Heritable variation and evolution under favourable and unfavourable conditions

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Heritable variation and evolution under favourable and unfavourable conditions

Ary A. Hoffmann and Juha Merilä

The minimum requirements for an evolutionary change are the occurrence of natural selection and the presence of heritable variation in the selected trait[1]. The narrow-sense heritability of a trait, defined as the proportion of the phenotypic variance V_P accounted for by additive genetic effects V_A (i.e. V_A/V_P), is an important indicator of the extent to which a trait can evolve. It is well known that trait heritabilities are not constant but can vary with environmental conditions, as well as with changes in gene frequency. Other measures of genetic variability, particularly measures of 'evolvability', which define the additive genetic variance relative to the mean (e.g. $V_A/\bar{x}^2$, $V_A/\bar{x}\sqrt{V_P}$, where $\bar{x}$ is the mean)[1,2], also vary with environmental conditions. Understanding this variation is important in determining the evolutionary potential and dynamics of populations inhabiting heterogeneous environments[3–5], and in predicting the fate of populations under environmental change[6,7].

Genetic variability in quantitative traits can change as a direct response to the environmental conditions in which they are expressed. Consequently, similar selection in different environments might not be equally effective in leading to adaptation. Several hypotheses, including recent ones that focus on the historical impact of selection on populations, predict that the expression of genetic variation will increase in unfavourable conditions. However, other hypotheses lead to the opposite prediction. Although a consensus is unlikely, recent *Drosophila* and bird studies suggest consistent trends for morphological traits under particular conditions.

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Recently, there has been discussion about whether some types of environmental condition have consistent effects on heritable variation[3,8,9]. Much of the focus has been on whether unfavourable versus favourable conditions increase or decrease heritable variation. Several hypotheses have been proposed to explain how unfavourable conditions might impact heritable variation, and empirical studies have attempted to test the predictions. The issue also relates to questions of whether laboratory estimates of heritable variation are similar to estimates obtained under field conditions[10] that are often assumed to be unfavourable, and whether evolutionary changes in one environment translate into changes in others, providing a link to phenotypic plasticity[11].

Hypotheses

Increased genetic variation in unfavourable conditions?

Several hypotheses have been proposed for why heritable variation (and particularly the heritability of a trait) might differ between unfavourable and favourable conditions (Table 1). First, stressful conditions (i.e. those leading to a drastic reduction in fitness) can directly increase genetic variation in traits by increasing rates of mutation and recombination (Table 1, hypothesis 1)[3]. These sources of variation might be important for understanding adaptation and long-term evolution, but they cannot explain, for instance, heritability differences between environments evident from parent–offspring or strain comparisons.

The second hypothesis (Table 1) is that heritability differences between environments arise because selection removes alleles with a low fitness. There are two versions of this hypothesis. One is that, under the favourable conditions commonly encountered by organisms, there is a rapid decrease of heritable variation in traits associated with fitness[12]. In contrast, in rare unfavourable conditions, selection on alleles resulting in lower fitness will be much less effective, resulting in a higher heritability under these conditions.

The other version of this hypothesis is based on the accumulation of mutations[5] and is a result of recent experiments that have shown that the effects of deleterious mutations are often environment-specific[13]. Deleterious mutations expressed in environments commonly encountered by organisms will be rapidly removed by selection, but mutations that are only deleterious in rare and unfavourable environments will persist and thereby increase the expression of genetic variation under these conditions[5,14]. Thus, mutations will indirectly contribute to heritability differences between environments if unfavourable conditions are rare.

A third hypothesis (Table 1) is based on the effects of selection on canalization (i.e phenotypic variation produced by different genotypes). As emphasized by Waddington[15] and, in a recent model, by Pàl[16], selection is expected to favour the suppression of variation in quantitative traits until an environmental change occurs and alters the adaptive landscape. The expression of phenotypic differences among genotypes will therefore be reduced under conditions normally encountered by organisms (i.e. favourable ones), and differences will tend to occur only under stressful conditions (Fig. 1a).

