genotypically set target phenotype from the optimum and the precision with which this target phenotype can be realized. The second component, the adaptive precision, has rarely been quantified as such. We survey the literature to quantify how much of the phenotypic variation in wild populations is due to imprecise development. We find that this component is often substantial and highly variable across traits. We suggest that selection for improved precision may be important for many traits.

Adaptation is usually modeled as the fit between a population mean and some phenotypic optimum, but this

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ignores several potential sources of maladaptation. First, even if the population mean is at the optimum, it does not follow that the individual organisms in the population are well adapted, even on average (Orzack and Sober 1994*a*, 1994*b*, 1996). Individual variation around a population mean implies that the average individual is some distance away from both the mean and the optimum. Second, individual adaptation itself has two components: the distance from the optimum of the target phenotype set by the genotype in a given environment and the precision with which organisms are able to develop toward their target values (Armbruster et al. 2004; Pélabon et al. 2004*b*). Selection does not operate independently on these two components; instead, fitness is determined by a combination of the two that we call adaptive accuracy. For example, under quadratic stabilizing selection, the adaptive accuracy is proportional to the expected squared deviance of an individual phenotype from its optimum. The smaller the squared deviance, the greater the adaptive accuracy.

Adaptive imprecision is caused by disturbances of the development of the organism. Such disturbances can have many causes, some of which are intrinsic to the organism and some of which are caused by external environmental factors. In general, it is hard to quantify the maladaptive effects of environmental variation, as many of the differences between individuals may reflect plastic responses, or condition or size dependencies, that are due to an adaptive norm of reaction. The reduced clutch size of a bird in poor condition does not imply maladaptation, and the smaller antlers of a smaller deer are not necessarily better or worse than the larger antlers of a larger deer. In general, detailed biological understanding is necessary to judge which components of individual variation are adaptive or maladaptive (e.g., Hallama and Reznick 2001). The maladaptive effects of intrinsic developmental stochasticity, however, may be quantified in a fairly consistent manner through the use of fluctuating asymmetry, that is, random undirectional differences between the two sides of a bilaterally symmetric structure (Van Valen 1962). For most bilateral characters, the adaptive optimum may be assumed to coincide with perfect symmetry, and random deviations from symmetry may be assumed to be maladaptive (Palmer 1996, 2004). We therefore restrict our

empirical quantification of adaptive imprecision to assessing the effects of intrinsic developmental instability. We want to make clear that this narrow focus is not because we consider variation in the external environment to be unimportant but merely because developmental stochasticity is more easily quantified and can be more reliably considered maladaptive.

Of course, there are situations where even imprecision may be adaptive. If the fitness function is convex (i.e., it has a positive second derivative), then any variation, including developmental noise, may increase the expected fitness of an individual. The model to be presented here applies to traits that are under stabilizing selection in the vicinity of a local fitness optimum. In this case the fitness function is expected to be concave, and selection acts against variation (Layzer 1980). When evaluating this assumption of stabilizing selection, it is, however, misleading to think of traits in isolation. Developmental disturbances can occur at all levels of organismal integration and are likely to have pleiotropic effects on many characters. It is less likely that a whole suite of developmentally linked characters will all cease to be under stabilizing selection at the same time. Still, imprecision could be advantageous in a changing environment, both as a bet-hedging strategy (Simons and Johnston 1997) and because it may contribute to decanalization of genetic effects and increase evolvability. We also note that developmental instability may be indirectly selected as a side effect of flexible development (e.g., Emlen et al. 2003), but this does not mean that developmental stochasticity per se is adaptive.

Our purpose with this article is twofold. First, we want to draw attention to and formalize some conceptual distinctions in the study of adaptation. This includes the distinction between population and individual adaptation and the distinctions among adaptive accuracy, adaptive precision, and target optimality. Second, we review empirical studies of developmental instability to assess its potential importance for adaptive imprecision. Previous studies, as reviewed by Lajus et al. (2003), have indicated that developmental stochasticity can explain a surprisingly large fraction of phenotypic variance (see also Lynch and Walsh 1998, pp. 112–116). These studies are, however, largely from lab populations, which are outside the environment to which they are adapted and which may be highly inbred. Because we want to assess the influence of developmental stochasticity on adaptive precision, we focus exclusively on studies of wild populations.

Theory

Defining Adaptive Accuracy and Precision

We may think of phenotypic target value and precision as properties of a genotype. The phenotypic target value

(Nijhout and Davidowitz 2003) can be operationally defined as the average phenotype reached by a particular genotype in a particular distribution of environments. Target optimality refers to the distance of the phenotypic target to an adaptive optimum, and adaptive precision refers to the reliability with which the genotype is able to attain its set target. Consider the quadratic fitness function $W(z) = W_{\max} - s(z - \theta)^2$, where θ is the trait optimum and s is the strength of stabilizing selection. Let the phenotypic expression of a trait, z, consist of a genotypically set target value, z_T, and a developmental error, z_d, as $z = z_T + z_d$, where z_d is a random variable with mean 0 and variance V_d. The expected fitness of this genotype is then

$$W_{\max} - sE_d[(z - \theta)^2] = W_{\max} - s(z_T - \theta)^2 - sV_d,$$

where $E_d[\ ]$ denotes expectation over developmental realizations of this genotype. Thus, as illustrated in figure 1, individual maladaptation has two components: one that is proportional to a measure of deviance of the target from the optimum, $(z_T - \theta)^2$, and one that is proportional to the developmental imprecision, V_d. These combine into the adaptive inaccuracy:

$$\text{adaptive inaccuracy} =$$
$$(\text{target deviance})^2 + \text{adaptive imprecision},$$

or

$$sE_d[(z - \theta)^2] = s(z_T - \theta)^2 + sV_d.$$

This is reminiscent of a fundamental relationship in statistical estimation theory where inaccuracy = bias^2 + imprecision. Just as accuracy is the fundamental property of a good estimator, natural selection acts on the adaptive accuracy and only indirectly on target deviance or imprecision. Also, in further analogy with estimation theory, when there is a biological trade-off between target deviance and precision, it is not necessarily true that the "unbiased" genotype will have the highest fitness.

On the population level, variation among individuals in their target phenotypes is another source of population maladaptation (or population load). If $E[z]$ is the population mean and V_T is the population variance in the target phenotype, the population maladaptation can be decomposed as follows:

$$\text{maladaptation} = (\text{population mean deviance})^2$$
$$+ \text{target variance} + \text{imprecision},$$

or

$$sE[E_d[(z_T + z_d - \theta)^2]] = s(E[z] - \theta)^2 + sV_T + sE[V_d],$$

where $E[\ ]$ without subscript denotes population expectation. Evolutionary biologists have given these three components very different degrees of attention. Orzack and Sober (1994*a*, 1994*b*) argued forcefully that the adaptationist program has been almost exclusively concerned with the first component, the population mean deviance, and has ignored the individual components of adaptation. Population geneticists have studied the second component, target variance, as a source of population maladaptation in terms of genetic and mutational loads, but the third component, adaptive imprecision, has rarely been formally considered as a source of maladaptation. In the following, we will make an attempt at assessing at least one aspect of this neglected component.

Measuring the Developmental Component of Adaptive Imprecision

Adaptive imprecision (V_d) is caused by developmental stochasticity and microenvironmental variation. Microenvironmental variation is important, but we will not attempt to quantify it in this article. Instead, we focus on developmental stochasticity, which can be quantified in a fairly objective way through the use of fluctuating asymmetry. As the environment and the genetic component of the two sides are very similar, the fluctuating asymmetry has a built-in control of genetic and environmental sources of variation. Provided directional asymmetry (systematic left-right asymmetries) and antisymmetry (systematic, but undirected asymmetries) are controlled for, fluctuating asymmetry is largely due to developmental stochasticity. We are aware that fluctuating asymmetry may have a significant microenvironmental component (Nijhout and Davidowitz 2003), but this is of minor concern in the present context, as the effects on the precision of adaptation are similar. An anonymous reviewer pointed out that the general lack of genetic variation and evolvability in fluctuating asymmetry also suggests that observed variation is largely developmental in origin.

Following Whitlock (1996, 1998) and Houle (1997, 2000), the right and left side of a trait can be modeled as

$$R = g + e + e_R,$$

$$L = g + e + e_L,$$

where e_R and e_L are the developmental errors (+ measurement error) in the two sides. Each of these, for estimation purposes, are assumed to be normally distributed with mean 0 and variance V_d such that

$$R - L = e_R - e_L \sim N(0, 2V_d).$$

The fluctuating asymmetry (FA) is measured as the absolute value of this, as $FA = |R - L|$. In appendix A, we describe this model in more detail and show how the following results can be derived.
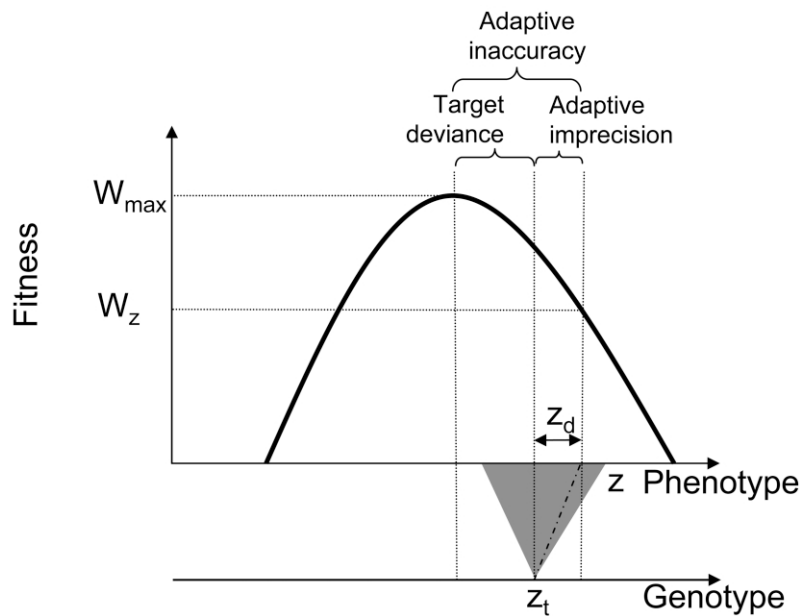

Figure 1: Components of adaptive accuracy.

