

Dependence of Phenotypic Variance in Body Size on Environmental Quality

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ABSTRACT: The recent “overhead threshold” model for optimal age and body size at maturity (Day and Rowe 2002) predicts that phenotypic variability in adult body size will be low under inferior environmental quality and will increase with improving conditions. The model is, however, based on a potentially restrictive assumption of a monotone increase of fecundity with increasing body size. On the basis of a numerical model, we show that introducing the concept of maximum adult body size changes the predictions of the model. The dependence of variability in adult body size on environmental quality becomes a concave function with a maximum at intermediate values. Depending on the range of environmental conditions considered, one may therefore expect to observe both increasing and decreasing functions. We test the predictions of our model on a literature-based database of 131 insect species covering all major orders. We demonstrate that, in most species, relative phenotypic variation in body size decreases when environment-specific average of adult body size increases. In the majority of cases at least, such a relationship can be interpreted as a decreased relative variation in better growing conditions. With some potentially meaningful exceptions (e.g., females of capital-breeding insects), the general pattern was largely invariable across different taxa, ecological subdivisions, and sexes.

Keywords: body size, canalization, growth rate, phenotypic plasticity, phenotypic variance, reaction norms.

Intraspecific phenotypic variance is an inherent feature of most quantitative traits. The relative role of different mechanisms that determine levels of variance is of obvious

interest for evolutionary biology, in particular because phenotypic differences form the raw material for natural selection. Even if evolvability of a trait is ultimately based on the genetic component of variance, response to selection is determined by heritability, a quantity that also depends on the environmental component (Houle 1992; Falconer and Mackay 1996). Nevertheless, environmentally induced differences in the levels of phenotypic variance are examined only infrequently (see, however, Gebhardt and Stearns 1988 for an example), which is in sharp contrast with the vast number of empirical studies that examine response of trait means to environmental variability (Pigliucci 2001). This is also true for body size, a trait of special interest for evolutionary biology given its close association with various components of fitness.

Attempts to theoretically analyze patterns of variance in body size have been hampered by an incomplete understanding of evolutionary forces that shape the reaction norms for body size and age at maturity (Blanckenhorn 2000). The classical models (reviewed in Roff 1992; Stearns 1992) lead to reasonable qualitative predictions (e.g., the “L-shaped reaction norms,” which imply a negative phenotypic correlation between adult body size and age at maturity). Despite this, several assumptions behind these models have remained largely phenomenological and are not based on proximate physiological principles (criticized, e.g., by Sevenster [1995]; Day and Taylor [1997]). Recently, however, Day and Rowe (2002) proposed an insightful approach to the explanation of the L-shaped reaction norms by relying on a different set of simple but biologically well-founded assumptions. A key feature of their “overhead threshold” (OT) model is the assumption of a fixed body size threshold that juveniles must reach to attain successful maturation (see, e.g., Davidowitz et al. 2003; Etilé and Despland 2008 for empirical examples).

As a by-product, the OT model predicts a uniform increase of variance in adult body size with increasing environmental quality (measured as juvenile growth rate). In inferior growth conditions, the variance in adult body size remains low: the best choice for all slow-growing individuals is to mature to just above the threshold size. This

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is because even a minor increase in size at maturity can only be achieved by a significant prolongation of development time, and mortality costs per unit size increment are, therefore, high. In contrast, under favorable growing conditions, individuals surpass the developmental threshold and continue to grow to gain the fecundity advantage of large body size. The OT model predicts that even slight incidental differences in growth rates of fast-growing individuals lead to considerable variability in (optimal) adult body size. Inspired by the OT model, Plaistow et al. (2004) analyzed reaction norms for body size and age at maturity in a soil mite and were able to confirm these predictions: variance in body size remained low in poor environments and increased with improving conditions.

The prediction of high variance in good growing conditions rests, however, on a particular assumption of the OT model: an unlimited linear increase of fecundity with adult body size. This is definitely a reasonable assumption for some organisms, such as capital-breeding insects, whose reproduction is completely based on resources accumulated during the larval stage (Tammaru and Haukioja 1996; Jervis and Ferns 2004). In these insects, fecundity may be proportional to body weight at the moment of adult eclosion (e.g., Honek 1993; Tammaru et al. 1996). Among capital-breeding females, a larger adult may indeed always be “better” (Tammaru et al. 2002). An implication is that, in capital breeders, adult body size should be limited solely by the costs associated with attaining a large adult body size and not by the costs of being a large adult (Blanckenhorn 2000).

However, an unlimited increase in realized fecundity with body size is not necessarily the case in all organisms. For instance, for income-breeding insects (Tammaru and Haukioja 1996; Jervis and Ferns 2004), it is reasonable to expect substantial costs associated with being a too-large adult. This is because, in these insects (butterflies are an example), realized fecundity is crucially dependent on adult foraging and, thus, behavioral performance (see Dunlap-Pianka et al. 1977 for an extreme example).