The same pattern can also arise if phenotypic differences among genotypes are not expressed unless resources become limiting, irrespective of selection for canalization (Table 1, hypothesis 4). This hypothesis helps to explain the increase in the expression of genetic effects on flux through biochemical pathways that are normally buffered[17]. Ward[18], in particular, has emphasized how differences in heritability between favourable and unfavourable conditions can arise because of the way environmental and genetic effects interact in producing phenotypes, regardless of the history of selection.

The predictions from these hypotheses are rather different. On the one hand, if selection history is important, a high heritability will occur in environments that are rare but favourable[12,19]; and, under the second hypothesis, genetic correlations between environments are expected to be lower (i.e. selection gains in one environment lead to little change in the other environment) because genes are largely environment-specific in their expression. On the other hand, under the other hypotheses (Table 1, hypotheses 1, 3 and 4), genetic correlations can be high, and selection responses under unfavourable conditions might enhance evolutionary rates regardless of environmental conditions.

Decreased genetic variation in unfavourable conditions?

Several hypotheses also lead to the opposite prediction – that genetic variation decreases in unfavourable conditions (Table 1, hypotheses 5 and 6). Foremost among these is that unfavourable conditions decrease heritability by increasing the environmental variance (hypothesis 5). This hypothesis originated from agricultural studies on plants[20] and predicts that both V_E (the environmental variance) and V_P will increase in unfavourable conditions while the evolvability remains relatively constant. A variant of this hypothesis[21] applies specifically to arthropods that undergo a variable number of larval instars before maturation. If unfavourable conditions increase the variability in instar number, an increase in phenotypic variability in size and sexual maturity can decrease the heritability of these traits.

The sixth hypothesis was proposed in relation to nutrition in birds[22]. Assume that the potential size an individual can reach is largely determined genetically by additive effects, but might not be realized under unfavourable conditions when the environment reduces growth rate. Thus, the narrow-sense heritability of a trait is lowered when conditions are unfavourable because of a decrease in V_A (Fig. 1b). This situation could also arise as a consequence of selection favouring the evolution of alleles in growth-promoting loci that are not expressed during periods of food shortage, leading to a decrease in V_A.

Finally, two hypotheses (Table 1, hypotheses 7 and 8) propose that the effects of environmental conditions on heritability can be variable. One of these[21] (Table 1, hypothesis 7) concerns the effect of measurement error on heritable variation. Traits are measured with error, and variation caused by error can remain constant even when the phenotypic variance changes with environmental conditions. Consequently, the heritability estimate of a trait in unfavourable conditions can appear to increase (or decline) if the phenotypic variance is higher (or lower) under these conditions.

The eighth hypothesis is that changes are unpredictable when genetic effects on plasticity are considered separately from genetic effects on the trait mean. Under a simple model[23], genotypes are set at an arbitrary environmental point to have a plasticity of zero. When the reaction norm is linear, plastic reactions are described by the slope of a line extending from this arbitrary point (Fig. 1c). The heritability of a trait will increase as environments move away from this point because the variance resulting from plasticity increases the overall genetic variance. In particular, if there is a negative or positive association between genes controlling plasticity and trait-mean effects, and the heritability for plasticity is high, then heritabilities will increase sharply with changes in environmental conditions. Thus, if there is genetic variation in the plasticity of a trait, changes in heritability depend on the environmental point at which reaction norms converge.

In summary, predictions about changes in heritable variation are difficult. In the simplest case, an increase in V_E under stress decreases the heritability. However, the environment might also impact on the expression of genetic variation, leading to an increase or decrease in heritability. If a trait mean is decreased under unfavourable conditions, its heritability might decrease because of persistent measurement error and because genes that control the maximum value have no impact on the final phenotype. Conversely,

