

COMMENTARY

Population size is not genetic quality

E. D. Brodie III

Department of Biology, Mountain Lake Biological Station, University of Virginia, Charlottesville, VA, USA

Correspondence

Edmund D. Brodie III, Department of Biology and Mountain Lake Biological Station, University of Virginia, Charlottesville, VA 22904, USA.

Email: bbrodie@virginia.edu

doi:10.1111/j.1469-1795.2007.00134.x

Inbreeding depression is a phenomenon largely taken for granted among evolutionary geneticists (Conner & Hartl, 2004). For conservation biologists, the most important source of inbreeding comes when small population size leads to nonrandom mating among genotypes, either because available mates are related or because drift has reduced heterozygosity. Either process leads to the over-expression of homozygotes throughout the genome. Because many of the resultant homozygotes will express deleterious phenotypes, inbreeding is expected to widely lead to reductions in phenotypic values and fitness for individuals spawned from such unions. Inbreeding itself does not lead to reductions in allelic diversity. Rather, it enables selection to more effectively weed out deleterious recessives, and linkage disequilibrium drags along alleles at linked loci, so that over time we often see declining genetic diversity in inbreeding populations. On the whole, populations with measurable inbreeding are predicted to have lower average fitness than comparable populations with random mating (i.e. 'inbreeding depression'), because of the expression of deleterious homozygotes rather than secondarily reduced allelic diversity (Conner & Hartl, 2004). Inbreeding level is variable; it may be severe, as when populations are so small so as to necessitate mating among close relatives, or may be subtle in any situation that results in a nonrandom association of mates. Thus, even populations of moderate, but not effectively infinite, size may experience some of the deleterious effects of inbreeding.

It seems obvious, then, that inbreeding is not a good thing for most populations (though there are certainly many taxa, especially plants, that make due with high levels of inbreeding). If inbreeding reduces fitness, should not we expect inbreeding to be one of the many factors that hasten the demise of declining populations? As Reed, Nicholas & Stratton (2007a,b) point out, the causal relationship between inbreeding and extinction risk is not clear. In extremely small populations, the very ones expected to be highly inbred, realities of demography and stochasticity are expected to blink out a population before inbreeding can make its mark (Lande, 1988). In somewhat larger populations, density-dependent mortality might lead to situations in

which population dynamics are largely unaffected by the level of inbreeding. In such cases, inbreeding might correlate with, but not contribute to, population growth (or decline) rates. It is exactly these kinds of populations – declining, but not perilously small – for which management decisions have a reasonable chance of protecting both the numbers of a species and its genetic potential.

Reed *et al.* (2007a) set out to test whether genetic diversity and inbreeding have measurable impacts on population dynamics of two species of wolf spiders across a range of population sizes. Using a 3-year dataset that they recently published in *Conservation Genetics* (Reed *et al.*, 2007b), they analyze a new independent variable, population growth, to discern whether inbreeding or genetic quality impacts population dynamics. Their analyses clearly show that habitat quality (as measured by prey capture rate) and population size impacts population growth rate. The effect of population size is most obvious (and significant) in years with low prey capture rate, leading the authors to the conclusion that inbreeding (or 'genetic quality,' or 'genetic diversity') impacts population dynamics under stressful situations. As a generality, I agree with the expectation that genetic factors will have negative effects on population growth, especially under stressful conditions. However, I found myself questioning whether this impressive dataset and analysis demonstrate such links. Moreover, I think it is critical to distinguish different genetic phenomena, their origins and their expected consequences.

Inbreeding might affect population growth rate through at least two distinct paths. For populations with little history of inbreeding and thus a wealth of deleterious recessives, inbreeding depression is expected to lower mean fitness (for populations with a history of inbreeding, as with many plant breeding systems, past selection would have reduced the number of deleterious recessives so that inbreeding depression is less marked). Inbreeding depression might also result from a reduction of heterozygosity at overdominant loci (Conner & Hartl, 2004). This reduction in mean fitness should lead to declines in the population growth rate unless density-dependent mortality results in

compensatory increases in survival rates. This process is different from the effect of reduced genetic diversity, which might be a secondary consequence of inbreeding when combined with selection or drift. The loss of allelic diversity, however, is not necessarily a primary source of inbreeding depression (in fact, the elimination of deleterious recessive alleles through selection should alleviate inbreeding depression). Instead, reduced allelic diversity is expected to limit adaptive evolutionary responses to changing environments. In a stable environment, a well-adapted population should suffer no loss in mean fitness due to loss of allelic diversity, particularly if the lost alleles are deleterious recessives. Of course, stable environments may be a theoretical construct and certainly do not fairly represent the situations that are typically represented by declining populations. In small populations, genetic drift can lead to a loss of genetic diversity through the random fixation of alleles. When the alleles approaching fixation are deleterious, small population size can result in an increase in deleterious homozygotes that act like inbreeding depression (Conner & Hartl, 2004). Only in this sense does genetic diversity lead to inbreeding depression and lower mean fitness. In most scenarios, reduced genetic diversity does not impact mean population fitness, and thereby population dynamics, in the same way that inbreeding depression is expected to. The labels 'inbreeding depression' and 'genetic diversity' are therefore not interchangeable. 'Genetic quality' is a bit more nebulous, but implicitly compares individuals to a local fitness optimum. Inbreeding depression could certainly be said to impact genetic quality, but I do not think the same could be said of genetic diversity, which is inherently a statement about populations.

