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Inbreeding depression in benign and stressful environments

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Understanding the consequences of inbreeding has important implications for a wide variety of topics in population biology. Although it is often stated in the literature that the deleterious effects of inbreeding (inbreeding depression) are expected to be more pronounced under stressful than benign conditions, this issue remains unresolved and controversial. We review the current literature on the relationship between the magnitude of inbreeding depression and environmental stress and calculate haploid lethal equivalents expressed under relatively benign and stressful conditions based on data from 34 studies. Inbreeding depression increases under stress in 76% of cases, although this increase is only significant in 48% of the studies considered. Estimates of lethal equivalents are significantly greater under stressful (mean = 1.45, median = 1.02) than relatively benign (mean = 0.85, median = 0.61) conditions. This amounts to an approximately 69% increase in inbreeding depression in a stressful *vs* a benign environment. However, we find strong lineage effects to be ubiquitous among studies that examine inbreeding depression in multiple environments, and a prevalence of conditionally expressed deleterious effects within lineages that are uncorrelated across environments. These results have important implications for both evolutionary and conservation biology.
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Introduction

Inbreeding depression refers to the reduction in the fitness of offspring produced by consanguineous mating, and the deleterious effects of inbreeding have been known for more than a century (Darwin, 1876). Understanding the causes and consequences of inbreeding depression is fundamental to a wide variety of topics in population biology, including the evolution of mating systems (Charlesworth and Charlesworth, 1987; Uyenoyama *et al*, 1993), dispersal strategies and social behavior (Thornhill, 1993), artificial breeding of agricultural stocks (Falconer and Mackay, 1996), and the maintenance of rare and endangered species (Hedrick and Kalinowski, 2000; Reed and Frankham, 2003).

Population biologists are also concerned with understanding how environmental variation might interact with inbreeding depression to affect the fitness of individuals (ie, is inbreeding depression more severe under environmental stress?, Figure 1). This interest is related to several issues. For example, how might inbreeding depression measured under artificial laboratory, greenhouse, or zoo conditions relate to the effects of inbreeding depression in presumably more stressful natural environments? Furthermore, how might spatial and/or temporal variation in environmental conditions interact with the effects of inbreeding depression over ecological or evolutionary time scales, and how might such interactions affect evolutionary dynamics and extinction processes?

It is frequently claimed that inbreeding depression is greater in more stressful environments (Roff, 1997; Frankham *et al*, 2002). However, over a wide range of taxonomic and biological groupings, studies that find statistically increased inbreeding depression under environmental stress are slightly less numerous than those that do not (see Results below). Thus, despite its immediate concern to evolutionary and conservation biologists, this subject remains controversial (Keller and Waller, 2002).

Herein, we review 34 studies, 14 of which have been published in the last 3 years, examining the interaction between inbreeding depression and environmental stress. We then calculate the haploid lethal equivalents expressed under relatively benign and stressful conditions in order to quantify the interaction between inbreeding depression and environmental stress. Although recent reviews on inbreeding depression in the wild (Keller and Waller, 2002), and inbreeding depression and conservation (Hedrick and Kalinowski, 2000) have touched on this issue, neither has explicitly focused on the environmental dependency of inbreeding depression nor presented a comprehensive evaluation of all the currently available literature on this topic.

Definitions

Stress

Nearly all studies either implicitly or explicitly recognize a 'stressful' environment as one that reduces fitness

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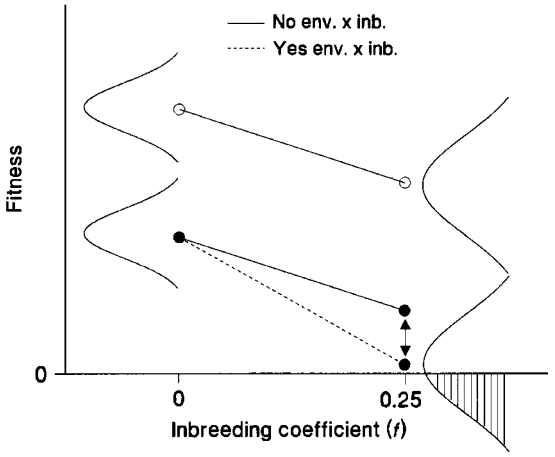