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Table 1. Hypotheses about the effect of unfavourable conditions on the genetic variation of a trait

| Hypothesis	Refs
Unfavourable conditions increase heritability	
(1) There are direct effects of stress on recombination and mutation rates	3
(2) A history of selection against low fitness alleles decreases trait heritability less in novel (unfavourable) environments	5,12,14,19
(3) A history of selection for canalization decreases phenotypic differences in common favourable conditions	15,16
(4) Stress conditions increase phenotypic differences between genotypes as resources become limiting	3,17
Unfavourable conditions decrease heritability	
(5) Environmental variation is increased by stress conditions	20
(6) Genetic potential of organisms is not reached under poor nutrition	22
Unfavourable conditions have unpredictable effects	
(7) Effects of measurement error are altered by the environment	21
(8) Genetic variation for a trait's plasticity influences heritability	23
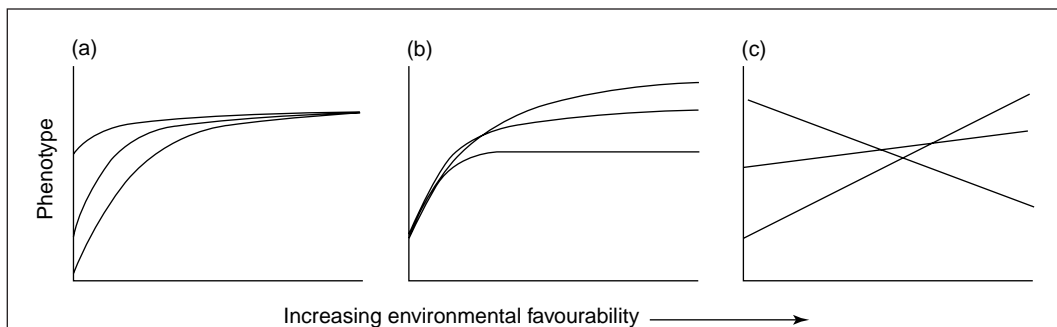
Fig. 1. Effects of environmental conditions on the phenotypic expression of three genotypes (curves) in three different hypothetical situations: (a) genotypic differences are expressed only under unfavourable conditions; (b) genotypic differences are expressed only under favourable conditions; (c) linear reaction norms are closest under intermediate conditions and diverge towards increasingly favourable and unfavourable conditions.

Box 1. Heritability and its causal components in different environments

The phenotypic variance (V_P) of a trait can be expressed as $V_P = V_A + V_D + V_I + V_E$: where V_A is the additive genetic variance; V_D, the dominance variance; V_I, the variance resulting from epistatic interactions between genes; and V_E, the environmental variance. Different components can be estimated from appropriate quantitative genetic breeding designs or from selection experiments[1], although the estimation of epistatic and dominance variance components is difficult, and they are usually assumed to be negligible (but see Ref. 31). Changes in the narrow- ($h^2 = V_A/V_P$) or broad- [$h^2 = (V_A + V_D + V_I)/V_P$] sense heritabilities can be caused by changes in the genetic or environmental components of variance. When comparing heritability estimates across two (or more) environments, heritabilities can differ even when V_D, V_I and V_E do not change across environments because (see figure): (a) there is a difference in V_A (= variance of breeding values) among the environments (V_A in environment 1 is less than V_A in environment 2); or (b) the genetic correlation across the environments is less than one (and V_A is the same in the two environments). In both cases, this occurs because of genotype × environment interactions, but only in the first case does the evolutionary potential between the two environments differ.
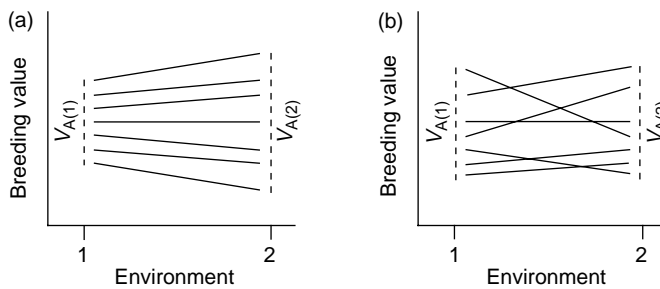
(Online: Fig. I)

decanalization might increase the expression of genetic variation. Alternatively, any changes in heritability might reflect a history of weak selection and/or the accumulation of deleterious mutations in unfavourable conditions.