Let z denote a trait measured on one side of the organism (i.e., z is R or L). The population variance component in z due to developmental imprecision is then $E[V_d]$. As detailed in appendix A, this can be computed in two ways. First, as half the variance in the right-left difference (i.e., signed FA),

$$E[V_d] = \frac{\text{Var}\,[R - L]}{2}.$$

Alternatively, it can be computed from the mean and variance of (unsigned) FA as

$$E[V_d] = \frac{E[\text{FA}]^2(1 + I[\text{FA}])}{2},$$

where $I[\ ]$ denotes the mean-standardized variance (i.e., $I[\text{FA}] = \text{Var}\,[\text{FA}]/E[\text{FA}]^2$, which equals the square of the coefficient of variation, $\text{CV}[\text{FA}]$). These two estimators are equally efficient with an asymptotic relative error of $(2/n)^{1/2}$ (see appendix). Note that $I[\text{FA}]$ has a theoretical minimum at $\pi/2 - 1 \approx (3/4)^2$, and if the coefficient of variation is elevated above 3/4, this indicates individual variation in developmental stability.

The estimation relies upon assumptions such as a normally distributed character (on the within-individual level), no directional asymmetry, no antisymmetry, and no measurement error. We remind the reader that z is the trait as measured in one side only and that the above should be divided by $\text{Var}[z]$ to yield the fraction of overall phenotypic variance explained by developmental imprecision.

Material and Methods

We carried out a survey of studies of fluctuating asymmetry in wild populations published since 1990 in the journals *American Naturalist*, *Animal Behavior*, *Ecology*, *Evolution*, *Heredity*, *Journal of Evolutionary Biology*, and *Proceedings of the Royal Society*. We augmented our survey with informal searches in the general literature and included a number of studies from other sources. Although this augmentation introduces an element of subjectivity, which is not ideal for a meta-analysis, this is unlikely to lead to a systematic bias in our case, as none of the studies we used were focused on or specifically tested hypotheses regarding amount of developmental stochasticity. To be included in our survey, a study had to provide information that made it possible to compute trait variance and developmental variance. The study must give this information on a sample of individuals collected at random in the wild. Data from individuals that were experimentally manipulated or allowed to complete a significant part of their life cycle in the lab were excluded. Museum collections were avoided. Since many studies of fluctuating asymmetry involve comparisons of different groups of individuals, such as "stressed" and "nonstressed," "mated" and "unmated," or "survivors" and "dead," it was often not possible to obtain a completely random sample from the population. We used our judgment to decide whether a particular set of measurements would be representative for the population or not. In a few cases we contacted authors for clarifications. When data were originally presented in groups, such as year, population, habitat, age, or sex, the groups were maintained in our analysis. We pooled data only when it was clear that the samples were obtained in the same way for the same population or when there were too many groups for meaningful analysis. To reduce rounding error we did not use data reported to a single significant figure when that figure was 5 or less (with the exception that we used 2 or less as a criterion for data used to compute Var [FA] for the correction term). Based on the description in the original article, we classified traits into categories for further analysis. We classified traits as sexually selected when it was clear that sexual selection was likely to be involved. We also classified vestigial and presumably nonfunctional traits as weakly selected, but almost all traits in this group are numbers of foramina.

Fluctuating asymmetry can be presented in a number of different ways (Palmer 1994). We mainly used the mean and variance of the absolute difference between left and right sides, $\text{FA} = |R - L|$ (Palmer's FA1), or the variance of unsigned FA, $\text{Var}\,[R - L]$ (Palmer's FA4). From a few studies we also used size-corrected FA (Palmer's FA2 or FA6) or FA measured on a log scale. We made sure to compute the variance due to FA and the variance in the trait on the same scale, and we used the original scale of measurements whenever possible. In some cases we also used the mean squares from two-way mixed-model ANOVAs (sensu Palmer 1994) to compute the amount of variation due to developmental instability. In an ANOVA with side as fixed effect and individual as random effect, the mean squares of the interaction effect equals $\text{Var}\,[R - L]$. Information about variances was sometimes obtained by back-calculating from published standard errors of the mean. If the trait size is computed as the average of the two sides, the variance of one side, z, is computed as $\text{Var}\,[z] = \text{Var}\,[(R + L)/2] + E[V_d]/2$.

Regardless of how they are obtained, estimates of developmental variation are upwardly biased by measurement error. Unfortunately, it was not possible to correct for measurement error in most of the studies. Following Palmer and Strobeck (1986) and Palmer (1994), most researchers test for statistical significance of FA relative to measurement error, but this does not provide a correction for its effects. Furthermore, when they were available, es-
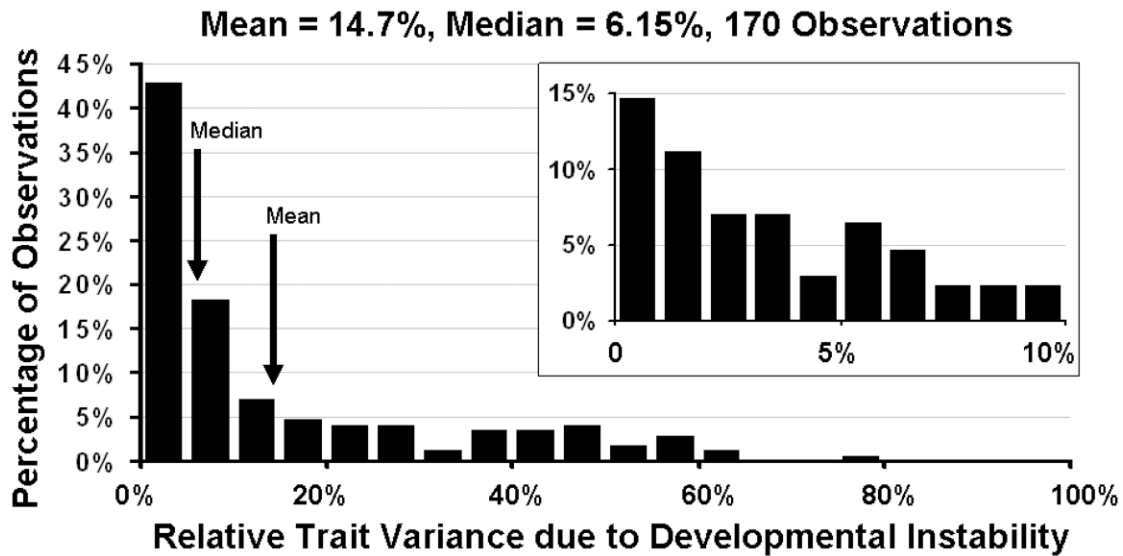
Figure 2: Distribution of fraction of phenotypic variance explained by developmental noise (bin size = 5%). Inset shows the distribution with extreme values removed (bin size = 1%).

timates of measurement variance were often from small subsets of the sample and were not reliable. For these reasons we did not correct for measurement error unless this was completely incorporated in the original study. We did report estimates of measurement variance when available, and we attempted to assess its overall effect in a separate analysis from a subset of studies. Likewise, measures of developmental variance may be upwardly biased by directional asymmetry or antisymmetry. We assumed antisymmetry was absent, and we corrected for directional asymmetry only when the original study did so.

The majority of the studies we surveyed could not be included due to missing information (most commonly trait variances, but often also basic statistics on FA), incomplete descriptions of methods, inconsistencies or errors in reported data, or sampling schemes that cannot be considered representative for our purposes. As our goal was to obtain a representative set of data for a number of traits and organisms and not to do an exhaustive review of the literature, we excluded a number of studies based on lack of clarity in the exact procedures or the character of the sample. No botanical studies are included, simply because we did not come across a single study that fulfilled our criteria.

Results

We were able to locate 34 studies that provided the necessary data for wild populations (see table B1 in the online edition of the *American Naturalist*). This furnished 170 individual estimates of developmental variance. The distribution of these data is shown in figure 2. The proportion of population variation due to developmental variation ranges from 0.1% to 76%. The mean and median are 14.7% and 6.2%, respectively. As shown in figure 3, it made little difference whether this was computed based on the mean and variance of FA or on the variance of the signed FA. The main conclusions to draw from this are that developmental imprecision is extremely variable across traits and populations and that developmental imprecision can often generate a substantial component of trait variation in wild populations. A quartile of the estimates was above 22%.