Figure 1 Hypothetical fitness distributions and mean fitness for control ($f=0$) and inbred ($f=0.25$) treatments in benign (○) and stressful (●) environments. Negative slopes connecting the mean fitness estimates in each environment indicate inbreeding depression. The solid lines indicate no environment-by-inbreeding interaction (No env. × inb.), the dashed line indicates an environment-by-inbreeding interaction is present (Yes env. × inb.). The double arrow (↕) illustrates the effect of the truncated portion of the fitness distribution for the inbred treatment in a stressful environment (indicated by cross-hatching (| | |)).

(or fitness components) relative to more benign conditions (Hoffmann and Parsons, 1991). However, it should be noted that this definition is not always applied correctly when citing other studies. For example, both Chen (1993) and Pray *et al* (1994) are sometimes cited as supporting the conclusion that inbreeding depression is more pronounced under stressful conditions. Chen (1993) reared outbred and inbred (one generation of full-sib mating) European land snails (*Arianta arbustorum*) in the laboratory and a garden, finding evidence for inbreeding depression for survivorship over 100 days in the garden environment but not the laboratory. However, survivorship of the snails was higher in the garden than in the laboratory. Pray *et al* (1994) found that inbreeding depression of both male and female *Tribolium castaneum* was more pronounced in a variable than a constant humidity environment. However, as noted by Pray *et al* (1994), both sexes actually had higher fitness in the variable rather than constant humidity environment, although the difference was only significant for males. According to the definition discussed above, inbreeding depression in these studies was actually more pronounced in the benign rather than stressful environment. These results, therefore, emphasize that laboratory and/or constant environments can actually be more stressful than more natural and/or variable environments. In our analysis, we define the stressful environment as one that reduces fitness relative to another environment.

Fitness

The most meaningful measurement of fitness in a constantly expanding population with overlapping generations is the Malthusian parameter, r (Charlesworth, 1980). However, unambiguously identifying a single parameter acting to maximize fitness in a natural population will often be difficult or impossible. Nevertheless, it seems reasonable to assume that composite indices of fitness, which integrate measures of performance over as many components of lifetime reproductive success as possible are most meaningful.

In some cases, authors will cite a study as supporting the hypothesis that stressful conditions increase inbreeding depression when an inbreeding-by-environment interaction is detected for one fitness component, but not overall performance. However, such conclusions may be misleading, because inbreeding depression affecting one component of the lifecycle may lead to reduced competition and/or enhanced growth and/or fertility in other portions of the lifecycle. For example, in a study of inbreeding in a natural population of the Great Tit (*Parus major*) in Holland, Van Noordwijk and Scharloo (1981) found evidence of substantial inbreeding depression for egg hatching success. However, inbred clutches had nonsignificantly higher fledgling recruitment relative to noninbred clutches, which may have been caused by reduced competition in clutches with low hatching rates. Such trade-offs between fitness components may be common (eg, Sinervo, 1990; Sinervo *et al*, 1992; Carriere and Roff, 1995; Preziosi *et al*, 1996; Reed and Bryant, 2000). These considerations underscore previous arguments that have been made (Charlesworth and Charlesworth, 1987) regarding the importance of measuring composite indices of fitness, rather than fitness correlates or components, when evaluating the consequences of inbreeding.

The literature

A literature survey was performed using key words and citation searches of the work available on inbreeding depression in plants and animals. In order to avoid publication bias, we have included studies that report nonsignificant effects of inbreeding under benign or stressful conditions. We have restricted our coverage to studies that perform direct experimental manipulation to measure inbreeding depression in more than one environment. We have omitted studies that rely on indirect comparisons of different populations of the same species (eg, Crnokrak and Roff, 1999) due to the large number of potentially confounding factors which may obscure the results of such comparisons and the emerging pattern that inbred populations and lineages from a single species often respond differently to inbreeding and/or environmental stress (eg Kärkkäinen *et al*, 1996; Cheptou *et al*, 2000a; Carr and Eubanks, 2002; Carr *et al*, 2003). We also have not included studies that rely on molecular marker data to infer relative levels of inbreeding, since these data often explain a low proportion of the variation in actual inbreeding (Hedrick *et al*, 2001). We have also excluded the substantial literature on heterosis by environment interactions. Despite common statements to such effect in the literature, inbreeding depression is not simply the reverse manifestation of heterosis (Lynch and Walsh, 1998; Whitlock *et al*, 2000).