Problems in testing the hypotheses

A considerable body of data on genetic variability under different conditions has accumulated from both agricultural and animal breeding studies, as well as from studies of natural populations. Previous attempts to summarize the patterns of genetic variability under favourable and unfavourable conditions suggest some trends[3,8,24]. However, several problems need to be overcome when undertaking comparisons and relating data to the hypotheses discussed here (Table 1).

Defining and comparing environmental conditions

Three problems relate to the nature of environmental variation. First, we need a method of distinguishing favourable and unfavourable conditions across a wide range of situations. One way of defining environmental quality is to characterize effects on fitness measures, but such information is rarely provided. Another approach is to define quality by considering environmental effects on the traits under examination (e.g. Ref. 25).

A second problem arises when environmental comparisons involve regression of offspring reared in one environment on parents reared in a different environment. When this occurs, it is difficult to distinguish differences in genetic variance between environments from genotype × environment interactions (crossing reaction norms, Box 1). The regression of offspring (*o*) from environment 1 on the midparent value (*p*) from environment 2 is given as:

$$\beta_{(o1,p2)} = \frac{\gamma \sigma_{A1} \sigma_{A2}}{\sigma_{P2}^2}$$

where γ is the additive genetic correlation between the trait in the two environments, σ_{A1}^2 and σ_{A2}^2 are the additive genetic variances in the offspring and parental environments respectively, and σ_{P2}^2 is the phenotypic variance in the parental environment[26]. Heritability estimates obtained from this equation will only equal the true heritability in environment 1 if γ is one (no genotype × environment interactions) and if the additive genetic variance is the same in the two environments. Nevertheless, a recent review[10] suggests that laboratory and field estimates of narrow-sense heritability are often similar, implying similar values of V_A across environments and genetic correlations close to 1.

Another problem when comparing heritabilities across environments concerns scale, which stems from the effect of unfavourable conditions on the mean and/or variance of a trait. This can lead to inflated or deflated heritability estimates when comparing generations exposed to different conditions. For instance, if offspring are exposed to conditions that lower the mean and variance of a trait compared with parental conditions, there will be a reduction in heritability values computed from parent–offspring comparisons even when heritabilities are similar in the two environments[27]. Because the parent–offspring covariance is the numerator and the parental variance is the denominator when computing heritability, a higher parental variance reduces the heritability estimate. For this reason, trait scores in parents and offspring will need to be standardized to equal variances before estimating heritability.

Environment-specific parental and nonadditive effects

When comparing genetic variability across environments, maternal, paternal and common environment effects (which are pervasive[28,29]) need to be controlled. By increasing nongenetic similarity among relatives, parental environmental effects can inflate heritability estimates. This becomes a problem when comparing environments because parental effects can be enhanced under unfavourable conditions (e.g. Ref. 30).

Likewise, nonadditive effects can affect genetic variability measures across environments[25,31]. Most studies of natural populations explicitly assume that the contribution of dominance and epistatic variance (Box 1) to sib-estimates of genetic variance are negligible. However, dominance effects are often large, especially for fitness related traits[31], and their expression can be environment dependent. Recent data also indicate an increased expression of epistatic effects under unfavourable conditions[25]. These effects might lead to apparent heritability differences between environments even when the narrow-sense heritabilities are the same.

Therefore, there are several potential confounding factors affecting heritability comparisons between favourable and unfavourable conditions. Consequently, experimental designs allowing the isolation of these effects from those caused by changes in V_A and V_E should ideally be undertaken.

Looking for trends
Size-related traits in Drosophila

The effects of unfavourable conditions on size-related traits have been investigated in several recent *Drosophila* studies (Table 2). Their emphasis has been on temperature extremes and nutrition, although some studies have also combined different conditions to generate stressful situations. Most *Drosophila* studies have involved comparisons of variation among isofemale lines (i.e. they have provided only broad-sense heritability estimates, Box 1). In general, these studies suggest that temperature extremes tend to increase the heritability of thorax length and, to a lesser

Table 2. Effect of unfavourable conditions on heritability for size-related traits in *Drosophila* and other invertebrates