Estimates of fluctuating asymmetry are infamous for their poor statistical precision (e.g., Palmer and Strobeck 1986, 2003; Palmer 1994, 1998, 2000; Houle 2000; and see app. A). There was, however, no indication that estimation error or publication bias systematically affected our results. Following Palmer (2000), a funnel plot (fig. 4) shows no tendency for estimated levels of developmental variation to vary with sample size. Fluctuating-asymmetry measures may also be biased due to measurement error, which was not controlled for in most of the studies. Using a subset of studies where reasonable estimates of measurement variance were available, we found that measurement error explains on average 0.8% and a median of 0.4% of the total trait variation. Furthermore, there was only a weak overall relationship between measurement variance and estimated developmental variance (fig. 5). Measurement-induced bias is therefore unlikely to have a large effect on
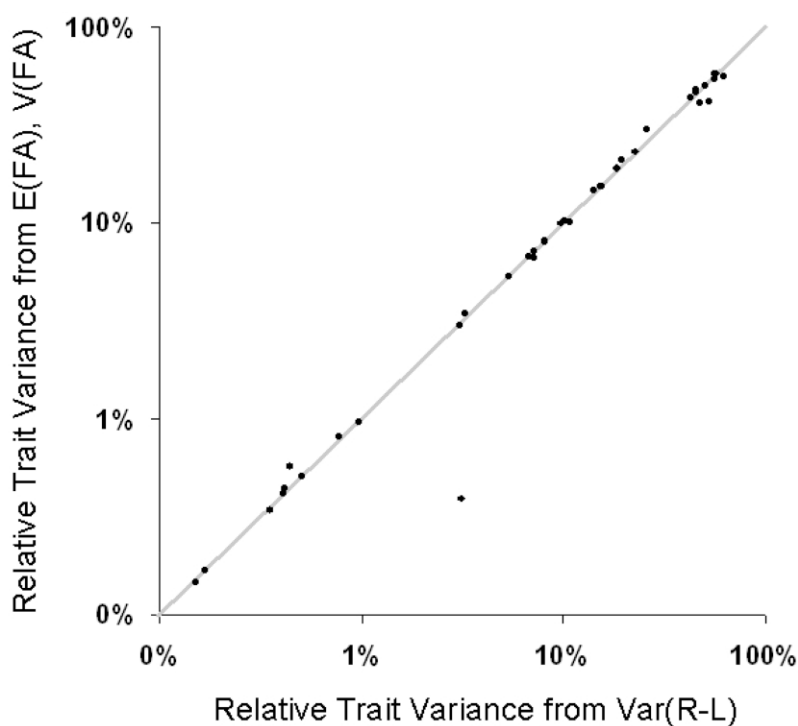
Figure 3: Plot of variance due to developmental stochasticity calculated from mean and variance of unsigned FA (on *Y*-axis) against variance due to developmental stochasticity calculated from variance of signed FA (on *X*-axis). Discrepancies are due to rounding errors and nonnormal distributions of FA. The strongly aberrant point comes from Nosil and Reimchen's (2001) study of water boatmen (*Callicorixa vulnerata*) and concerns number of tarsal spines in one sample, but other samples of the same trait were normal.

our general qualitative conclusions but may still be important in some individual studies.

In table 1 we present the mean and median fractions of developmental variance for various trait and species categories. We caution that such broad comparisons suffer from pseudosampling from traits, species, and studies and should at most be taken as suggestions for further investigation. Still, there are some patterns that may deserve further attention. It is perhaps most striking that meristic characters appear to have much larger fractions of developmental variation than quantitative characters. We also observed differences between characters under different selection regimes. Traits classified as being influenced by sexual selection had higher components of developmental variance than traits classified as being under natural selection, and the few traits classified as weakly selected had even higher values. Interestingly, there was practically no relationship between fraction of developmental variance and the CV of the trait itself ($R^2 = 4.2\%$). We observed slightly larger fractions of developmental variance in males than in females.

We did not find much evidence for differences among taxonomic categories. The raw data did indicate lower developmental precision in mammals than in birds and insects, but this difference disappears if data from foramina and antlers are removed from the mammalian data set, as shown in table 1. The high values for "other vertebrates" are also inconclusive as they are based on a small sample size and include many meristic characters.

Discussion

Our survey of the literature revealed that developmental imprecision often generates a surprisingly large fraction of observed phenotypic variation. Developmental imprecision could explain more than 22% of the phenotypic variance in a full quartile of the estimates. Add to this the fact that adaptive imprecision may have other sources stemming from microenvironmental variation, and we reach the conclusion that adaptive imprecision may constitute an important fraction of maladaptation in many traits in natural populations. This conclusion is also supported by the findings of Lajus et al. (2003). Their review was based on 17 studies of which only one (Juste et al. 2001) fulfilled the criteria for inclusion in our study. Based on their table 19.1, the percent of phenotypic variance
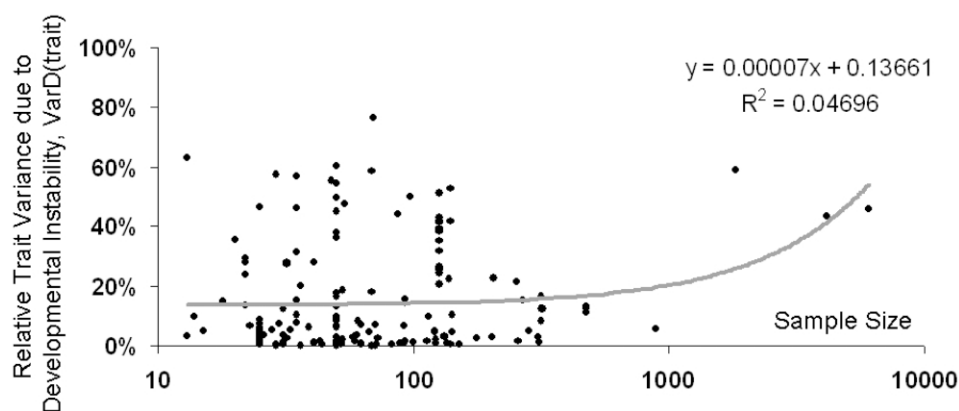
Figure 4: Funnel plot of fraction of trait variation due to developmental variation against sample size. The line is from a linear regression, with the apparent nonlinearity being due to plotting on a log scale. If the four points with the largest sample sizes are removed, the R^2 drops from 4.7% to 0.2%.

explained by developmental variation had a mean of 31% and a median of 26%. This is much higher than our values of about 15% and 6%, respectively. Their higher values may be due to their inclusion of a number of studies of inbred populations in standardized lab environments. Both inbreeding and lab environments are likely to reduce phenotypic variation and may also increase developmental instability. Nevertheless, their results and ours combined strongly support the idea that developmental imprecision is capable of generating substantial phenotypic variation.

The large variation in developmental precision across traits raises questions about the types of traits and species that are more or less precise. We found a very large difference between meristic and quantitative traits, indicating that meristic traits may be less developmentally precise, although it is possible that there is a bias against studying fluctuating asymmetry in invariant meristic characters. Our data set also supports the notion that sexually selected characters may be less precise than naturally selected characters, as suggested by Møller and Höglund (1991). We found that males had slightly higher fractions of developmental variation than females, which may be due to many of the male characters studied being under sexual selection. We caution again that these comparisons are weak tests of hypotheses, as they suffer from pseudo-sampling. Unfortunately, we did not have enough data to meaningfully test hypotheses with controlled contrasts between trait categories within studies. We also note that the basis for the idea that sexually selected characters should be more unstable, that directional selection favors decanalization and developmental instability, has questionable theoretical support. Directional selection can lead to either canalization or decanalization depending on the pattern of epistasis in the trait (Carter et al. 2005), and empirical

studies have failed to find a decrease in development stability for traits under artificial directional selection (Leamy 1986; Pélabon et al. 2006).

It is possible that imprecise traits tend to be under weaker selection. This is underscored by some of the extreme cases in our data set. The highest fractions of developmental variation were seen in foramina numbers in the skulls of harbor seals (58% and 76%; Schandorff 1997). Relatively low precision of foramina numbers were also indicated by Blagojevic and Vujosevic's (2004) study of *Peromyscus* (20%–50%). While the presence of foramina is doubtlessly important, the exact number of foramina may neither be important nor under precise genetic control. Numbers of feather barbs may be a similar case. Price et al. (1991) found that 53% of the phenotypic variation in feather barbs in a warbler was due to developmental variation. A very informative case comes from Crespi and Vanderkist's (1997) study of vestigial wing length in soldier morphs in a thrips, where 63% of the variation in males and 32% of the variation in females were due to developmental variation. This contrasts with 6% and 3%, respectively, in disperser morphs with functional wings. More puzzling is spur length, which shows around 50% variation attributable to developmental variation in both pheasants (Grahn and von Schantz 1994) and wild turkeys (Badyaev et al. 1998). As younger individuals are less asymmetric, this may be due to wear or to rapid, poorly controlled growth. A rather extreme case comes from two studies of the number of antler tines in reindeer (Markusson and Folstad 1997; Lagesen and Folstad 1998). Here, about 56% of the variation is due to developmental imprecision, but we caution that these data come from very young individuals, which usually have only two or three tines per antler. Variation at this stage is unlikely to be
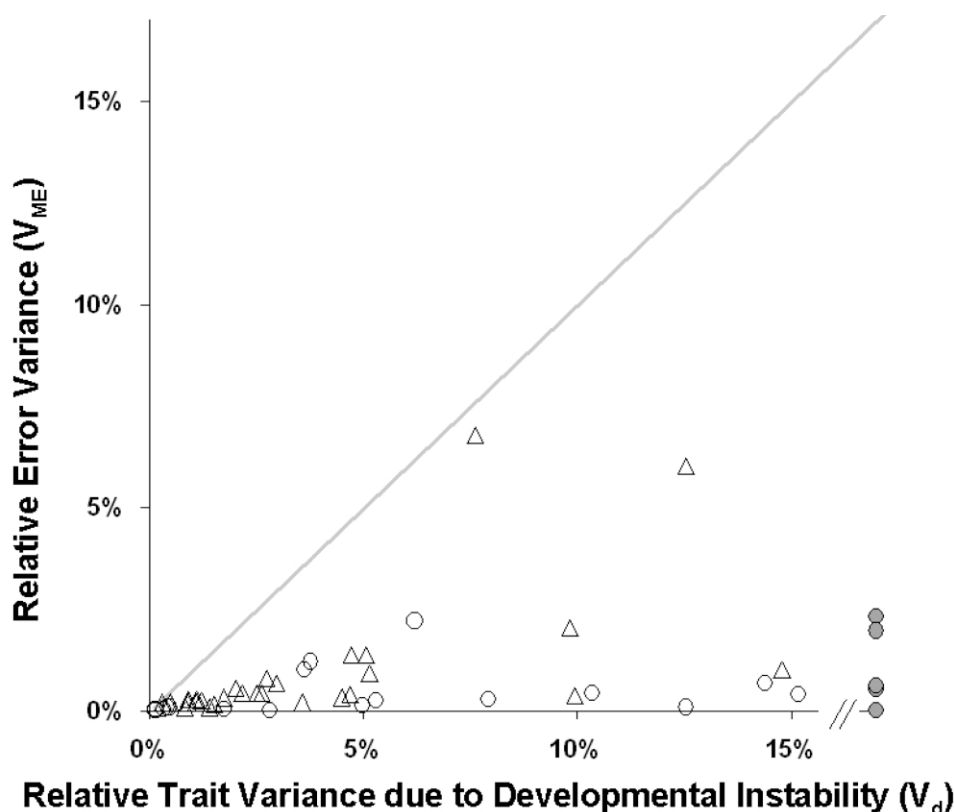
Figure 5: Plot of 75 estimated measurement variances against estimated variances due to developmental variation (both given in percent of total trait variance). Circles are from studies that did not correct for measurement error in estimates of developmental variance, and triangles are from studies that did correct for it. Filled symbols represent studies where more than 20% of the trait variance was due to developmental variation. Not all studies that report measurement error variance were used because some report these values to a single significant figure, causing extreme relative rounding errors and unrealistic estimates of measurement variance. Circle data from Simmons and Ritchie (1996), Pélabon and van Breukelen (1998), and Kruuk et al (2003). Triangle data from Lens and Van Dongen (1999), Van Dongen et al. (1999), Lens et al (2000), and Juste et al. (2001). The two points with very high measurement variance are from Juste et al. (2001).