A summary of the papers, we considered is outlined in Appendix A1. They include studies on 11 plant, nine invertebrate, and one vertebrate species. The stress factors include exposure to insecticides and other noxious or toxic chemicals, nutrient deprivation, temperature and desiccation stress, the effects of competition

and parasitism, and comparisons between laboratory and field environments.

For each study, we computed B, the number of haploid lethal equivalents (Morton *et al*, 1956) under benign and stressful conditions as:

$$B = -\frac{1}{f}\ln\left(\frac{w_f}{w_o}\right) \quad (1)$$

where f is the inbreeding coefficient, and w_f and w_o are the mean fitness of inbred and outbred (control) individuals, respectively (Hedrick, 2000). The number of haploid lethal equivalents, B, describes the rate at which the logarithm of fitness (or fitness components) declines with inbreeding, and is equal to 0 when there is no inbreeding depression. Calculating lethal equivalents is a common method for comparing the effects of inbreeding among studies, taxa and/or environmental conditions (Ralls *et al*, 1988; Keller *et al*, 2002) because it provides a measure which standardizes the effects of different levels of inbreeding (f).

In many instances, the data sets that we used in this study measured more than one fitness component. In these cases, we used the single fitness component expected to most closely correlate with total fitness in our analysis (ie, composite measures such as lifetime reproductive success were favored over fecundity or survival, and fecundity or survival were given preference over growth rates or biomass). Several studies measured inbreeding depression under benign and stressful conditions in more than one species (see Appendix A1). Furthermore, several of the studies measured the effects of inbreeding under one benign environment and multiple stressful environments. In these cases, we included estimates of lethal equivalents expressed under multiple, independent stressful environments in our analysis, and thus the number of estimates of B from stressful environments ($n=52$) exceeds the number of estimates of B from benign environments ($n=39$, see Appendix A1).

In order to evaluate the consequences of inbreeding under benign and stressful conditions we performed a paired t-test to evaluate the null hypothesis that the expression of haploid lethal equivalents (B) was equal under benign and stressful conditions. Estimates of B expressed under relatively benign and stressful conditions were subjected to the transformation $\ln(x+1)$ and the degrees of freedom were determined based on the number of independent estimates of B_{benign} ($n=39$). In order to examine factors that might influence the change in levels of inbreeding depression under benign *vs* stressful conditions, we calculated the proportional change in inbreeding depression as $B_{\text{stress}}/B_{\text{benign}}$. The distribution of $B_{\text{stress}}/B_{\text{benign}}$ was highly skewed, but a natural log transformation of $(B_{\text{stress}}+1)/(B_{\text{benign}}+1)$ produced an approximately normal distribution. We performed analysis of variance (ANOVA) on $\ln[(B_{\text{stress}}+1)/(B_{\text{benign}}+1)]$ with fitness measurement (composite *vs* noncomposite, df = 1), stress type (see Appendix A1, df = 4), and taxa (plant *vs* animal, df = 1) as fixed effects. Similar to the paired t-test described above, residual degrees of freedom were determined based on 39 independent estimates of B_{benign}. All statistical analyses were performed in S-Plus 6.2 (Insightful, 2001).

Results

Inbreeding depression increased under relatively stressful conditions in 76% of the cases we examined, although this increase was only statistically significant in 48% of cases. The mean haploid lethal equivalents expressed under benign conditions was 0.85 (SE = 0.14, $n=39$), while under stressful conditions the mean B was 1.45 (SE = 0.17, $n=52$). Because the distribution of B under both benign (B_{benign}) and stressful (B_{stress}) conditions was markedly non-normal (Figure 2), the median value should be considered a better estimate of central tendency. Median B_{benign} was 0.61, and median B_{stress} was 1.02. This difference was highly significant by paired t-test ($t=4.49$, df = 38, $P<0.001$). Using either the mean or the median produced a number of haploid lethal equivalents that was approximately 69% greater, on average, in a stressful environment than in a benign environment (mean = 70%, median = 68%).

