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NEWS AND COMMENTARY

Population biology

The ecology of inbreeding depression

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The idea that the environment might have an influence on the negative effects of inbreeding in populations is not a new one, but work recently published in *Heredity* provides, for the first time, strong evidence that inbreeding depression is more likely in stressful environments.

Inbreeding depression (ID), that is, the reduction of fitness due to consanguineous mating, has long fascinated population biologists, because it impacts on diverse topics including the role of mutations and the evolution of adaptive traits, such as mating systems, dispersal and sociality. In 'the effects of cross- and self-fertilization in the vegetable kingdom' (Darwin, 1876), Darwin had already anticipated the main issues: 'With Nicotiana the crossed were to the self-fertilized in height, when grown extremely crowded together in pots, as 100 to 54; when grown much less crowded in pots as 100 to 66, and when grown in the open ground, so as to be subjected to but little competition, as 100 to 72'.

However, despite a recent surge of interest, strong evidence that the environment influences ID was still lacking. Armbruster and Reed (2005) reviewed 34 studies from various taxa (almost half of which have been published in the last 3 years) to test the widely held view that a stressful environment increases ID. Their meta-analysis clearly established that estimates of lethal equivalents (a standardized measure of inbreeding effect) are significantly greater under stressful conditions than under benign ones.

It has been implicitly assumed for many years that the environment influences ID. However, the strong evidence from Ambruster and Reed's paper will modify our vision of ID. Previously, most empirical studies of ID have focused on the genetic basis of ID (mutation/selection balance) as a determinant of ID values (Carr and Dudash, 2003). There has also been a tendency to consider environment as a nuisance or a side effect. Environment-dependent aspects have sometimes been considered as mere 'complications' that ought to be avoided when studying inbreeding depression (Barrett and Harder, 1996). Armbruster and Reed champion a broader view that encompasses the sources of variation of ID and their evolutionary implications in natural populations.

More work is still needed: Armbruster and Reed refer to stressful environment as reducing fitness (compared to benign environment), which may cover many different ecological situations. This development should be carried one step further: we need to think about the different sources of 'stress' in natural populations. The different environmental factors considered in empirical studies of ID might be classified into the two major categories, which are typically distinguished in demographic analysis (Caswell, 2001): those arising from intrinsic factors such as the density or the relative frequency of inbred individuals (frequency-dependent factors) and those arising from extrinsic factors such as environmental variation (eg nutrients or water) (see Dole and Ritland, 1993 for a striking example in a natural population).

An important case in point arises when the environmental conditions experienced by individuals in a population are linked to the evolution of the reproductive system itself (frequency-dependence). For example, Cheptou and Schoen (2003) found that the relative composition of inbred and outbred plants in competing stands (which is determined directly by population selfing rate under natural conditions) substantially influences the magnitude of inbreeding depression in the genus *Amsinckia*. In this context, selfing variation can modify the competitive environment in which ID is expressed, which would, in turn, condition the evolution of selfing. Clearly, we should consider population dynamics when studying ID and its role in wild populations. As Armbruster and Reed (2005) suggest, models may need to incorporate both genetics and demography.

ID depends on the environment, so we would in turn expect the purging of deleterious mutations from a population to covary with environment. Indeed, we have empirical evidence from *Drosophila* that the environment influences the purging process (Bijlsma *et al*, 1999). The environment dependence of ID could, then, be that attributable to mutations that are globally more deleterious under some environment. An alternative explanation is that different loci are expressed in different kinds of environment. As yet, the relative importance of these phenomena is unknown.

In summary then, Armbruster and Reed's (2005) work answers a critical question: does the environment significantly influence inbreeding depression? Overall, the answer is yes. The challenge is now to incorporate the different sources of variation of ID in a single framework, in order to analyse its dynamics in natural populations and formulate expectations. Obviously, the characteristics of deleterious mutations as well as the selective environment play a joint role in shaping the genetic architecture of inbreeding depression and the assessment of their role might be allowed by coupling demography and population genetics. However, we need to avoid over complication in modelling: simple conceptual models are often most helpful when trying to understand complex realities.

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