Behavioral performance is typically body size dependent, and for active and mobile adults, there is necessarily an optimal body weight for any given body design. Unlike for females of capital breeders, one should not expect an unlimited increase in realized fecundity with increased body size. Instead, the fecundity function of body size should be concave, or it may reach a plateau (Blanckenhorn et al. 1999; Jiménez-Pérez and Wang 2004; Gotthard et al. 2007). This implies that the assumptions of the OT model may not always be met.

To examine the effect of the two different fecundity functions of body size (i.e., linear increase and a plateau function) on the corresponding patterns of variance in adult body size, we introduced the concept of “ultimate

optimum” of adult body size into the OT model (Day and Rowe 2002). Ultimate optimum was defined as a value of body size that is solely determined by the costs and benefits of being an adult of certain size and disregarding the costs of attaining any particular value of adult body size. As an analogy, there may be such an ultimate optimum home size for each human family that is perhaps primarily determined by the balance of needs and maintenance costs. The practical optimum, which additionally includes the costs of purchasing the home, should typically be much lower than the ultimate optimum. In other words, any juvenile should stop growing no later than when its size has reached the ultimate optimum; by definition, nothing will be gained from surpassing this limit. Introducing such an ultimate optimum into a respective life-history model should intuitively lead to low variance in adult body size in good growing conditions simply because all juveniles will reach the ultimate optimum (defined below as common for all individuals). We confirmed this prediction through an analysis of the respective simulation model (as described below).

Furthermore, we tested the prediction of the overhead threshold model (Day and Rowe 2002) in regard to the relationship between variance in body size and quality of growth conditions using a large set of empirical data derived from published case studies. We sought to determine whether environmental variability in adult body size uniformly increases with improving growing conditions or whether there were alternative patterns. We focused on insects because there are a vast number of published case studies for these animals, furnishing data sets that are highly suitable for testing the associations between various parameters of individual growth (e.g., Teder and Tammaru 2005). In particular, it is a common practice in insect ecology to subject different subsets of individuals to different environmental conditions during their juvenile development. Typical response parameters recorded in this type of research include various indices of body size. However, most of these studies discuss the effect of rearing conditions on trait means only, whereas the response of trait variance has usually been left uninterpreted. To fill this gap, we conducted a systematic survey of the literature to compile a database of studies that report some index of mean final (pupal or adult) size and some statistic describing its variability for at least two samples of conspecific insects reared under different conditions. These data formed the basis for our analysis of the response of phenotypic variance of body size to environmental quality.

In insects, juvenile growth rate is the most widely used and relatively uncontroversial measure of environmental quality. In our analyses of empirical data, however, we used environment- or treatment-specific mean body size as a proxy of environmental quality—that is, we analyzed

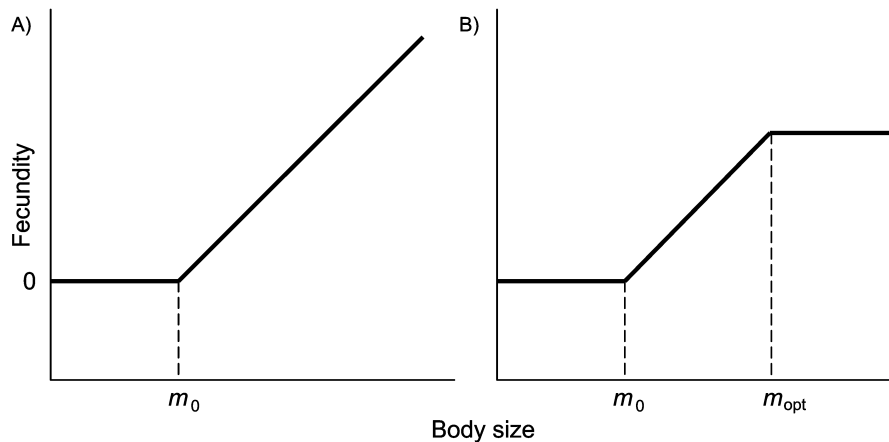


Figure 1: An assumption (A) of the overhead threshold (OT) model by Day and Rowe 2002, and that of (B) a modified model presented in this study. The two models differ in the fecundity function of body size: the former assumes an unlimited increase of fecundity with body size, whereas the latter postulates that fecundity will reach a plateau at a certain value of body size, called ultimate optimum (m_{opt}) in this study; m_0 is the minimum threshold size introduced in the OT model.

the dependence of variance in final body size on average body size attained in respective environments. Larger final body size was ultimately considered to indicate exposure to more favorable conditions during juvenile development (a common practice in insect ecology; see Awmack and Leather 2002). Choosing final body size as the index of environmental quality, rather than growth rate per se, was inevitable because of the nature of the data that are typically reported in the relevant case studies. No qualitative bias is expected because a positive relationship (or, at least, a nonnegative relationship—see above) between growth rate and final body size is generally predicted by life-history models and is commonly observed in nature (Roff 1992; Stearns 1992). Exceptions may occur under special circumstances—for example, when a higher growth rate co-occurs with a higher time stress (De Block and Stoks 2004). Similarly, a higher growth rate is not necessarily associated with larger body size when temperature is the environmental variable that is being manipulated (Angilletta et al. 2004). The cases in which such special scenarios were likely to be observed (different photoperiods, i.e., the likely cues of time stress, as treatments; different temperatures) were, however, not numerous in the data analyzed; we present these results separately.