ANOVA indicated that $\ln[(B_{\text{stress}}+1)/(B_{\text{benign}}+1)]$ was not significantly affected by the fitness measurement (composite *vs* noncomposite, see Appendix A1) employed in a study ($F_{1,27}=0.47$, $P=0.50$), stress type ($F_{4,27}=0.32$, $P=0.58$), taxa ($F_{1,27}=0.87$, $P=0.36$), stress-by-taxa ($F_{2,27}=0.71$, $P=0.50$) nor stress-by-fitness interaction ($F_{3,27}=1.56$, $P=0.22$). The conclusions of the same analysis with nontransformed data were qualitatively equivalent.

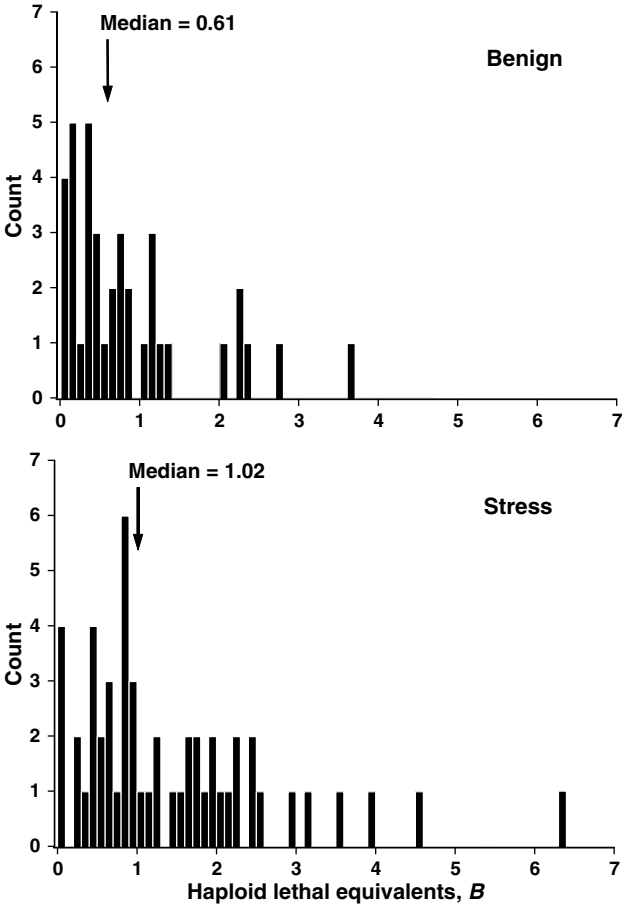

Figure 2 Haploid lethal equivalents (B) under relatively benign ($n=39$) and stressful ($n=52$) conditions from 34 studies described in Appendix A1.

The 'file drawer' problem (ie unpublished data) is a concern with any meta-analysis (Osenberg *et al*, 1999). In this study, the distribution of effect sizes displays the funnel shape indicative of a lack of publication bias (Palmer, 2000) and the number of studies reporting nonsignificant results outnumbers those reporting significant results. Thus, publication bias seems extremely unlikely.

Discussion

Is inbreeding depression greater in more stressful environments?

We find that, on average, inbreeding depression is greater in relatively stressful environments (Figure 2). The median number of lethal equivalents expressed under environmental stress was 69% greater than under relatively benign environmental conditions. Factors contributing to the lack of clarity on this subject prior to this study are: (1) The large amount of variation in expression of lethal equivalents from different studies (Figure 2) and sometimes among different measures in a single study (see below). (2) The low statistical power associated with the small sample sizes and/or a limited number of inbred lineages used in single experiments. Suggestions have been made elsewhere that a minimum of between 20 (Keller and Waller, 2002) and 100 (Lynch, 1988) inbred lineages should be examined in studies of inbreeding depression, but 64% of the studies we examined employed less than 20 inbred lineages. (3) Studies are often cited in an inconsistent manner. Definitions of 'stress' are often not considered carefully, the distinction between fitness components and overall fitness is neglected, or studies are cited as reporting increased inbreeding under stress when only one or a few of many traits display such a pattern.