selectively important or representative of antler-tine variation in adults. A very anomalous case is the extreme asymmetry found by Brown and Brown (1998) in the wings of cliff swallows that died during a winter storm. This seems biologically implausible to us and may conceivably be explained by asymmetrical postmortem changes in the wings.

Our results provide little support for taxonomic differences. We could neither support nor reject Palmer's (2004) suggestion that mammalian development was more canalized due to an internal gestation period, which protects the embryo from environmental variation during critical periods of development. Further investigations are needed on this point, and these need to contrast similar traits in different taxa.

In addition to its contribution to adaptive imprecision, developmental instability may also affect fitness in more direct ways. Indeed, fluctuating asymmetry is often used

as a bioindicator of stress and reduced fitness, and many studies have reported surprisingly large effects. Based on meta-analyses of the published literature, Leung and Forbes (1996) reported that the average correlation of fitness components with fluctuating asymmetry across studies would explain 6.7% of the variation, and Møller (1999) reported that it would explain 2.1%, 6.0%, and 12.3% of the variation in growth, fecundity, and survival, respectively. The average amount of variation in fitness explained in these studies must be even larger than this, since the average R^2 is larger than the square of the average R. There are, however, reasons to be skeptical about these figures. Palmer (2000) has provided evidence of publication bias in these meta-analyses by showing the correlation with fitness decreases with the sample size of the study. Additionally, a strong direct link between fluctuating asymmetry and fitness is theoretically implausible because fluctuating asymmetry tends to be weakly correlated across

Table 1: Developmental variation (% total variation) in different traits and taxa

Trait category	V_d[a]	FA[b]	CV (FA)	CV (trait)
Meristic	27.1%, 24.5% (51)	7.9%, 5.1% (37)	100.0%, 96.1% (31)	21.2%, 18.7% (39)
Quantitative	9.4%, 3.8% (119)	3.1%, 1.4% (85)	116.6%, 106.7% (46)	11.3%, 7.5% (85)
Colors	5.9%, 4.7% (22)	4.2%, 4.0% (14)	82.6%, 83.0% (10)	16.9%, 17.6% (14)
Limbs	8.6%, 3.4% (76)	1.8%, 1.1% (60)	140.0%, 126.0% (20)	6.9%, 4.2% (62)
Selection regime:				
Naturally selected	11.1%, 4.5% (90)	2.3%, 1.1% (71)	118.9%, 112.8% (30)	9.1%, 5.0% (71)
Sexually selected	15.7%, 9.1% (51)	7.4%, 5.1% (49)	104.2%, 96.1% (47)	20.4%, 16.6% (49)
Weakly selected	40.6%, 39.0% (16)	15.5%, 15.5% (2)	…	35.6%, 42.8% (4)
Sex:				
Males	14.7%, 6.8% (89)	5.2%, 2.9% (84)	105.4%, 95.9% (64)	14.6%, 10.1% (84)
Females	8.9%, 3.4% (27)	3.1%, 1.0% (24)	146.4%, 121.2% (8)	11.0%, 4.2% (24)
Taxonomic group:				
Mammals[c]	3.7%, .7% (6)	.9%, .9% (4)	92.4%, 100.2% (3)	13.9%, 13.7% (4)
Mammals[d]	24.7%, 21.0% (34)	9.9%, 7.5% (18)	97.5%, 95.6% (17)	27.0%, 24.5% (20)
Birds	11.6%, 4.9% (42)	3.6%, 2.5% (18)	104.8%, 108.1% (15)	14.3%, 10.9% (18)
Other vertebrates	20.5%, 12.8% (10)	8.9%, 8.0% (10)	106.5%, 105.8% (4)	21.7%, 17.7% (10)
Insects	11.5%, 3.7% (84)	3.0%, 1.3% (76)	117.2%, 108.3% (41)	10.3%, 8.6% (76)
Total	14.7%, 6.2% (170)	4.6%, 2.0% (122)	109.9%, 103.1% (77)	14.2%, 9.7% (126)

Note: Mean and coefficient of variation (CV) of (unsigned) FA, as well as the coefficient of trait variation, are also shown. For each column we show the mean and median of the statistics across all traits. Pseudosampling of traits from same study, same type, or same species, as well as the differing precision of different studies, are not taken into account. The sample size (number of traits) is given in parentheses.

[a] % trait variance.
[b] % trait mean.
[c] Excluding foramina and antlers.
[d] All data.

traits (Houle 1998; Palmer 2000; Clarke 2003). Note, however, that even if the link between FA and fitness is largely spurious, this does not mean that developmental instability is unimportant as a source of adaptive imprecision, which is caused by trait variation and not directly by the asymmetry itself.

Outside comparative and phylogenetic approaches, adaptation is usually conceived as the fit of the population mean to an optimum. Orzack and Sober (1994*a*, 1994*b*, 1996, 2001) identified only two study systems where the degree of individual optimality, as opposed to population adaptation, have been explicitly assessed: Brockman et al.'s (1979; Brockman and Dawkins 1979) study of reproductive behavior in digger wasps of the genus *Sphex* and Orzack et al.'s (1991; Orzack 1990; Orzack and Parker 1990) work on sex-ratio adaptation in parasitic wasps of genus *Nasonia*. This situation may have several causes. One is that the optimality approach to adaptation does not explicitly consider population or individual variation. Thus, there is no theoretical distinction between adaptation of the population or type and adaptation of the individual organism. Individual adaptation may also be ignored because it is viewed as empirically unimportant. It can be unimportant in two senses. Most obviously, it could be that individual variation of any sort normally constitutes

a minor part of maladaptation, thereby justifying a focus on the population mean. Less obviously, it could be that adaptive accuracy is not easily evolvable beyond optimization of the population mean and therefore does not fit easily into the adaptationist program.

We have presented evidence that one component of individual accuracy, namely, developmental precision, is likely to be empirically important in at least some cases. This implies that natural selection for increased accuracy may act on both the optimality of the target phenotype and on adaptive precision. Selection for increased developmental stability is thus a potentially important factor in the evolution of organismal robustness and canalization (e.g., de Visser et al. 2003; Flatt 2005). In general, we need a better empirical and theoretical understanding of what determines the precision of different traits. While it is clear that better precision of traits under stabilizing selection would be favored, we also note that selectively important traits are more likely to have optimal target phenotypes with less population variation and may therefore be the very traits for which adaptive imprecision is relatively most important. For similar reasons, it is also unclear whether traits under stronger stabilizing selection should be more genetically canalized (Wagner et al. 1997; Hermisson et al. 2003), but we note that the relationship between genetic

canalization and developmental stability is unclear, and some evidence suggests they are not closely linked (Debat et al. 2000; Rutherford 2000; Milton et al. 2003; Pélabon et al. 2004*a*).

The low evolvability of developmental stability found in most studies (e.g., Whitlock and Fowler 1997; Palmer 2000; Van Dongen and Lens 2000; Fuller and Houle 2003; Pélabon et al. 2004*b*; but see Clarke and McKenzie 1987; Polak and Starmer 2001) implies that pattern of selection may not be the best predictor of adaptive precision and suggests the alternative hypothesis that adaptive precision may be an intrinsic consequence of developmental architecture. Structural features that may be related to precision include trait complexity and the level of phenotypic integration among traits. More complex traits have more varying parts and may therefore be expected to be more prone to developmental stochasticity. On the other hand, better integration of the different parts of a trait may allow better precision by automatically adjusting and aligning developmental errors in the different parts so as to maintain functional relationships (Klingenberg 2003; Armbruster et al. 2004). Additional comparative studies may clarify whether more complex and integrated characters are generally more or less developmentally stable. In our data set, we were unfortunately not able to categorize the complexity and integration of enough characters to make this comparison.