The Model

The OT model of Day and Rowe (2002) deduces the L-shaped reaction norms for body size and age at maturity from quite straightforward, basic assumptions. In partic-

ular, they postulate that growth of juveniles follows a linear function of time. Growth is assumed to be determinate; that is, there is an abrupt switch from growth to reproduction. The timing of a respective maturation decision is subject to natural selection.

As the key assumption, fecundity is postulated to be proportional to the fraction of adult size that exceeds a certain threshold value (fig. 1A). The threshold is interpreted as the minimum possible size of a viable adult. Fitness is calculated as the product of fecundity and is the probability of survival to adulthood. Formalizing these assumptions, fitness (w) thus depends on development time (t) as $w = s'(kt - m_0)$, in which s is survival per unit of time, m_0 is the minimum threshold body size, and k defines the growth rate (i.e., $kt = m$, the size attained). Day and Rowe (2002) demonstrated that, for every k , there exists an optimal value of t that maximizes the fitness function. The combinations of t_{opt} and the corresponding optimal final body size m_{opt} form the optimal reaction norms for body size and age at maturity, the graph of which is L shaped.

To introduce the concept of ultimate optimum of final body size, we changed just one assumption of the OT model. In particular, we assumed that fecundity reaches a plateau—that is, that it stops increasing after a certain value of body size has been reached (fig. 1B). The ultimate adult optimum is assumed to be independent of the environment experienced by the juvenile. Such an assumption is perfectly realistic for a holometabolous insect species, for example, in which larval and adult individuals live in completely different environments. Necessarily, the

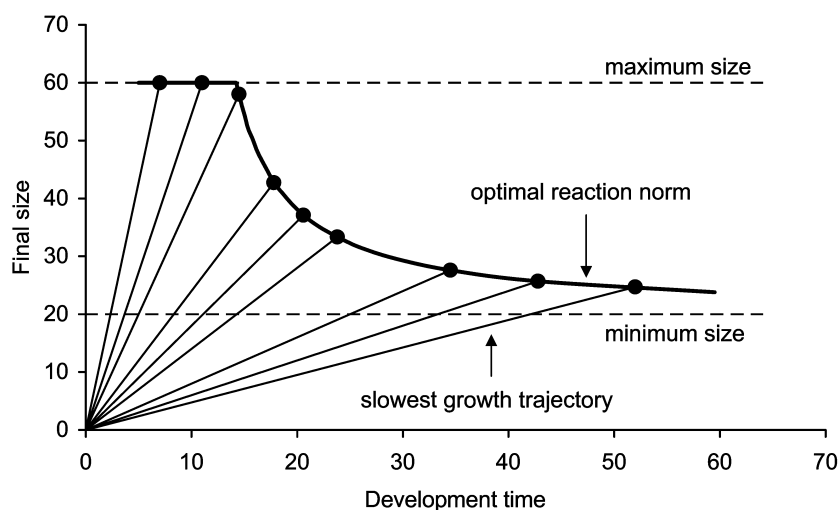


Figure 2: Individual growth trajectories (*straight lines*) and optimal maturation decisions (*filled circles*) in a model assuming two threshold sizes: a lower threshold size below which maturation is not possible and an upper threshold that corresponds to maximum adult fecundity (the ultimate optimum). The convex part of the optimal reaction norm was numerically derived on the basis of the overhead threshold model by Day and Rowe (2002). Accordingly, fitness (w) depends on development time (t) as $w = s'(kt - m_0)$, in which s is survival per unit time, m_0 is the lower threshold size, and the slope of a linear growth trajectory, k , defines the growth rate (i.e., $kt = m$, the size attained). Values of t that maximize the fitness function were found for the range of $k = 0.5$ – 5.5 (e.g., assuming $s = 0.9$ and $m_0 = 20$). The overhead threshold model was amended, assuming that fecundity reaches a plateau (fig. 1)—that is, that it remains constant at $m \geq 60$. Nothing is to be gained from exceeding the maximum size, and the obvious result is the horizontal part of the reaction norm. Low variance in final sizes in pessimal growing conditions (three rightmost trajectories) is predicted by the overhead threshold, whereas the low variance at the upper threshold (three leftmost trajectories) in optimal conditions is a straightforward consequence of the existence of maximum adult size. Growth trajectories form three groups that correspond to three different environmental qualities. The within-group differences can be seen as reflecting individual variation within the environments, which allows visualizing within-environment variation in final sizes.

quality of the juvenile environment (i.e., the growth rate in relation to daily mortality) determines whether it is beneficial to attain the ultimate optimum; however, it is never beneficial to exceed the ultimate optimum. In other words, the ultimate optimum is the maximum body size to be attained in any environment. One can alternatively assume that the maximum size is determined by some constraint rather than being an ultimate optimum in the sense described above. The proximate nature of the maximum size is irrelevant to the discussion below.