Variation in response to inbreeding under stress

It is important to note the large number of instances in which inbreeding did not increase under stress. In 24% of the data sets, inbreeding depression actually decreased in the stressful environment. ANOVA examining fitness measurement, stress type, and taxa did not identify any of these factors as significantly affecting the increase of inbreeding depression under stress, although we note that this particular analysis has somewhat limited statistical power. Furthermore, part of this unexplained variation is likely due to the idiosyncrasies of the study organism or population, variation among the environmental conditions used, experimental procedures, and specific lineage effects (see below). This large amount of unexplained variance emphasizes a recurrent theme (see below), that accurate predictions regarding the response of specific populations or lineages to inbreeding under stress will often be difficult or impossible.

Lineage effects

Genetic variance *among* lineages is expected to increase under inbreeding (Falconer and Mackay, 1996; Lynch and Walsh, 1998). Of the 22 studies where lineage effects could be tested for, 17 (77%) found significant among-lineage variation. Most commonly, investigators testing the effects of inbreeding under multiple environmental conditions generate replicate inbred lineages by full-sib mating while maintaining a control (ie, noninbred) population. After one or more generations of full-sib mating the performance of inbred and control offspring is measured under two or more sets of environmental conditions. Under a purely additive model of gene action the total genetic variation across all replicate lineages is expected to increase according to $(1+f)$Vg where f is the inbreeding coefficient, and Vg is the genetic variance in the control (noninbred) population (Falconer and Mackay, 1996). If nonadditive genetic effects (dominance and epistasis) contribute to gene expression, inbreeding can actually increase (rather than decrease) within-lineage variance (Goodnight, 1987), and the increase in among-lineage variance with inbreeding can be substantially larger than the additive expectation (Goodnight, 1988).

One potential implication of an increase in total population genetic variation with inbreeding for detecting inbreeding by environment interactions is illustrated in Figure 1. Figure 1 illustrates a hypothetical situation in which an inbred population in a stressful environment contains a large number of individuals who cannot survive and/or reproduce (ie, fitness of zero). The combination of increased variance in the inbred population and the fact that individuals cannot have fitness less than zero means that as environmental conditions become increasingly severe, the expression of inbreeding depression is diminished. This is because the increased variance in fitness in the inbred population allows natural selection to act against the least fit genotypes, reducing the cumulative loss of fitness predicted to occur in the benign environment. In many studies that have failed to detect inbreeding by stress interactions the fitness (components) of inbred treatments in the stressful environments do indeed approach zero, as illustrated in Figure 1 (Dahlgaard *et al*, 1995; Norman *et al*, 1995; Hauser and Loeschcke, 1996; Armbruster *et al*, 2000).

One very clear pattern to emerge from the studies we reviewed is that different populations of a single species, and different inbred lineages from the same population, often exhibit highly variable responses to inbreeding under stressful conditions (Pray *et al*, 1994; Bijlsma *et al*, 1999; Dahlgaard and Hoffmann, 2000; Fowler and Whitlock, 2002; Reed *et al*, 2002; Carr *et al*, 2003; Haag *et al*, 2003). The implication of this result is that different alleles and/or loci are determining susceptibility to stresses in different inbred lineages and/or populations. These results emphasize the difficulty in predicting how managed populations may respond to inbreeding, particularly under environmentally variable conditions (Hedrick and Kalinowski, 2000). Inbred lineages that have relatively high fitness under benign farm, laboratory, or zoo conditions may fare relatively poorly in a natural environment, and therefore are will not necessarily be the most suitable for reintroduction programs (Pray *et al*, 1994; Bijlsma *et al*, 2000; Reed and Bryant, 2000). Furthermore, attempts to 'purge' inbreeding depression by deliberately inbreeding managed populations under relatively benign conditions (eg, Templeton and Read, 1983) are unlikely to be successful since alleles causing susceptibility to environmental stress will be unlikely to be effectively removed from such populations (Bijlsma *et al*, 2000; Reed and Bryant, 2001).

Do the same loci contribute to stress resistance in different environments?

Even if different alleles are fixed or drift to high frequency in different inbred lineages as described above, it is possible that individual alleles might have general stress-resistance effects across different types of stresses. Such an effect would cause individual inbred lineages to have highly correlated norms of reaction across different stressful environments.