Although it is occasionally argued that evolutionary theory could benefit from paying more attention to maladaptation (e.g., Bradshaw 1991; Williams 1992; Crespi 2000; Hansen and Houle 2004), there are few empirical attempts at quantifying lack of adaptation. We hope that conceptualizing adaptation as accuracy may invite more attention to maladaptation and its components. By conceiving adaptation as accuracy in place of optimality, it becomes apparent that adaptation is a property of individuals with two components, precision and target optimality, that can be expressed in a common currency. On the population level, this translates into three distinct components of maladaptation: deviance of the population mean from the optimum, individual variation in the target phenotype, and imprecision. Our survey is far from providing a final answer as to the importance of precision for maladaptation, but it does suggest that it should not be ignored. More focused studies may be necessary to develop an understanding of biological underpinnings of adaptive imprecision.

Finally, we note that the data gathered in this study are but a small sample from the literature on developmental stability. Most published studies lack fundamental details such as means, variances, or clearly described methods. We urge authors, reviewers, and journal editors to insist on the publication of these important details along with the main conclusions of a study. As is the case in so many other areas of evolution and ecology, haphazard standards of reporting and the lack of attention to the meaning of estimates greatly impairs our ability to generalize on the basis of past work (cf. Hereford et al. 2004).

APPENDIX A

Notes on the Model and the Statistical Properties of the Estimators

Given the model in the main text, the fluctuating asymmetry is distributed as

$$\text{FA} = |R - L| = |e_R - e_L| \sim \sigma\chi(1), \tag{A1}$$

where $\chi(1)$ is a χ-distributed random variable with one degree of freedom, and the parameter σ is a measure of developmental stability. (In the appendix we follow the convenient notation of Houle [1997]; σ^2 is equal to $2V_d$ in the main text and equal to V_N in Whitlock [1996].) Conditional on a value of σ, the mean and variance of this distribution are

$$\text{E}[\text{FA}|\sigma] = \sigma\sqrt{\frac{2}{\pi}}, \tag{A2}$$

$$\text{Var}[\text{FA}|\sigma] = \sigma^2\left(1 - \frac{2}{\pi}\right). \tag{A3}$$

The unconditional mean and variance are

$$E[FA] = EE[FA|\sigma]$$

$$= E[\sigma] \sqrt{\frac{2}{\pi}}, \tag{A4}$$

$$Var[FA] = E[Var[FA|\sigma]] + Var[E[FA|\sigma]]$$

$$= E[\sigma^2]\left(1 - \frac{2}{\pi}\right) + Var[\sigma]\left(\frac{2}{\pi}\right)$$

$$= E[\sigma^2] - \left(\frac{2}{\pi}\right)E[\sigma]^2$$

$$= E[\sigma^2] - E[FA]^2. \tag{A5}$$

The signed FA has variance $Var[R - L] = E[\sigma^2]$. Thus, $E[\sigma^2]$ can be computed either as $Var[R - L]$ or as $E[FA]^2 + Var[FA]$.

An estimator of population mean FA is

$$\underline{E[FA]} = \frac{\sum_i |L_i - R_i|}{n}, \tag{A6}$$

where n is sample size. We will use underline to signify estimators. With a large sample, we can approximate the distribution of this estimator with a normal distribution:

$$\underline{E[FA]} \sim N\left(\sigma\sqrt{\frac{2}{\pi}}, \frac{\sigma^2}{n}\left(1 - \frac{2}{\pi}\right)\right). \tag{A7}$$

The standard error of $\underline{E[FA]}$ is estimated as

$$SE \underline{E[FA]} = \underline{E[FA]} \sqrt{\frac{\pi - 2}{2n}}. \tag{A8}$$

The component of trait variation that is due to developmental variation is $E[\sigma^2]/2$. This can be estimated from either signed or unsigned FA. First, we look at the use of signed FA. Since $Var[R - L]$ is equal to $E[\sigma^2]$, we can use $\sum_i (R_i - L_i)^2/(n - 1)$ as a direct estimator:

$$\underline{E[\sigma^2]} = \frac{\sum_i (R_i - L_i)^2}{(n - 1)} \sim \frac{E[\sigma^2]}{(n - 1)}\chi^2(n - 1), \tag{A9}$$

since $R - L \sim N(0, \sigma^2)$. Thus, the standard error is

$$SE[[\underline{E[\sigma^2]}]] = \frac{\underline{E[\sigma^2]}\sqrt{2}}{\sqrt{(n - 1)}}. \tag{A10}$$

Another estimator of $E[\sigma^2]$ based on unsigned FA is

$$^*\underline{E[\sigma^2]} = \underline{E[FA]}^2 + \underline{Var[FA]}$$

$$= \underline{E[FA]}^2(1 + \underline{I[FA]}). \tag{A11}$$

Assuming $\underline{Var[FA]}$ is estimated as $\sum_i (FA_i - \underline{E[FA]})^2/(n - 1)$, we rearrange (A11) to obtain

$$^*\underline{E[\sigma^2]} = \underline{E[\sigma^2]} - \frac{\underline{E[FA]}^2}{n - 1}. \tag{A12}$$

Thus, the estimator based on unsigned FA will be slightly biased and have slightly lower precision than the one based on relative FA, but as the second term is of order $1/n$, the two estimators are practically equivalent for moderate sample sizes. Note that this contrasts with the remarks of Palmer (1994), who pointed out that unsigned FA is only 87.6% as efficient as signed FA in estimating the between-sides variation. While it is true that an estimator based on only mean unsigned FA (i.e., $[\pi/2]E[FA]^2$) is 87.6% as efficient, as well as biased if there is variation among individuals, the use of the mean-scaled variance as a correction factor improves the precision of the estimator to make it approximately equivalent to the use of signed FA.

Based on (A10), the relative error of the two estimators is $[2/(n - 1)]^{1/2}$. This allows us to assess the necessary sample sizes for studying developmental precision. If $n = 50$, the relative error is about 20%; if $n = 100$, the relative error is about 15%; and with $n = 1,000$, relative error is about 5%. Clearly, individual studies should aim for sample sizes in the hundreds to be reliable. We also note that our estimates of the fraction of population variation due to developmental stochasticity also have an additional source of error stemming from estimation error in the population variance.

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Appendix B from T. F. Hansen et al., "On Adaptive Accuracy and Precision in Natural Populations"

Table B1

Data

Common name, species name, source, and trait	DANM[a]	Sex[b]	Trait type[c]	Age/group[d]	n	E(z)	Var(z)[e]	Var(R − L)	E(FA)	Var(FA)	ME[f]	CV(FA)	Relative V_d[g]
Mammals:													
Yellow-necked mouse *Apodemus flavicollis* (Blagojevic and Vujosevic 2004):													
No. squamae frontalis foramina	DAN	NR	Mer/nat/for	0B-chrom.	126		.296	.303	.302				.512, …
No. squamosis foramina	DAN	NR	Mer/nat/for	0B-chrom.	126		.281	.233	.183				.415, …
No. diastemae foramina	DAN	NR	Mer/nat/for	0B-chrom.	126		1.072	.827	.595				.386, …
No. palatinum foramina	DAN	NR	Mer/nat/for	0B-chrom.	126		1.722	.889	.651				.258, …
No. hypoglossum foramina	DAN	NR	Mer/nat/for	0B-chrom.	126		.708	.454	.405				.320, …
No. orbitalis anterior foramina	DAN	NR	Mer/nat/for	0B-chrom.	126		.719	.566	.444				.393, …
No. orbitalis superior foramina	DAN	NR	Mer/nat/for	0B-chrom.	126		.659	.566	.429				.429, …
No. alveolaris maxillaris foramina	DAN	NR	Mer/nat/for	0B-chrom.	126		2.786	1.363	.937				.245, …
No. alisphenoideum foramina	DAN	NR	Mer/nat/for	0B-chrom.	126		1.442	.767	.563				.266, …
No. ovale foramina	DAN	NR	Mer/nat/for	0B-chrom.	126		.969	.806	.587				.416, …
No. mentale foramina	DAN	NR	Mer/nat/for	0B-chrom.	126		1.977	1.389	.698				.351, …
No. mentale b foramina	DAN	NR	Mer/nat/for	0B-chrom.	126		2.548	1.043	.683				.205, …
Reindeer *Rangifer tarandus* (Markusson and Folstad 1997):													
Antler length (cm)	DANM	M	Qnt/sex/fnc	1.5 years	53	78.1	295.81	108.38	8.05	46.83		85.0	.183, .189
Antler weight (g)	DANM	M	Qnt/sex/fnc	1.5 years	50	163.3	2,582.3	417.61	16.21	153.13		76.3	.081, .081
Antler volume (10 mL)	DANM	M	Qnt/sex/fnc	1.5 years	50	11.5	14.77	2.88	1.28	1.280		88.4	.097, .099
No. antler tines	DANM	M	Mer/sex/fnc	1.5 years	48	1.8	.96	1.08	.75	.480		92.4	.565, .545
Jaw length (mm)	DANM	M	Qnt/nat/fnc	1.5 years	44	223.2	54.32	.44	.54	**.158**		73.7	.004, .004
Reindeer *Rangifer tarandus* (Lagesen and Folstad 1998):													
Antler length (cm)	DAN, non-n	M	Qnt/sex/fnc	1.5 years	35	67.05	214.77	66.65	6.66	21.160		69.1	.155, .153
Mean beam length (cm)	DAN	M	Qnt/sex/fnc	1.5 years	35	37.6	27.513	5.60	1.88	2.0736		76.6	.102, .102
No. antler tines	DAN, lep	M	Mer/sex/fnc	1.5 years	35	3.23	1.784	2.02	1.03	.9801		96.1	.565, .572
Jaw length (cm)	DAN	M	Qnt/nat/fnc	1.5 years	31	21.53	.465	.01	.08	**.0025**			.010, .010