If there is such an ultimate optimum for adult body size, it is quite trivial to expect that body size at maturation ceases to increase with improving growth conditions when an optimum is attained (fig. 2). In other words, body size is canalized under growing conditions that are sufficient to allow all individuals to reach a maximum adult body size. On the other hand, the result that final sizes are canalized in pessimal conditions (Day and Rowe 2002) remains unaffected by our additional assumptions. It is, therefore, quite straightforward to predict that, at a qualitative level, such a growth model with two different threshold body sizes (i.e., the lower and the upper thresh-

olds, corresponding to the minimum viable body size and the ultimate optimum) will result in high variance of final body sizes at intermediate values of growth rate, whereas variance at both extremes will remain low (fig. 2). To quantitatively model body size variance in different conditions, we assumed some individual variation in the values of individual growth rates (i.e., k) around the environment-specific mean of this variable. Such within-environment variability in growth rates (fig. 2) should be viewed as resulting from genetic differences among individuals or from unavoidable differences in environmental conditions specific to the individuals.

Our numerical analysis revealed that, consistent with expectations, variance is a concave function of body size (fig. 3). If the graph of the overall relationship is concave, the empirical, sample-based relationships can be both increasing or decreasing, depending on the range of growth rates being considered. In the model, we have assumed that growth rates (k) are determined exogenously and do not result from any “adaptive decision making” by the juveniles themselves (cf. Abrams et al. 1996). “Higher growth rate” can, therefore, also be read as “better envi-

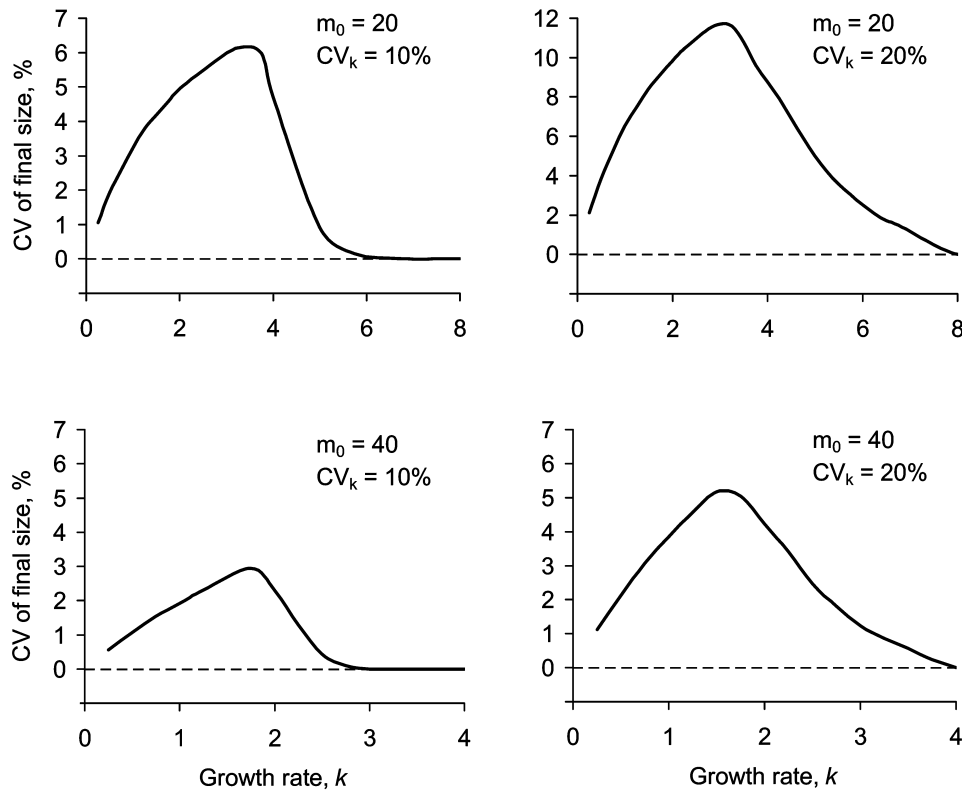


Figure 3: Results of a numerical analysis of the model assuming two threshold body sizes (see fig. 2 for rationale and basic parameters): relative variability (CV, vertical axis) of optimal adult sizes is a concave function of environmental quality. The X-axis variable k defines environmental quality in terms of environment-specific mean growth rate. Within each environment (i.e., for each mean k), individual-specific values of k (not shown) were assumed to be variable (with $CV_k = 10\%$ or $CV_k = 20\%$, which are realistic values for insects) and normally distributed around the environment-specific mean. If growth rates are low, CV in final body size is low, because all individuals mature to body sizes that only slightly exceed the lower threshold value m_0 . In turn, if growth rates are high, all individuals reach the maximum body size, resulting in zero variance (fig. 2). The qualitative pattern of the concave relationship was determined to be robust to changing the parameters of the model: the within-sample CV of k and the relative magnitude of the two threshold values (m_0) was varied and the ultimate optimum was fixed at 60; see fig. 2).

ronmental quality,” which, at least in the case of herbivorous insects, is primarily determined by food quality.