Although the number of available studies addressing this question is small, preliminary results suggest that the expression of deleterious recessive alleles underlying inbreeding depression may often depend on specific environmental conditions (Heywood, 1993; Bijlsma *et al*, 1999; Dahlgaard and Hoffmann, 2000; Reed and Bryant, 2001; Haag *et al*, 2003; Reed *et al*, 2003).

Recent studies by Vermeulen and Bijlsma (2004a, b) have demonstrated lineage- and temperature-specific adult mortality in inbred *Drosophila melanogaster* lines caused by the expression of temperature-sensitive lethals and semi-lethals. These studies thus provide an example of a specific mechanism underlying lineage- and environment-specific inbreeding depression, although the precise genetic basis (ie one *vs* multiple loci, chromosomal location(s)) has not yet been determined (Vermeulen and Bijlsma, 2004b).

The implications of these results is that different alleles and/or loci determine resistance to different stresses, and thus it will be difficult or impossible to select for general 'stress-resistant' lineages which perform well under multiple environmental challenges. The large degree of variation in how species and populations respond to different sorts of stress means that *a priori* predictions will almost always be unreliable.

In their review of inbreeding depression in wild populations, Keller and Waller (2002) wrote that 'Although it is often asserted in the literature that inbreeding depression in greater under stress or field conditions, this pattern is neither universally supported nor theoretically resolved'. Results of our analysis indicate that averaging across a wide range of taxa, inbred lineages, and environmental stress conditions, the effects of inbreeding depression do tend to increase under environmental stress. However, lineage- and stress-specific responses to inbreeding are widespread.

To develop a more unified framework regarding the effects of inbreeding under stress, we suggest first that studies identifying the specific loci contributing to inbreeding depression, and characterizing their environmental sensitivity will be important (eg Vermeulen and Bijlsma, 2004a, b). Also important will be studies of inbreeding under natural conditions (ie see Appendix A1). Many of the studies we examined used artificial stress factors such as chemicals or heavy metals (Bijlsma *et al*, 1999, 2000; Dahlgaard and Hoffmann, 2000; Reed *et al*, 2002; Kristensen *et al*, 2003). Resistance to these types of stress will often be determined by alleles at a single or few genetic loci (Hoffmann and Parsons, 1991), and may provide a poor reflection of the consequences of inbreeding under more natural conditions when a wide variety of physiological and/or behavioral challenges confront organisms, and potentially a much wider suite of genetic loci are involved in resistance. Another important area of future research is to develop a theoretical framework for investigating inbreeding depression by environmental interactions. Few models establishing such a framework currently exist (but see Cheptou and Schoen, 2002). Models incorporating both genetics and demography (eg Mills and Smouse, 1994), and explicitly modeling interactions between inbreeding depression and environmental variation should play an important role in guiding experimental work.

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Appendix A1

Summary of studies examined to calculate the expression of haploid lethal equivalents (*B*) under benign and stressful conditions are referred in Table A1.

Table A1 Summary of studies examined to calculate the expression of haploid lethal equivalents (*B*) under benign and stressful conditions