Table B1 (*Continued*)

Common name, species name, source, and trait	DANM[a]	Sex[b]	Trait type[c]	Age/group[d]	*n*	E(z)	Var(z)[e]	Var(R − L)	E(FA)	Var(FA)	ME[f]	CV(FA)	Relative V_d[g]
Roe deer *Capreolus capreolus* (Pélabon and van Breukelen 1998):													
Antler length (cm)	DANM, lep	M	Qnt/sex/fnc	Age 1	206	8.95	9.88	4.51	1.36	2.677	.52	120.4	.228, .229
Antler length (cm)	DANM, lep	M	Qnt/sex/fnc	Age 2	35	13.39	11.17	1.79	.87	1.000	.29	114.8	.080, .079
Antler length (cm)	DANM, lep	M	Qnt/sex/fnc	Age ≥3	270	17.63	8.51	2.59	.92	1.728	.41	142.6	.152, .151
Red deer *Cervus elaphus* (Kruuk et al. 2003):													
Brow tine length (cm)	M	M	Qnt/sex/fnc		320	20.53	24.10		1.78	2.88	.09	95.6	…, .125
Antler length (cm)	M	M	Qnt/sex/fnc		285	66.49	121.91		2.41	6.43	.14	105.3	…, .050
Dry weight (g)	M	M	Qnt/sex/fnc		203	642.76	54,236.4		41.59	1,330.0	.01	87.7	…, .028
No. antler tines	M	M	Mer/sex/fnc			4.79	1.04		.41	.28	.00	129.8	…, .215
Mountain goat *Oreamnos americanus* (Côté and Festa-Bianchet 2001):													
Horn length (mm)	DANM	M	Qnt/sex/fnc		52	187.2	2,200.1	11.98	2.52	6.37		100.2	.0027, .003
Horn length (mm)	DANM	F	Qnt/sex/fnc		82	192.5	2,137.9	19.69	3.15	10.63		103.5	.0046, .005
Straw-colored fruit bat *Eidolon helvum* (Juste et al. 2001):													
Average cranial morphometrics (log)		NR	Qnt/nat/fnc		31						.06		.125
Egyptian fruit bat *Rousettus egyptiacus* (Juste et al. 2001):													
Average cranial morphometrics (log)		NR	Qnt/nat/fnc		30						.07		.076
Harbor seal *Phoca vitulina* (Schandorff 1997):													
No. hypoglosi foramina	DAN	NR	Mer/nat/for	1988 adults	69	1.600	**.478**	**.559**					.585, …
No. dorsal condylar foramina	DAN	NR	Mer/nat/for	1988 adults	70	1.560	**.555**	.847					.763, …
Birds:													
Black grouse *Tetrao tetrix* (Rintamaki et al. 1997):													
Tarsus length (mm)	DANMR	M	Qnt/nat/fnc	Age >2 years	61	58.7	1.814		.37	.160		108.1	…, .082
Tarsus length (mm)	DANMR	M	Qnt/nat/fnc	Age >2 years	69	22.75	2.156		.58	.449		115.5	…, .182
Cliff swallow *Petrochelidon pyrrhonota* (Brown and Brown 1998):													
Wing length (mm)	DANMR, DA-L, lep	NR	Qnt/nat/fnc	1992-surv.	62	108.53	4.340	.620	.42	**.397**		150.0	.071, .066
Wing length (mm)	DANMR, DA-L, lep	NR	Qnt/nat/fnc	1992-dead	41	108.74	6.176	3.214	1.58	1.185		68.9	.260, .298
Wing length (mm)	DANMR, DA-L, lep	NR	Qnt/nat/fnc	1996-surv.	891	106.87	**5.186**		.49	**.356**		121.8	…, .058
Wing length (mm)	DANMR, DA-L, lep	NR	Qnt/nat/fnc	1996-dead	1,832	107.53	**5.332**	**6.595**	1.20	**4.580**			.618, .565
Outer tail length (mm)	DA-L, lep	NR	Qnt/nat/fnc	1992-surv.	62	48.68	70.685	.6200	.55	**.5022**		128.8	.004, .006
Outer tail length (mm)	DA-L	NR	Qnt/nat/fnc	1992-dead	41	47.07	402.53	6.2361	2.05	2.3616		75.0	.008, .008
Tarsus length (mm)		NR	Qnt/nat/fnc	1996-surv.	62	10.50	**6.705**		.25	**.0558**			…, .009
Tarsus length (mm)	DA-L	NR	Qnt/nat/fnc	1996-dead	41	10.38	**8.494**		.34	**.0656**			…, .011
Buff-breasted sandpipers *Tryngites subruficollis* (Lanctot et al. 1998):													
Wing length (mm)	DANM, DA-corr	M	Qnt/nat/fnc		93	136	6.830	2.0925	1.123	.9115		85.0	…, .159
Tarsus length (mm)	DANM	M	Qnt/nat/fnc		92	32.84	1.609	.2209	.361	.0884		82.4	…, .068
Red-collared widowbird *Euplectes ardens* (Pryke et al. 2001):													
Tail length (mm)	DAN	M	Qnt/sex/fnc		43	213.5	1299.7		5.500	10.30		58.4	…, .016
Yellow-browed warbler *Phylloscopus inornatus* (Price et al. 1991):													

Table B1 (*Continued*)

Common name, species name, source, and trait	DANM[a]	Sex[b]	Trait type[c]	Age/group[d]	*n*	E(z)	Var(z)[e]	Var($R-L$)	E(FA)	Var(FA)	ME[f]	CV(FA)	Relative V_d[g]
Wing feather barb 1	M	NR	Qnt/nat/fnc		140			.046					.529, …
Wing feather barb 2	M	NR	Qnt/nat/fnc		140			.018					.419, …
Wing feather barb 10	M	NR	Qnt/nat/fnc		139			.022					.222, …
Wild turkey *Meleagris gallopavo* (Badyaev et al. 1998):													
Spur length (mm)	DANR		Qnt/nat/fnc	Age 1 year	71	5.54	7.28	1.040	.620	.66		130.6	.071, .071
Spur length (mm)	DANR		Qnt/nat/fnc	Age >2 years	97	20.91	18.05	17.978	2.490	11.90		138.6	.498, .501
Ring-necked pheasant *Phasianus colchicus* (Grahn and Von Schantz 1994):													
Spur length (mm)		M	Qnt/sex/fnc	1-year-old	32	16.7	4.05		.710	1.69		183.1	…, .271
Spur length (mm)		M	Qnt/sex/fnc	Adult	35	20.8	8.67		2.600	1.28		43.5	…, .464
Red-billed streamertails *Trochilus polytmus* (Evans et al. 1994):													
Tail streamer length (mm)		M	Qnt/sex/fnc		39	164.6	254.44		4.350	12.89		82.5	…, .063
Taita thrush *Turdus helleri* (Lens et al. 2000):													
Tarsus length (mm)	DANMR, lep	NR	Qnt/nat/fnc	CH pop	18		.508	.15		.097	.99		.148, …
Tarsus length (mm)	DANMR, lep	NR	Qnt/nat/fnc	NG pop	67		.645	.06		.044	.31		.045, …
Tarsus length (mm)	DANMR, lep	NR	Qnt/nat/fnc	MB pop	152		1.522	**.01**		**.008**	.20		.003, …
Postocular patch width (mm)	DANMR, lep	NR	Qnt/?/fnc	CH pop	14		1.610	.32		.270	.37		.099, …
Postocular patch width (mm)	DANMR, lep	NR	Qnt/?/fnc	NG pop	53		1.598	**.07**		**.05**	.44		.022, …
Outer rectrix length (mm)	DANMR, lep	NR	Qnt/?/fnc	CH pop	15		17.345	1.78		.980	.92		.051, …
Outer rectrix length (mm)	DANMR, lep	NR	Qnt/?/fnc	NG pop	58		16.445	.98		.830	.67		.030, …
Outer rectrix length (mm)	DANMR, lep	NR	Qnt/?/fnc	MB pop	122		17.478	.71		.710	.57		.020, …
Taita thrush *Turdus helleri* (Lens and Van Dongen 1999):													
Tarsus length (mm)	DANR, lep	NR	Qnt/nat/fnc		113		.979	.034		.027	.31		.017, …
Post-ocular patch width (mm)	DANR, lep	NR	Qnt/?/fnc		100		6.808	.190		.143	.07		.014, …
Outer rectrix lth (mm)	DANR, lep	NR	Qnt/?/fnc		73		18.848	.990		.800	.44		.026, …
Taita white eye *Zosterops silvanus* (Lens and Van Dongen 1999):													
Tarsus length (mm)	DANR, lep	NR	Qnt/nat/fnc		142		.502	.047		.035	.40		.047, …
Max width eye ring (mm)	DANR, lep	NR	Qnt/?/fnc		121		.656	.062		.049	1.37		.047, …
Max height eye ring (mm)	DANR, lep	NR	Qnt/?/fnc		121		.513	.052		.040	1.36		.051, …
White-starred robin *Pogonocichla stellata* (Lens and Van Dongen 1999):													
Tarsus length (mm)	DANR, lep	NR	Qnt/nat/fnc		312		2.021	.044		.035	.20		.011, …
Max width preocular spot (mm)	DANR, lep	NR	Qnt/?/fnc		176		1.418	.071		.043	.42		.025, …
Max height preocular spot (mm)	DANR, lep	NR	Qnt/?/fnc		115		.147	.029		.019	2.04		.098, …
Olive sunbird *Nectarinia olivacea* (Lens and Van Dongen 1999):													
Tarsus length (mm)	DANR, lep	NR	Qnt/nat/fnc		309		.619	.034		.029	.81		.027, …
Pectoral tuft (mm)	DANR, lep	NR	Qnt/?/fnc		257		4.233	.130		.087	.17		.015, …
Stripe-cheeked greenbul *Andropadus milanjensis* (Lens and Van Dongen 1999):													
Tarsus length (mm)	DANR	NR	Qnt/nat/fnc		136		2.902	.049		.037	.07		.008, …
Cheek patch (mm)	DANR	NR	Qnt/?/fnc		123		8.325	.140		.120	.10		.008, …