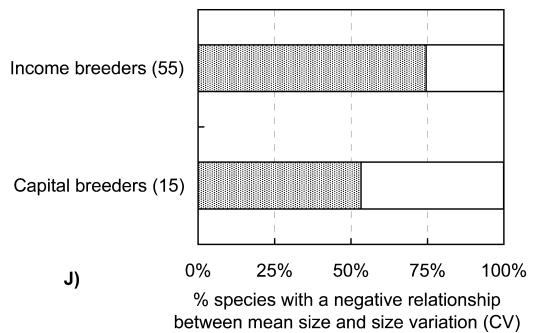
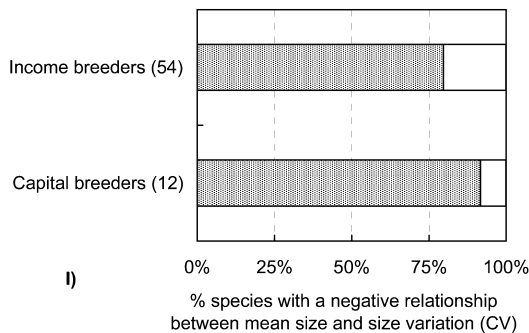
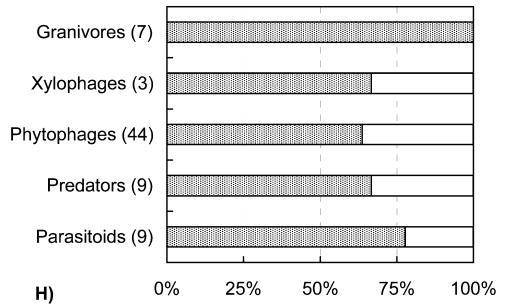
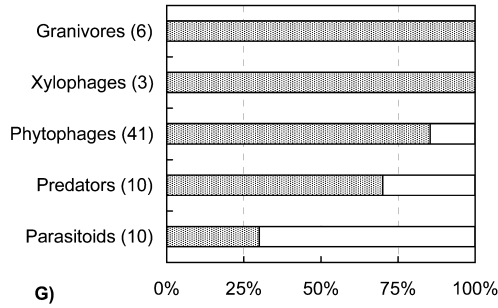
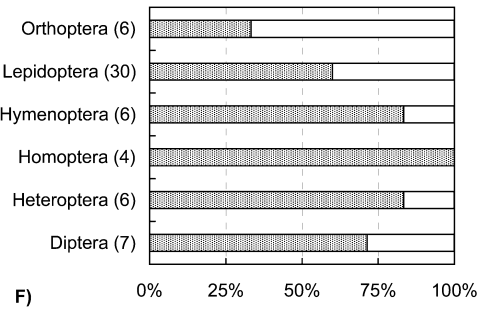
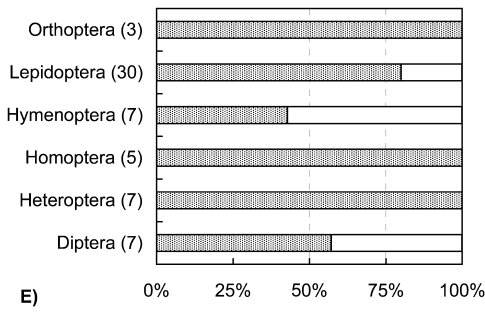
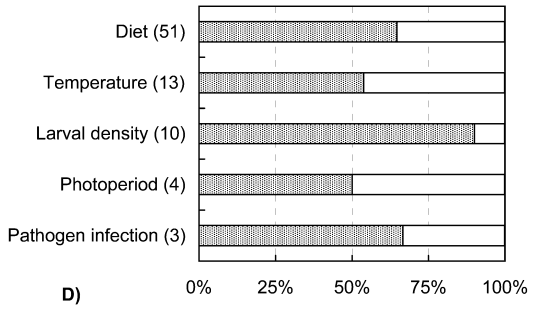
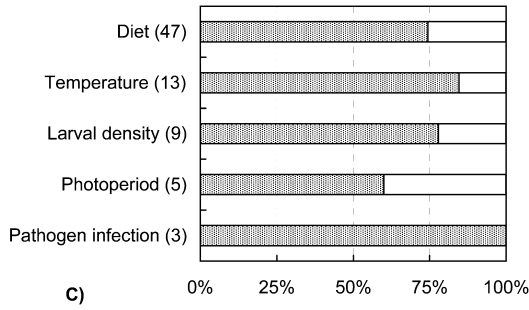
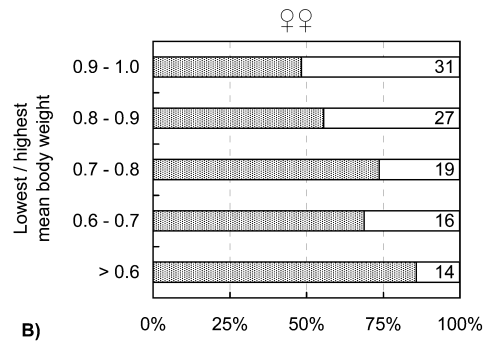
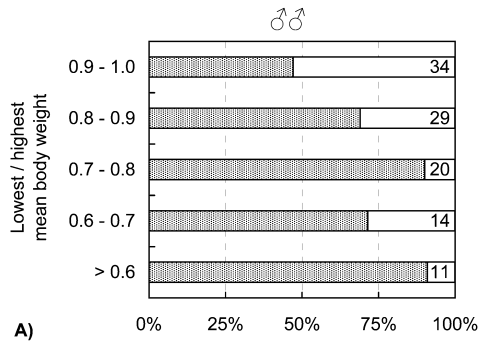
Material and Methods: Reviewing the Literature