Reed *et al.* (2007a,b) use 'population size' as a shorthand for all three of these terms, hence, it bears considering whether or not this is appropriate. Effective population size (N_e), the concept of Wright's meant to bridge simple counts of individuals (N) to the population genetic consequences of idealized populations, is fundamental to estimating the impact of inbreeding, drift and selection. N_e is always smaller than a raw count of individuals, and considers factors such as sex ratio and variance in mating success. Reed *et al.*'s estimates of spider censuses are impressive, but do not constitute estimates of 'long term effective population size' as suggested. Nonetheless, correlations between population size and inbreeding are certainly expected, at least at smaller population sizes (the relationship is likely to be non-linear because above some population size inbreeding should be negligible). This relationship is born out in their first paper (2007b), wherein population size is positively correlated with a measure of heterozygosity at micro-satellite loci. In the same paper, a positive correlation between an average measure of 'heritability' and population size is also reported. Heritability is intended to be a standardized measure of additive genetic variation for a specific trait. It is notoriously specific to environmental conditions (including any source of environmental variance), breeding system and allele frequencies. Averaging heritabilities over a number of traits will make most quanti-

tative geneticists bristle, because the factors influencing each heritability are so varied. How this metric bears on allelic diversity, genetic quality or inbreeding is unclear; at best it is a measure of evolutionary potential and so most likely to inform us about impacts on the adaptive prospects of a population.

Taking these measures at face value, it seems that population size is a reasonable correlate of inbreeding or diversity in the wolf spider system. However, as one of the authors points out elsewhere (Reed, 2007), 'Any declining population sampled should have reduced genetic variation regardless of whether inbreeding depression is a contributing factor in the decline.' That is, population size, genetic diversity and heterozygosity are all expected to be correlated without a single exclusive path. As with any set of inter-correlated variables, it is difficult to attribute causality to one variable by showing association with another. The results of Reed *et al.* (2007a) show clear associations between population growth and population size (not N_e) in some years, but do not show significant improvement of models when heterozygosity or 'average heritability' are included. It is therefore difficult to conclude from these data whether genetic factors are causally related to population declines. Other factors influence population size and population size has ramifications beyond the genetics. In some instances, it is even possible that small population size is inversely related to genetic diversity and inbreeding, such as when invasions from multiple sources mix genotypes (Kolbe *et al.*, 2004).

There is a conceptually simple way to experimentally test whether inbreeding depression is leading to population declines in the wolf spider system. When drift and inbreeding occur together, different populations should fix for alternative deleterious alleles. Crossing two populations should then lead to heterosis and a gain in mean fitness. This is a classic result from population genetics and is the basis of 'genetic rescue' plans (e.g. Madsen *et al.*, 1999). If such crosses then lead to increased population growth rates in nature (as in the Madsen study), it would be strong evidence that inbreeding depression contributed to the population declines.

The most important aspect of many real-world conservation problems is not whether inbreeding contributes to population declines, but what the relative impact of demographic, ecological and genetic factors is. Management decisions rarely have the luxury of optimizing all considerations, and often the most important factors must be addressed first. The clearest message from the data of Reed *et al.* (2007a,b) is that the major impact on population growth of wolf spiders is habitat quality (as measured by prey capture rate). Population size or perhaps heterozygosity sometimes interact or have lesser explanatory effects. This observation suggests that attention to ecological factors might have more dramatic results than attempts to manipulate the genetic makeup of populations (of at least moderate size). The question of whether or not inbreeding adversely affects growth rate in declining populations is an interesting one, and a difficult one to tease apart from other

correlated factors. On the practical side, however, it may be less critical to demonstrate because the high degree of correlation between population size and inbreeding means that practices that stem the numerical decline of populations also ameliorate inbreeding.

References

- Conner, J.K. & Hartl, D.L. (2004). *A primer of ecological genetics*. Sinauer Associates, Inc.
- Kolbe, J.J., Glor, R.E., Shettino, L.R., Lara, A.C., Larson, A. & Losos, J.B. (2004). Genetic variation increases during biological invasion by a Cuban lizard. *Nature* **431**, 177–181.
- Lande, R. (1988). Genetics and demography in biological conservation. *Science* **241**, 1455–1460.
- Madsen, T., Shine, R., Olsson, M. & Witzell, H. (1999). Restoration of an inbred adder population. *Nature* **402**, 34–35.
- Reed, D.H. (2007). Extinction of island endemics: it is not inbreeding depression. *Anim. Conserv.* **10**, 145–146.
- Reed, D.H., Nicholas, A.C. & Stratton, G.E. (2007a). Genetic quality of individuals impacts population dynamics. *Anim. Conserv.* **10**, 275–283.
- Reed, D.H., Nicholas, A.C. & Stratton, G.E. (2007b). Inbreeding levels and prey abundance interact to determine fecundity in natural populations of two species of wolf spider. *Conserv. Genet.*, DOI 10.1007/s10593-006-9260-4.