Reference	*Organism*	*Stress*[a]	*Fitness measurement*	B_{benign}	B_{stress}
Armbruster *et al* (2000)	*Aedes geniculatus*	Field	Composite fitness	3.62	3.91
Bijlsma *et al* (1999)	*Drosophila melanogaster*	Chem.	Composite fitness	0.81	1.23
		Chem.	Composite fitness	—	0.86
		Temp.	Composite fitness	—	1.23
		Biotic	Composite fitness	—	0.94
Bijlsma *et al* (2000)	*Drosophila melanogaster*	Temp.	Extinction	1.06	3.55
		Chem.	Extinction	—	2.58
Carr and Eubanks (2002)	*Mimulus guttatus*	Biotic	Number flowers	0.40	0.86
Carr *et al* (2003)	*Mimulus guttatus*	Biotic	Number flowers	0.43	0.85
Chen (1993)	*Arianta arbustorum*	Field	Survival	0.18	0.07
Cheptou *et al* (2000a)	*Crepis sancta*	Misc.	Survival	0.08	0.02
Cheptou *et al* (2000b)	*Crepis sancta*	Biotic	Composite fitness	2.26	0.89
Cheptou *et al* (2001)	*Crepis sancta*	Biotic	Composite fitness	0.08	0.63
		Biotic	Composite fitness	0.36	1.79
Dahlgaard and Hoffmann (2000)	*Drosophila melanogaster*	Temp.	Composite fitness	1.11	1.99
Dahlgaard and Loeschcke (1997)	*Drosophila melanogastger*	Temp.	Egg-to-adult survival	0.65	0.62
Dahlgaard *et al* (1995)	*Drosophila melanogaster*	Temp.	Adult survivorship	0.11	0.21
Dudash (1990)	*Sabatia angularis*	Field.	Composite fitness	2.75	1.49
Eckert and Barrett (1994)	*Decodon verticillatus*	Biotic	Survival	0.38	0.88
		Biotic	Survival	0.11	0.88
Fowler and Whitlock (2002)	*Drosophila melanogaster*	Temp.	Survival	0.33	0.41
		Biotic	Survival	—	0.33
		Misc	Survival	—	0.44
Haag *et al* (2002)	*Daphnia magna*	Biotic	Composite fitness	0.46	2.21
Haag *et al* (2003)	*Daphnia magna*	Biotic	Composite fitness	2.37	2.43
		Biotic	Composite fitness	—	3.17
Hauser and Loeschcke (1996)	*Lychnis flos-cuculi*	Misc.	Composite fitness	2.21	4.58
Henry *et al* (2003)	*Physa acuta*	Field	Survivorship	0.06	0
Ivey *et al* (2004)	*Mimulus guttatus*	Biotic	Composite fitness	0.76	1.75
Jiménez *et al* (1994)	*Peromyscus leucopus*	Field	Survival	0.23	6.32
Johnston (1992)	*Lobelia cardinalis*	Field	Composite fitness	0.42	0.42
		Field	Composite fitness	0.01	0.50
Joron and Brakefield (2003)	*Bicyclus anynana*	Field	Male mating success	0.83	2.24
Koelewijn (1998)	*Plantago coronopus*	Field	Seed production	0.16	1.92
Kristensen *et al* (2003)	*Drosophila buzzati*	Chem.	Composite fitness	0.33	0.21
		Temp.	Composite fitness	—	1.59
		Temp	Composite fitness	—	0.72
Miller (1994)	*Drosophila melanogaster*	Temp.	Composite fitness	1.14	0.92
		Temp.	Composite fitness	—	1.04
		Chem.	Composite fitness	—	1.16
Norman *et al* (1995)	*Schiedea lydgatei*	Misc.	Composite fitness	2.01	1.88
Pray *et al* (1994)	*Tribolium castaneum*	Misc.	Composite fitness	0.56	0.45
Reed and Bryant (2001)	*Musca domestica*	Misc.	Viability	1.23	2.98
		Temp.	Viability	—	2.47
Reed *et al* (2002)	*Drosophila melanogaster*	Chem.	Extinction	1.15	1.68
		Chem.	Extinction	—	2.08
		Chem.	Extinction	—	2.13

Table A1 Continued

Reference	*Organism*	*Stress*[a]	*Fitness measurement*	B_{benign}	B_{stress}
Schemske (1983)	*Costus laevis*	Misc.	Composite fitness	0.71	0.99
	Costus guanaiensis	Misc.	Composite fitness	0.68	0.86
	Costus allenii	Misc.	Composite fitness	1.35	1.64
Schmitt and Ehrhardt (1990)	*Impatiens capensis*	Biotic	Biomass	0.15	0
Waller (1984)	*Impatiens capensis*	Biotic	Biomass	0.73	0.65
Wolfe (1993)	*Hydrophyllum appendicilatus*	Biotic	Growth rate	0.12	0.59

[a]Biotic = increased inter- or intra-specific density, exposure to parasites, herbivory, or light deprivation; Chem. = exposure to noxious or toxic chemical; Field = natural as opposed to lab or greenhouse conditions; Misc. = nutrient deprivation, desiccation, or a combination of Biotic, Chem., Field, and/or Temp.; Temp. = Temperature.