Database

To test the predictions of Day and Rowe’s (2002) OT model, as well as our extension to that model, a database was compiled on the basis of an extensive literature survey of major entomological and ecological journals (see Teder and Tammaru 2005 for the list of journals). The final version of the database included case studies of insects in which some measure of final body size, as well as some statistic describing its variability, had been presented for at least two samples of the same insect species. In most of the original studies, different rearing conditions had

been manipulatively created (e.g., different diets or different larval densities). Observational studies were included only if they could be considered to be natural experiments, that is, if original authors had explicitly specified a factor that was responsible for size differences among different samples.

A data set was extracted from each included case study that consisted of three parameters (mean body size, a measure describing size variability [standard deviation, variance, standard error, confidence intervals, or coefficient of variation (CV)], and sample size) for as many subsets of individuals (i.e., samples or separated by treatment group) as had been presented. If any of these parameters were unavailable, the corresponding data set was ignored. Samples with fewer than five individuals for either sex were excluded. The database was limited to numerical presen-



tations of body size indices, and graphical presentations were not considered. Any data on larval size were ignored. Body size measures in units of mass (adult or pupal weight) were preferred over linear measurements.

Only data that were presented separately for male and female individuals were accepted. This is because joint measures of variability necessarily include an often considerable sex-specific component of variance: female insects are typically larger (often much larger) than males within a species (Teder and Tammaru 2005).

Data sets for one species that had been extracted from multiple studies were analyzed as different data sets. Where justified, subsets of data presented for one species in a single study were also treated as separate data sets; this occurred primarily with studies in which an identical experimental design had been assigned to subsets of individuals from two or more different populations. However, when more than one data set was available for a particular species, only the one with the largest number of individuals was used.

Data were ignored if samples were determined on the basis of a factor other than conditions experienced during immature development (e.g., mated vs. nonmated individuals, large individuals vs. small individuals [classified as such by the experimenter], or groups that differed genetically). The database did not include social species and species with complex, size-related caste systems (primarily aphids).

Data Analysis

Because we were interested in the relative variability of body size under different conditions, all measures used to describe size variability in the original studies were transformed into CVs. Body size was used in the analyses as a proxy to describe environmental quality: a larger final body size was considered to indicate more favorable conditions during juvenile development (see above). This assumption was supported by numerous studies in our database. In particular, in species for which both final body size and age at maturity had been presented (i.e., for about 50% of the species in our database), phenotypic correlations between final size and development time were typically negative (for about 75% of the species examined). Quite ob-

viously, a negative relationship between final body size and age at maturity implies a positive correlation between growth rate and final body size.

The dependence of size variability on mean body size was examined by plotting size variability (CV) of the samples against mean body size of respective samples (for each species and for the two sexes within each species, independently). Main conclusions with regard to the dependence of size variability on mean body size—and, thus, environmental quality—were made at the metalevel. The vote-counting method (Wang and Bushman 1999) was used for this purpose; that is, a “vote” cast by a particular species was determined by the sign of the Pearson correlation between body size and CV of body size, irrespective of the statistical significance of each particular correlation. The actual proportions of these votes (i.e., positive vs. negative correlations) were tested against a 1 : 1 ratio using a χ^2 test. Such an approach was used because, in most species, the number of independent samples was insufficient to draw meaningful conclusions about the statistical significance of the relationships at the intraspecific level. In addition to analyses that included all species, separate analyses were performed for different taxa (i.e., major insect orders) and ecological subdivisions (e.g., different feeding guilds and capital breeders vs. income breeders) to determine if body size variability in different groups resulted in similar patterns.