Trait	Species	Method[a]	Condition	Heritability[b]	Means[c]	Refs
Wing length	*D. buzzatii*	il	High temperature	+	+	46
	D. melanogaster	il	High temperature	(−)	++	47
	D. melanogaster	il	Low temperature	(−)	++	47
	D. melanogaster	il	High temperature	+	++	36
	D. melanogaster	il	Low temperature	−	++	36
	D. melanogaster	il	High temp./nutrition	+	?	32
	D. melanogaster	il	Low temp./nutrition	−	?	32
	D. melanogaster	po	Cold/ethanol/nutrition	++	+	33
Thorax length	*D. buzzatii*	il	High temperature	−	=	46
	D. melanogaster	il	High temperature	(−)	++	47
	D. melanogaster	il	Low temperature	(+)	+	47
	D. melanogaster	il	High temperature	−	++	36
	D. melanogaster	il	Low temperature	−	++	36
	D. melanogaster	il	High temp./nutrition	−	?	32
	D. melanogaster	il	Low temp./nutrition	− −	?	32
Dry weight	*Callosobruchus maculatus* (cowpea weevil)	hs	Low temp./humidity	−	+	41
Pupal weight	*Lymantria dispar* (gypsy moth)	fs	Nutrition	+	+	48
Body width	*Harmonia axyridis* (ladybird beetle)	fs	Nutrition	− −	+	34
Adult weight	*Dysdercus fasciatus* (cotton stainer bug)	hs	Moisture	+	++	37
Adult length	*Daphnia magna*	cl	Food availability	(+)	?	21

[a]Key: il = isofemale line comparison; po = parent–offspring regression; fs/hs = full/half sib analysis; cl = clone comparison.
[b]Direction of affect (favourable versus unfavourable) and magnitude of difference in heritability estimates: − or + = less than 2 SE; − − or ++ = greater than 2 SE; brackets indicate that magnitude could not be estimated.
[c]Direction of effect (favourable versus unfavourable) and magnitude of difference in trait means: + = less than 1 SD; ++ = more than 1 SD; ? = information not available.

Table 3. Effect of unfavourable growth conditions on the full-sib heritability estimates and trait mean of size-related traits in birds

Trait	Species	Growth factor[a]	Heritability[b]	Means[c]	Refs
Head length	*Branta leucopsis* (barnacle goose)	year	++	+	49
	Larus canus (common gull)	year	++	+	50
Tarsus length	*Parus major* (great tit)	year	−	+	22
	Parus caeruleus (blue tit)	brood	++	+	35
	B. leucopsis	year	++	++	49
	Ficedula albicollis (collared flycatcher)	brood	+	+	24
Weight	*P. major*	year	++	++	22
	B. leucopsis	year	−	++	49

[a]Growth conditions varied either because of year-to-year variation in natural conditions (year) or because of brood manipulation (brood).
[b]Direction of effect (favourable versus unfavourable) and magnitude of heritability difference: + or − = less than 2 SE; ++ = greater than 2 SE.
[c]Direction of effect (favourable versus unfavourable) and magnitude of difference in trait means + = less than 1 SD; ++ = more than 1 SD.

extent, wing length, particularly when combined with poor nutrition. The effects are relatively small in some studies, but in one case[32] estimates differed by several standard errors. Heritability differences tend to involve changes in both the genetic variance (V_G) as well as in V_E. There appears to be little correlation across different studies between the effects of favourable and unfavourable conditions on trait means and heritabilities (Table 2). Despite the trends, an increased heritability under unfavourable conditions has not been evident in all studies: one of the combined conditions led to a marked decrease in the heritability of wing length, mainly because of an increase in environmental variance[33].

Increases in heritability under unfavourable conditions have also been demonstrated in other invertebrate studies, such as the study of nutrition stress in ladybird beetles (Coccinellidae)[34], where a change in V_G was involved. However, in water fleas (*Daphnia*) exposed to different food levels there was a decrease in heritability under reduced food

levels[21], perhaps because of environmental effects on the number of instars (Table 1, hypothesis 5). Findings have therefore not been consistent across studies (Table 2).

