Heredity (2010) 104, 124

www.nature.com/hdy

NEWS AND COMMENTARY

Inbreeding depression

Inbreeding in the wild really does matter

R Frankham

Heredity (2010) **104,** 124; doi:10.1038/hdy.2009.155; published online 18 November 2009

The Crnokrak and Roff (1999) paper was a seminal contribution to conservation genetics as it resolved the controversial issue of whether inbreeding had deleterious impacts on life history traits among wild species in their natural habitats. Their meta-analysis established that inbreeding depression occurred in 90% of the 157 valid data sets (omitting data sets from *Malurus splendens*, for which paternity attributions were largely incorrect) involving 34 taxa. Furthermore, they showed that inbreeding was similarly deleterious across major plant and animal taxa. Crnokrak and Roff's paper has been cited 222 times in the Web of Science (as of September 2009).

The background to this issue is that inbreeding has been known to cause deleterious effects since Darwin (1876) and even earlier. Darwin studied this issue in 57 species of plants and showed that the impacts were overwhelmingly deleterious. Subsequent studies have shown inbreeding depression in all well-studied sexually reproducing laboratory and domestic animals and plants (Frankham *et al*., 2009).

In spite of this, controversy broke out in the 1970 s when it was suggested that inbreeding would have deleterious effects on wildlife in captivity. That issue was resolved by Ralls and Ballou (1983), who reported that 41 of 44 mammalian populations showed higher juvenile mortality among inbred than among outbred individuals. The controversy subsequently shifted to the impacts of inbreeding on wild species in natural habitats. It was at this point that the Crnokrak and Roff study made a telling entry. Their estimate of inbreeding depression in the wild was approximately seven times greater than the impacts of inbreeding on wildlife in captivity. This was in line with the presumption that inbreeding typically has more severe effects in stressful conditions, a hypothesis that was later confirmed in a meta-analysis by Armbruster and Reed (2005).

Subsequently, several other studies have supported Crnokrak and Roff's (1999) conclusions (Keller and Waller, 2002; Frankham, 2005). For example, hatching failure rates across 99 species of birds increased with the genetic similarity of parents (Spottiswoode and Møller, 2004). Briskie and Mackintosh (2004) showed that hatching failure rates were higher in bottlenecked than in non-bottlenecked populations of both native and introduced birds in New Zealand.

The controversy next moved on to whether inbreeding depression had impacts on population viability in the wild. Elevated extinction risks due to inbreeding have been documented for the Glanville fritillary butterfly in Finland, *Clarkia pulchella* in the United States and *Silene littorea* in Spain (Newman and Pilson, 1997; Saccheri *et al*., 1998; Vilas *et al*., 2006). I am not aware of any other studies on this issue. Furthermore, Brook *et al*. (2002) and O'Grady *et al*. (2006) showed that the inclusion versus exclusion of inbreeding depression in realistic computer models (population viability analyses (PVAs)) caused substantial reductions in median times to extinction. For example, adding inbreeding depression at realistic levels reduced the median time to extinction by an average of 37% across 30 taxa. The evidence is now so compelling that it is unrealistic to omit inbreeding depression from PVA models, nor is it credible to ignore the genetic effects in wild population management for outbreeding species (Frankham, 2005). Nevertheless, both these things are still happening.

It has also been argued that non-genetic factors will drive a species to extinction before genetic factors can affect them, a view that is attributed to Lande (1988) and was promoted by Caughley (1994), Caro and Laurenson (1994), and others. This was rejected for most species in an experimental test involving levels of genetic diversity in 170 comparisons of threatened and related non-threatened taxa (Spielman *et al*., 2004). There is now ample evidence to conclude that the controversy about inbreeding depression in wild species in natural habitats has been resolved (Frankham, 2005).

The most pressing deficiency in our knowledge about the impacts of inbreeding depression relates to estimates of the full impacts on the whole lifecycle in the wild, which is a critical input for PVAs. O'Grady *et al*. (2006) concluded that the impact averaged 12 lethal equivalents; however, the data available for the assessment were very limited. The issue of whether inbreeding depression in polyploids is lesser or greater than that in diploids also remains unresolved, although the former is more likely.

Professor R Frankham is at the Department of Biological Sciences, Macquarie University, New South Wales 2109, Australia and is at the Australian Museum, 6 College Street, Sydney, New South Wales 2010, Australia.

e-mail: rfrankha@els.mq.edu.au

Armbruster P, Reed DH (2005). *Heredity* **95**: 235–242.
Briskie JV, Mackintosh M (2004). *Proc Natl Acad Sci USA* **101**: 558–561.
Brook BW, Tonkyn DW, O'Grady JJ, Frankham R (2002). *Conserv Ecol* **6**: 16.
Caro TM, Laurenson MK (1994). *Science* **263**: 485–486.
Caughley G (1994). *J Anim Ecol* **63**: 215–244.
Crnokrak P, Roff DA (1999). *Heredity* **83**: 260–270.
Darwin C (1876). *The Effects of Cross and Self Fertilisation in the Vegetable Kingdom*. John Murray: London.
Frankham R (2005). *Conserv Biol* **126**: 131–140.
Frankham R, Ballou JD, Briscoe DA (2009). *Introduction to Conservation Genetics*, 2nd edn. Cambridge University Press: Cambridge, UK.
Keller LF, Waller DM (2002). *Trends Ecol Evol* **17**: 230–241.
Lande R (1988). *Science* **241**: 1455–1460.
Newman D, Pilson D (1997). *Evolution* **51**: 354–362.
O'Grady JJ, Brook BW, Reed DH, Ballou JD, Tonkyn DW, Frankham R (2006). *Conserv Biol* **133**: 42–51.
Ralls K, Ballou J (1983) In: Schonewald-Cox CM, Chambers SM, MacBryde B, Thomas L (eds). *Genetics and Conservation: A Reference for Managing Wild Animal and Plant Populations*. Benjamin/Cummings: Menlo Park, CA. pp 164–184.
Saccheri I, Kuussaari M, Kankare M, Vikman P, Fortelius W, Hanski I (1998). *Nature* **392**: 491–494.
Spielman D, Brook BW, Frankham R (2004). *Proc Natl Acad Sci USA* **101**: 15261–15264.
Spottiswoode C, Møller AP (2004). *Proc Roy Soc Lond B* **271**: 267–272.
Vilas C, Miguel ES, Amaro R, Garcia C (2006). *Conserv Biol* **20**: 229–238.

Editor's suggested reading

Rijks JM, Hoffman JI, Kuiken T, Osterhaus ADME, Amos W (2008). Heterozygosity and lungworm burden in harbour seals (Phoca vitulina). *Heredity* **100**: 587–593.
Tokarska M, Marshall T, Kowalczyk R, Wójcik JM, Pertoldi C, Kristensen TN *et al*. (2009). Effectiveness of microsatellite and SNP markers for parentage and identity analysis in species with low genetic diversity: the case of European bison. *Heredity* (e-pub ahead of print 22 July 2009; 10.1038/hdy.2009.73).
Alcaide M, Serrano D, Negro JJ, Tella JL, Laaksonen T, Müller C *et al*. Population fragmentation leads to isolation by distance but not genetic impoverishment in the philopatric Lesser Kestrel: a comparison with the widespread sympatric Eurasian Kestrel. *Heredity* **102**: 190–198.