Table B1 (*Continued*)

Common name, species name, source, and trait	DANM[a]	Sex[b]	Trait type[c]	Age/group[d]	n	E(z)	Var(z)[e]	Var($R-L$)	E(FA)	Var(FA)	ME[f]	CV(FA)	Relative V_d[g]
Other vertebrates													
Iberian rock lizard *Lacerta monticola* (Martin and Lopez 2000):													
No. femoral pores	DNM	M	Mer/sex/fnc		20	18.35	2.186		.800	.905	118.9		…, .353
Swordtail fish *Xiphophorus cortezi* (Morris and Casey 1998):													
No. lateral bars	D, non-n	M	Mer/sex/fnc		23	6.49	14.190	1.932	1.000	.909	95.3		.068, .067
Three-spine stickleback *Gasterosteus aculeatus* (Reimchen and Nosil 2001):													
No. lateral plates	DAN, DA-L, lep	M	Mer/sex/fnc		6,059	3.33	.819	.740	.590	.410	108.5		.451, .462
No. lateral plates	DAN, DA-L, lep	F	Mer/sex/fnc		4,145	3.29	1.000	.865	.650	.449	103.1		.432, .436
Bluegill sunfish *Lepomis macrochirus* (Felley 1980):													
No. lateral line scales	DAN, non-n	NR	Mer/nat/fnc	*L.m.macr.*	475	44.17	13.34	3.257	1.393				.122, …
No. lateral line scales	DAN, non-n	NR	Mer/nat/fnc	Fl subspecies	318	47.98	13.71	3.386	1.441				.123, …
No. B scale radii	DAN, non-n	NR	Mer/nat/fnc	*L.m.macr.*	475	8.80	8.39	2.238	1.058				.133, …
No. B scale radii	DAN, non-n	NR	Mer/nat/fnc	Fl subspecies	318	10.59	10.25	3.410	1.235				.166, …
No. pectoral fin rays	DAN, lep	NR	Mer/nat/fnc	*L.m.macr.*	475	13.16	.76	.166	.153				.110, …
No. pectoral fin rays	DAN, lep	NR	Mer/nat/fnc	Fl subspecies	318	13.66	1.00	.165	.159				.082, …
Insects:													…, …
Fruit fly *Drosophila buzzatii* (Norry et al. 1998):													
Wing length (mm)	None	M	Qnt/sex/fnc	Mating	71	1.504	.016		.002	.00003	264.3		…, .001
Wing length (mm)	None	M	Qnt/sex/fnc	Single	72	1.491	.020		.006	.00006	141.8		…, .002
Fruit fly *Drosophila buzzatii* (Santos 2001):													
ln(wing length)	None	M	Qnt/sex/fnc	Mating	92	1.932							.01
ln(wing length)	None	M	Qnt/sex/fnc	Single	89	1.893							.008
Fruit fly *Drosophila simulans* (Markow and Ricker 1992):													
Wing length (NA)	D	M	Qnt/sex/fnc	1988-mating	50	51.61	22.625		.560	**.405**	113.6		…, .016
Wing length (NA)	D	M	Qnt/sex/fnc	1988-single	50	48.89	25.302		.380	**.245**	130.3		…, .008
Wing length (NA)	D	M	Qnt/sex/fnc	1989-mating	50	46.16	16.481		.930	**.080**			…, .029
Wing length (NA)	D	M	Qnt/sex/fnc	1989-single	50	46.75	18.139		.689	**.080**			…, .015
No. aristal branches	D	M	Mer/nat/fnc	1989-mating	50	7.30	1.985		1.200	.720	70.7		…, .544
No. aristal branches	D	M	Mer/nat/fnc	1989-single	50	7.31	2.003		.900	.720	94.3		…, .382
No. head bristles	D	M	Mer/nat/fnc	1989-mating	50	9.68	**.458**		.480	**.320**	117.9		…, .601
No. head bristles	D	M	Mer/nat/fnc	1989-single	50	9.86	**.539**		.362	**.405**	175.9		…, .497
No. sternopleural bristles	D	M	Mer/sex/fnc	1989-mating	50	13.20	2.846		1.200	1.125	88.4		…, .451
No. sternopleural bristles	D	M	Mer/sex/fnc	1989-single	50	12.91	3.229		1.100	1.125	96.4		…, .362
Fruit fly *Drosophila mojavensis* (Markow and Ricker 1992):													
Wing length (NA)	D	M	Qnt/sex/fnc	1989-mating	22	28.20	4.136		.895	1.522	137.8		…, .281
Wing length (NA)	D	M	Qnt/sex/fnc	1989-single	22	27.28	3.048		.905	.961	108.3		…, .292
No. sternopleural bristles	D	M	Qnt/sex/fnc	1989-mating	22	26.36	13.046		1.545	1.215	71.3		…, .138
No. sternopleural bristles	D	M	Qnt/sex/fnc	1989-single	22	25.55	6.023		1.273	1.257	88.1		…, .239

Table B1 (*Continued*)

Common name, species name, source, and trait	DANM[a]	Sex[b]	Trait type[c]	Age/group[d]	*n*	E(*z*)	Var(*z*)[e]	Var(*R* − *L*)	E(FA)	Var(FA)	ME[f]	CV(FA)	Relative V_d[g]
Fruit fly *Drosophila simulans* (Markow et al. 1996):													
No. sternopleural bristles	DM	M	Mer/sex/fnc	Mating	50	24.45	17.40		1.87	1.13		56.7	…, .133
No. sternopleural bristles	DM	M	Mer/sex/fnc	Single	50	26.11	24.22		1.67	1.62		76.2	…, .091
No. sex combs	DM	M	Mer/sex/fnc	Mating	50	20.88	4.62		.96	.72		88.4	…, .178
No. sex combs	DM	M	Mer/sex/fnc	Single	50	21.98	4.59		.90	.72		94.3	…, .167
Fruit fly *Drosophila pseudoobscura* (Markow et al. 1996):													
No. sternopleural bristles	DM	M	Mer/sex/fnc	Mating	50	31.93	26.09		1.64	.85		56.1	…, .068
No. sternopleural bristles	DM	M	Mer/sex/fnc	Single	50	29.62	32.22		1.83	.72		46.4	…, .063
No. sex combs	DM	M	Mer/sex/fnc	Mating	50	20.68	51.05		.24	.13		147.3	…, .002
No. sex combs	DM	M	Mer/sex/fnc	Single	50	19.02	58.36		.20	.13		176.8	…, .001
Fly *Dryomyza anilis* (Otronen 1998):													
Wing length (mm)	DAM	M	Qnt/nat/fnc		69	7.4	**.442**		.021	**.00062**			…, .001
Damselfly *Calopteryx maculata* (Pither and Taylor 2000):													
Forewing prox. segment length (mm)	DANM, DA-R	M	Qnt/nat/fnc	Forsyth crk	25	12.992	.2656	.0324	.152				.061, …
Forewing prox. segment length (mm)	DANM, DA-R	M	Qnt/nat/fnc	Peterson crk	25	13.396	.1474	.0156	.130				.053, …
Forewing prox. segment length (mm)	DANM, DA-R, lep	M	Qnt/nat/fnc	Black crk	25	12.946	.2836	.0484	.184				.085, …
Forewing prox. segment length (mm)	DANM	F	Qnt/nat/fnc	Forsyth creek	25	14.091	.3081	.0210	.111				.034, …
Forewing prox. segment length (mm)	DANM, DA-R	F	Qnt/nat/fnc	Peterson crk	25	14.233	.2451	.0090	.098				.018, …
Forewing prox. segment length (mm)	DANM, DA-R, lep	F	Qnt/nat/fnc	Black crk	25	14.102	.3034	.0462	.179				.076, …
Hindwing prox. segment length (mm)	DANM	M	Qnt/nat/fnc	Forsyth crk	25	11.433	.2013	.0240	.119				.060, …
Hindwing prox. segment length (mm)	DANM, DA-R	M	Qnt/nat/fnc	Peterson crk	25	11.822	.1269	.0132	.117				.052, …
Hindwing prox. segment length (mm)	DANM	M	Qnt/nat/fnc	Black crk	25	11.386	.1849	.0121	.091				.033, …
Hindwing prox. segment length (mm)	DANM	F	Qnt/nat/fnc	Forsyth crk	25	12.390	.2150	.0256	.136				.060, …
Hindwing prox. segment length (mm)	DANM, DA-R	F	Qnt/nat/fnc	Peterson crk	25	12.555	.1606	.0156	.112				.049, …
Hindwing prox. segment length (mm)	DANM	F	Qnt/nat/fnc	Black crk	25	12.407	.1893	.0210	.115				.056, …
Forewing length (mm)	DANM	M	Qnt/nat/fnc	Forsyth crk	25	32.280	2.5202	.0676	.142				.013, …
Forewing length (mm)	DANM	M	Qnt/nat/fnc	Peterson crk	25	33.380	.8696	.0650	.160				.037, …
Forewing length (mm)	DANM	M	Qnt/nat/fnc	Black crk	25	32.405	.9278	.0196	.078				.011, …
Forewing length (mm)	DANM	F	Qnt/nat/fnc	Forsyth crk	25	35.623	1.7738	.0462	.150				.013, …