Size-related traits in birds

Several recent studies have considered the effects of growth conditions on the heritability of size-related traits in birds. Table 3 lists heritability estimates based on full-sib analyses. In general, these data, together with parent–offspring estimates (Fig. 2), indicate that size-related heritabilities tend to be higher in favourable compared with unfavourable conditions[24]. Although there are exceptions to this pattern, all the heritability differences exceeding two standard errors involve a decrease in unfavourable conditions. In some cases[22], these differences were linked to changes in environmental variance (Table 1, hypothesis 5), but for most studies, a decreased additive genetic component was implied. There was a correspondence between
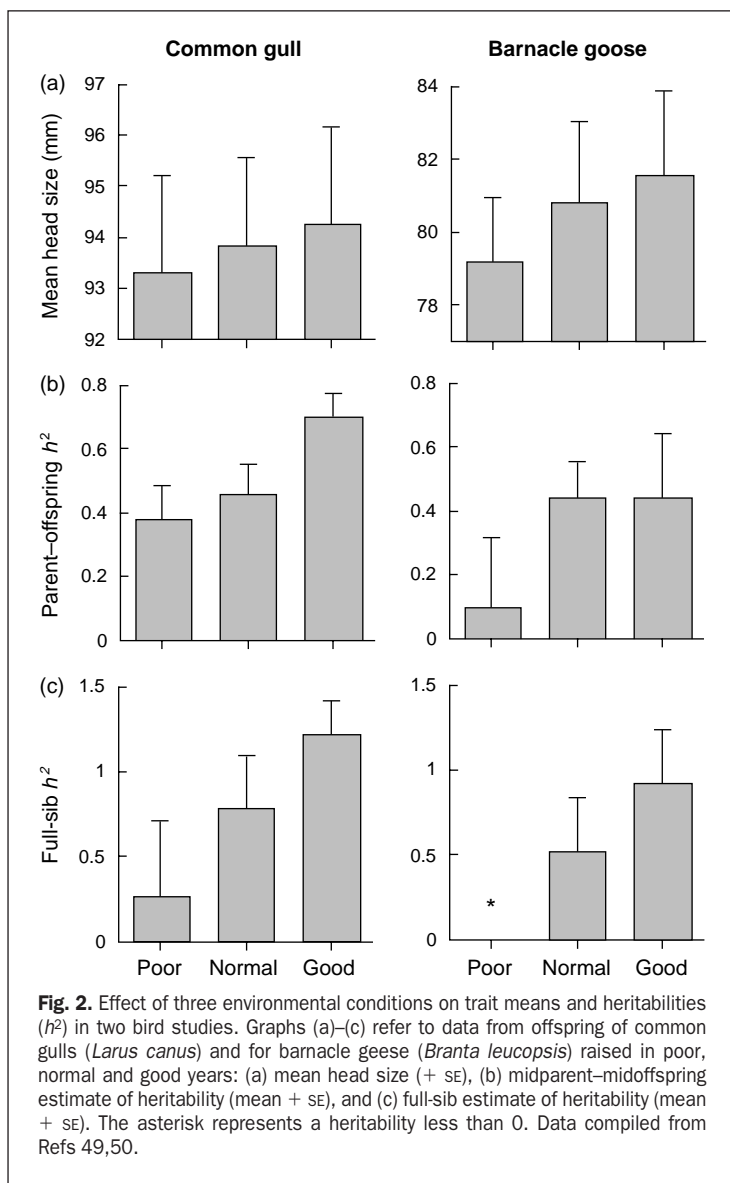
Fig. 2. Effect of three environmental conditions on trait means and heritabilities (h^2) in two bird studies. Graphs (a)–(c) refer to data from offspring of common gulls (*Larus canus*) and for barnacle geese (*Branta leucopsis*) raised in poor, normal and good years: (a) mean head size (+ SE), (b) midparent–midoffspring estimate of heritability (mean + SE), and (c) full-sib estimate of heritability (mean + SE). The asterisk represents a heritability less than 0. Data compiled from Refs 49,50.

environmental effects on trait heritabilities and trait means in some studies (Fig. 2).