Nevertheless, a subset of “strong” studies was identified in which significant intraspecific differences in body size variability among different samples were observed. Differences in body size variability among environments were regarded as statistically significant at the intraspecific level if CVs of the samples with the lowest and the highest mean body sizes were statistically different (Zar 1999, pp. 144–146). Comparing samples chosen on the basis of mean body size (and not, e.g., selecting pairs on the basis of extreme body size variability) allowed us to consider the contrasts as planned comparisons, with no post hoc adjustments necessary.

In our study, species were regarded as independent observations; this approach is known to be problematic (Harvey and Pagel 1991; Martins 1996). Unfortunately, because of the unsystematic character of the data that were retrieved, and because reliable phylogenies are still available

Figure 4: Proportion of insect species in which relative variation in final body size was observed to decrease with increasing final body size, the latter reflecting improving environmental quality (*shaded bars*). Graphs in the left column represent male individuals; graphs in the right column represent female individuals. *A, B*, Species grouped by the degree of among-samples environmental variation, determined by the ratio of the lowest sample-specific mean size to the highest sample-specific mean size (a ratio equal to unity implies no variability among samples). *C, D*, Species classified according to the environmental factor used to generate body size variation among samples in the original studies. *E, F*, Species grouped by their taxonomic affiliation. *G, H*, Species divided into feeding guilds. *I, J*, Species classified according to the presence of adult feeding. Numbers within the bars (*A, B*) or those next to categories in the Y-axis (*C–J*) are the numbers of species examined.

only for a limited number of insect taxa, phylogenetically explicit comparative methods could not be used. This shortcoming was mitigated by the large number of species, widely spread over most major insect orders, that was used in this study. More importantly, our main focus was to detect patterns that are invariant across taxa, and any argument of invariance is robust to disregarding phylogenetic relationships.

Results

Data sets that met the selection criteria (i.e., mean body size, body size variability, and sample size for at least two different samples, reported separately for males and females) were retrieved for 131 insect species, representing 55 families of nine orders. Linear body measurements were available for 21 species, and pupal or adult weights were available for 110 species.¹ The number of samples per a within-species data set ranged from two to 17 (median, 3; mean, 4.2). These data sets were used to examine the response of body size variability to an environmentally induced change in mean body size, as described above.

The proportion of species in which CV of body size decreased with increasing mean body size was considerably larger than the proportion of species that displayed the opposite trend. For both males and females, the ratio of negative and positive relationships differed significantly from a ratio of 1 : 1. In males, a negative relationship was found in 93 species (71.5%), whereas the relationship was positive only in 37 species (29.5%; $\chi^2 = 24.1$, $P < .001$, $df = 1$). Similarly, analysis of females revealed a negative relationship in 86 species (66.7%) and a positive relationship in 43 species (33.3%; $\chi^2 = 14.3$, $P < .001$, $df = 1$). Among the species for which size CVs of different samples differed significantly (the "strong cases"; see "Data Analysis" for calculation), both negative and positive relationships were represented. However, the ratio of negative and positive trends was even more biased toward negative ones (females, 34 : 8; males, 35 : 6). All further analyses were limited to data sets on the basis of body weight to avoid dimensionality problems associated with using different body size indices.

The larger the relative difference between mean body weights among samples in a particular data set, the higher was the probability of detecting a negative trend between mean weight and its variability (fig. 4A, 4B). Among the data sets with a <10% size difference between conspecific samples (calculated as the ratio of the lowest mean body size to the highest mean body size), the proportions of negative and positive trends were almost equal (fig. 4A,

4B). This is not surprising, because any trend emerging from data sets with small differences among samples was necessarily strongly affected by chance. For this reason, data sets with <10% body size difference between samples were ignored in further analyses, that is, when trends in different subsets of the data were examined.

Decrease in body size variability with increasing body size was the predominant pattern observed, irrespective of the environmental factor that had been used to generate size differences between intraspecific samples (diet, larval crowding, temperature, photoperiod, or pathogen infection; fig. 4C, 4D). Negative relationships between mean body size and body size variability prevailed in most taxa when either males or females were analyzed (fig. 4E, 4F). Broadly, the same applies to different feeding guilds (with the possible exception of male parasitoids, in which the proportion of positive relationships tended to be higher, although not significantly so [fig. 4G, 4H]).

As expected, notable deviations from the general patterns were observed when species were classified by the presence or absence of adult feeding (i.e., income vs. capital breeders; Tammaru and Haukioja 1996; fig. 4I, 4J). Among capital-breeding females, the ratio of the two opposite trends was nearly 1 : 1, whereas in income-breeding females, the typical negative relationships were far more common than positive ones (fig. 4J). In males, the proportions of negative and positive relationships were similar among income breeders and capital breeders (fig. 4I). Consistently, proportions of negative and positive relationships were statistically significantly different between females and males of capital breeder species (Fisher's exact test, $P = .04$; fig. 4I, 4J). Obviously, however, before any definitive conclusions can be drawn, these patterns must be confirmed by analyses that explicitly account for phylogenetic relatedness.