Table B1 (*Continued*)

Common name, species name, source, and trait	DANM[a]	Sex[b]	Trait type[c]	Age/group[d]	n	E(z)	Var(z)[e]	Var($R-L$)	E(FA)	Var(FA)	ME[f]	CV(FA)	Relative V_d[g]
Forewing length (mm)	DANM, DA-R	F	Qnt/nat/fnc	Peterson crk	25	36.118	2.4110	.0812	.173				.017, …
Forewing length (mm)	DANM	F	Qnt/nat/fnc	Black crk	25	36.179	1.0973	.0812	.206				.037, …
Hindwing length (mm)	DANM	M	Qnt/nat/fnc	Forsyth crk	25	31.024	2.3458	.1190	.189				.025, …
Hindwing length (mm)	DANM	M	Qnt/nat/fnc	Peterson crk	25	32.114	.7796	.0420	.128				.027, …
Hindwing length (mm)	DANM	M	Qnt/nat/fnc	Black crk	25	30.996	.7789	.0342	.112				.022, …
Hindwing length (mm)	DANM	F	Qnt/nat/fnc	Forsyth crk	25	34.260	1.7101	.1089	.168				.032, …
Hindwing length (mm)	DANM	F	Qnt/nat/fnc	Peterson crk	25	34.685	1.9279	.0756	.146				.020, …
Hindwing length (mm)	DANM	F	Qnt/nat/fnc	Black crk	25	34.700	1.0202	.0900	.187				.044, …
Damselfly *Ischnura elegans* (Carchini et al. 2000):													
No. foreleg spiniform setae	DANM	M	Mer/nat/fnc	Mating	87	42.25	11.71	11.11	2.69	2.42		57.9	.474, .412
No. foreleg spiniform setae	DANM	M	Mer/nat/fnc	Single	54	42.20	17.79	18.93	3.49	2.84		48.3	.532, .422
Field cricket *Gryllus campestris* (Simmons and Ritchie 1996):													
Harp area (mm²)	DANR, DA-L, lep	M	Qnt/sex/fnc	France	60	14.84	2.206		.313	.061	1.01	79.2	…, .036
Harp area (mm²)	DANR, DA-L, lep	M	Qnt/sex/fnc	Italy	39	15.49	1.304		.288	.079	2.19	97.6	…, .062
Harp area (mm²)	DANR, DA-L, lep	M	Qnt/sex/fnc	Germany	26	14.16	3.063		.357	.103	1.22	90.0	…, .038
Water boatmen *Callicorixa vulnerata* (Nosil and Reimchen 2001):													
Tarsal length (mm)	DANM, lep	M	Qnt/nat/fnc	Pond 1	141	.94	.011	.0023	.019	.0018	.46	221.1	.107, .101
Tarsal length (mm)	DANM	M	Qnt/nat/fnc	Pond 2	36	.83	.011	.0044	.046	.0025	.61	108.7	.196, .208
Tarsal length (mm)	DANM, lep	M	Qnt/nat/fnc	Pond 3	25	.91	**.005**	.0042	.034	.0034	1.96	170.6	.450, .482
Tarsal length (mm)	DANM, lep	F	Qnt/nat/fnc	Pond 1	93	.96	**.005**	.0015	.016	.0013	.67	225.0	.141, .147
Tarsal length (mm)	DANM, lep	F	Qnt/nat/fnc	Pond 2	28	.91	.026	.0028	.022	.0023	.24	218.2	.053, .053
Tarsal length (mm)	DANM, lep	F	Qnt/nat/fnc	Pond 3	29	.93	.017	.0196	.071	.0144	2.32	169.0	.577, .572
No. tarsal spines	DANM, lep	M	Mer/nat/fnc	Pond 1	140	10.1	3.581	.0358	.123	.0213	.07	118.7	.005, .005
No. tarsal spines	DANM	M	Mer/nat/fnc	Pond 2	36	11.99	6.662	.0225	.103	.0117	.02	104.9	.002, .002
No. tarsal spines	DANM	M	Mer/nat/fnc	Pond 3	25	11.6	1.880	.0132	.070	.0079	.05	127.1	.004, .003
No. tarsal spines	DANM, lep	F	Mer/nat/fnc	Pond 1	93	10.76	2.393	.1488	.090	.0108	.05	115.6	.031, .004
No. tarsal spines	DANM	F	Mer/nat/fnc	Pond 2	29	12.55	7.568	.0227	.100	.0121	.02	110.0	.002, .001
No. tarsal spines	DANM	F	Mer/nat/fnc	Pond 3	29	11.28	10.262	.0846	.186	.0557	.06	126.9	.004, .004
Gall thrips *Oncothrips tepperi* (Crespi and Vanderkist 1997):													
Wing length (mm)	DAM, trunc-n	M	Qnt/nat/fnc	Disp. morph	33	.774	.002		.011	.00012			…, .055
Wing length (mm)	DAM, trunc-n	F	Qnt/nat/fnc	Disp. morph	59	.785	.002		.008	.00004			…, .034
Femur length (mm)	DAM, trunc-n	M	Qnt/nat/fnc	Disp. morph	32	.284	.001		.006	.00002			…, .023
Femur length (mm)	DAM, trunc-n	F	Qnt/nat/fnc	Disp. morph	59	.366	.002		.006	.00002			…, .017
Wing length (mm)	DAM, trunc-n	M	Qnt/nat/vst	Soldier morph	13	.604	.003		.042	.00213			…, .633
Wing length (mm)	DAM, trunc-n	F	Qnt/nat/vst	Soldier morph	35	.360	.023		.086	.00716			…, .315
Femur length (mm)	DAM, trunc-n	M	Qnt/nat/fnc	Soldier morph	13	.272	.001		.006	.00001			…, .034
Femur length (mm)	DAM, trunc-n	F	Qnt/nat/fnc	Soldier morph	32	.350	.000		.007	.00004			…, .281
Winter moth *Operophtera brumata* (Van Dongen et al. 1999):													

Table B1 (*Continued*)

Common name, species name, source, and trait	DANM[a]	Sex[b]	Trait type[c]	Age/group[d]	n	E(z)	Var(z)[e]	Var($R-L$)	E(FA)	Var(FA)	ME[f]	CV(FA)	Relative V_d[g]
Prototibia length (mm)	DNM	M	Qnt/nat/fnc	Parents	31		2.210	.041		.018	.27		.009, …
Prototibia length (mm)	DNM	F	Qnt/nat/fnc	Parents	31		2.616	.063		.026	.23		.012, …
Mesotibia length (mm)	DNM	M	Qnt/nat/fnc	Parents	31		2.807	.027		.015	.21		.005, …
Mesotibia length (mm)	DNM	F	Qnt/nat/fnc	Parents	31		2.512	.046		.021	.20		.009, …
Metatibia length (mm)	DNM, DA	M	Qnt/nat/fnc	Parents	31		2.011	.045		.025	.30		.011, …
Metatibia length (mm)	DNM	F	Qnt/nat/fnc	Parents	31		2.648	.190		.062	.19		.036, …
Sphragis-bearing butterfly *Luehdorfia japonica* (Tsubaki and Matsumoto 1998):													
Forewing radius	DANR	M	Qnt/nat/fnc		133	17.19	**.663**	.043	.164	.0192		84.4	.033, .035
Hindwing radius	DANR	M	Qnt/nat/fnc		133	11.72	**.486**	.030	.126	.0133		91.5	.031, .030

Note: Data that are in boldface come from reported data that are given to only one significant digit and are thus prone to rounding error. Relative V_d values for three studies (Price et al. 1991; Juste et al. 2001; Santos 2001) come from ANOVA tables; hence, missing data. "prox." indicates proximate

[a] DANM indicates whether the study tested for directional asymmetry (D), antisymmetry (A), normality of signed FA (N), and magnitude of measurement arror (M). DA-L, DA-R, and DA indicate the presence of directional asymmetry for larger values on the left side, on the right side, and unreported sides, respectively. "Lep" indicates a significant degree of leptokurtosis, "trunc-n" indicates that the distribution was described as "truncated normal" in the study, and "DA corr" indicates that the data was corrected for directional asymmetry. "non-n" indicates nonnormal.

[b] Gender given as male (M), female (F), or not reported (NR), which is typically a mixed sample.

[c] Trait type: quantitative (qua) or meristic (mer)/naturally (nat) or sexually selected (sex)/functional (fnc) or vestigial (vst) or foramina (for).

[d] Age/group given for studies in which a subset of data was used or different classes of data were reported. Refer to relevant articles for meaning of terms and abbreviations.

[e] Var(z) calculated from reported variance of side $+ V_d/2$.

[f] ME reports the percentage of total trait variance that is due to measurement error.

[g] Relative V_d reported first as the value estimated from the variance of signed FA and second from the mean and variance of unsigned FA.