Nevertheless, these findings should be interpreted cautiously. Heritabilities based on full-sib analysis can be confounded by common environment and nonadditive genetic effects, although the latter might make these conclusions conservative. Furthermore, parent–offspring estimates were obtained in situations where offspring raised in poor- and good-growth conditions are compared with parents from undefined conditions[24], making it difficult to separate changes in genetic variance across environments from a lack of genetic correlation. An analysis of body-size variation in blue tits (*Parus caeruleus*)[35] revealed that apparent heritability differences between environments were mostly caused by environmental heterogeneity, rather than differences in V_A. Finally, maternal effects changing in different conditions can affect the results. For example, in a study of cross-fostered great tits (*Parus major*) there was resemblance among foster-nestlings and their foster-parents under unfavourable but not favourable conditions[22].

In conclusion, the data from natural bird populations appear largely consistent with hypothesis 6 and to some degree with hypothesis 5 (Table 1), although the patterns are open to alternative interpretations until several assumptions are checked.

Other studies

The effects of unfavourable conditions on heritable variation in life history traits and other traits have been considered in several studies with variable results. Under unfavourable conditions, there was a relatively large decrease in heritability for development time in *Drosophila melanogaster*[36] and for fecundity in cotton-stainer bugs (*Dysdercus fasciatus*)[37] (conditions being high culture temperatures and low moisture, respectively). In both cases, the decrease was associated with lowered genetic variance. Other studies, such as the effect of crowding on heat resistance in *Drosophila*[38], have found little impact of unfavourable conditions. Finally, an increased heritability has been demonstrated as a result of increased V_G in unfavourable conditions. Examples include fecundity in *D. melanogaster* exposed to a combined stress[39], early reproduction in the same species selected under crowded conditions[40] and development time in cowpea weevils (*Callosobruchus maculatus*) experiencing low temperature and humidity[41]. In the cowpea-weevil study, results were interpreted in terms of selection history (hypothesis 2) because the unfavourable conditions were novel. As previously mentioned, life-history heritabilities across environments need to be interpreted cautiously because of the likely importance of nonadditive effects on the traits[31].

Although the focus here has been on animal studies, much of the relevant literature on environmental effects is from plants. Previous agricultural studies suggested that heritabilities for yield and other traits tended to be higher under favourable conditions than unfavourable ones, but a recent review by Ceccarelli[42] suggests that the opposite result is just as likely. Data from natural plant populations are scarce. However Bennington and McGraw[9] estimated heritabilities in a reciprocal-transplant experiment between populations of the balsaminaceous plant *Impatiens pallida* from a floodplain (favourable environment) and a hillside (unfavourable environment). Estimates of narrow-sense heritabilities for morphological and fitness-related characters were low, but for both populations estimates tended to be higher on the floodplain compared with the hillside. This suggests a relatively low heritability in unfavourable conditions, regardless of selection history. Site differences reflected a decrease in V_A under unfavourable conditions following hypothesis 6 (Table 1).

Conclusions and future directions

Several hypotheses have been invoked to explain heritability differences between environments, but predictions are variable. Data from recent studies suggest frequent changes in additive genetic variance, but no consistent effects of unfavourable conditions on the heritability of traits. There appear to be trends for size-related traits specific to conditions and organisms, but life-history data are too limited to make any conclusions.

More work is needed to address specific hypotheses, such as the effect of novelty on genetic variance. At this stage, there are data supporting an increase in V_G in novel conditions[12,19], but contrary data also exist[43,44]. More work is also needed on phenotypically invariant traits, such as the segmental and wing vein traits in *Drosophila* first used by Waddington and others to illustrate the process of genetic assimilation. These traits are of particular interest because they could show little selection response unless organisms are exposed to extreme conditions[45].

The inconsistent empirical patterns discussed here could reflect two factors. First, there are several methodological problems involved in estimating and comparing heritabilities under different conditions and, because these

have been overcome in only a few studies, general patterns might be masked. Second, the effects of unfavourable conditions on heritability estimates might be diverse, as suggested by the different hypotheses. It then becomes important to identify those specific conditions that produce consistent patterns, because it is these that have the potential to influence evolutionary rates.

Acknowledgements

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