Discussion

This study revealed numerous documented cases of both negative and positive cross-environment relationships between body size and its relative variability, thereby indicating the lack of a uniform general pattern. In most case studies, however, relative variability in body size was found to decrease with increasing body size. This trend was highly consistent across the class of insects: species with a negative relationship between body size and its variability prevailed in nearly all larger taxa, as well as in most ecological subdivisions that were considered. Moreover, the qualitative result was largely insensitive to the nature of environmental factors that had generated cross-environment variability in mean body size, with the possible exception of photoperiod and temperature. In typical situations, which were quite prevalent in our data set, an increase in insect

¹ A table containing species list and sources of information is available from the first author upon request.

body size is synonymous with an improvement in environmental quality for growing juveniles. However, in the case of temperature and photoperiod, the interpretation may be complicated by the possibility that these factors may serve as seasonal cues correlated with the levels of time stress, rather than being indices of environmental quality (Roff 1983; Tauber et al. 1986; Danks 2007).

In conclusion, comparative data assembled over nine insect orders did not support the idea of variability in adult body size being positively correlated with the quality of environment for growing juveniles (Day and Rowe 2002; Plaistow et al. 2004); rather, the opposite pattern appeared to prevail. Nevertheless, our results should not be seen as disproving the overhead threshold model for reaction norms for body size and age at maturity (Day and Rowe 2002). In particular, we demonstrated that this model can easily be modified, without losing biological realism, to produce qualitatively different predictions with respect to the relationship between environmental quality and variability of final body size. The model with two different size thresholds (fig. 2) predicts that, at the favorable end of growing conditions, the relationship between variability in final body size and environmental quality should be negative (fig. 3). It is easy to see that, if there is a certain maximum of final body size that any growing individual does not surpass, one would expect final sizes to be canalized (zero variance) as soon as all individuals in the sample will grow fast enough. The reason for such a maximum body size may be either some constraint or just an ultimate optimum for adult body size. In other words, growth trajectories are expected to converge at the maximum body size under good conditions, whereas some variance in final body size is still expected to occur under less favorable conditions as a consequence of perhaps inevitable variability in individual growth rates.

Quite surprisingly, there seems to be only indirect empirical evidence that, at best, allows one to decide if such convergence at the maximum really occurs in insects (Amano 1983; Nylin 1988). For the time being, we are unable to directly support the ultimate optimum model (fig. 2) with rigorous empirical data. However, an indirect way to test this model could be to compare the relationship between mean and CV of body size at the stressful end (the relationship predicted to be positive) and the favorable end (predicted to be negative) of an environmental gradient. It seems likely (and, in fact, is often evident from original studies) that most of the experiments that form the basis of our review were performed under conditions that were more or less favorable for the insects being reared, and thus the prevailing negative relationship between mean size and size variability is, indeed, an expected outcome. A more direct way to confirm the hypothesis would be to prove the existence of the predicted concave

reaction norms. However, available literature data were insufficient to fulfill this task within the framework of this study: in most cases retrieved, only two environments could be compared with respect to variance in body size.

Nevertheless, a particular result of the literature survey may deserve attention in the context of the model, assuming an ultimate optimum for adult body size (fig. 2). Namely, the subset of females—but not males—of capital-breeding species (i.e., those not feeding as adults) formed an exception to the general pattern: in this group, variability of body size often increased with increasing body size. This is consistent with the hypothesis under consideration and was predicted a priori. In these organisms, no convergence at maximum body size is expected to occur, because no ultimate optimum apparently exists: because of the crucial role of resources accumulated in the larval stage and the simplification of adult behavior, larger size is always favored in females (e.g., Honek 1993; Tammaru et al. 1996, 2002). In contrast, there is no reason to expect capital-breeding males to deviate from the general pattern (in fact, they did not).

The model that had two different threshold sizes was able to explain both negative and positive relationships between environment-specific body size and its variance. Considering the scarcity of suitable published data, further experimental work is needed to critically evaluate this hypothesis and its possible alternatives. One such alternative factor with the potential to affect the relationship in question would be the dependence of within-environment variability of growth rates on environmental quality. Our practical experience with herbivorous insects indicates that, if rearing conditions are good, all conspecific larvae in an experimental rearing pass through the larval stage highly synchronously. However, as soon as adverse conditions are imposed, major differences in individual growth rates appear. The generality of this observation, as well as the potential of the environment-specific variance in growth rates to be reflected in the variance in final body size, may deserve further attention.

In summary, we conclude that qualitatively different relationships between environmental quality and variability in adult body size do occur in insects. The negative relationship, however, tends to prevail. We proposed a way to explain these different outcomes, but alternative explanations may also exist. Attention to this question is welcome, because it would necessarily contribute to our general understanding of determination and of adaptive significance of body size. On the other hand, knowing when and why the environmental component of variance is increased and when the genetic differences are displayed allows us to predict when and why natural (or artificial) selection for body size is most effective.

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