Recovery of the Florida panther – genetic rescue, demographic rescue, or both? Response to Pimm *et al*. (2006)

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Pimm, Dollar & Bass (2006) address difficult issues in their evaluation of the release of Texas panthers to mingle with the last 30 Florida panthers. This release was almost unique, because it was designed to let a hybrid swarm (Allendorf *et al*., 2001) swamp a population that was genetically unique, but inbred. Trading off against this loss of unique evolutionary potential is, hopefully, a reduction of inbreeding depression that improves the population's demography and dynamics.

It is this benefit ('genetic rescue') that Pimm *et al*. (2006) seek to demonstrate, but the issue is more complex than it first appears. Intuitively, the population's growth from ~30 to 87 cats seems to resolve the question, but we should consider the possibility that population growth was because of simple demographic rescue rather than genetic effects. As shown by the restoration of wolves to Yellowstone (Smith *et al*., 2003), small introductions of carnivores can produce dramatic population growth in cases where the initial population size was zero, which removes genetic rescue from consideration. The release of 31 wolves yielded a greater than fourfold increase in 5 years, substantially faster growth than the panthers have shown. Pimm *et al*. (2006) also note that 'hybrid cats are beginning to expand their ranges to areas previously thought unsuitable', but a growing population will often expand into new habitats, so this response may also be demographically driven.

To test for genetic rescue more directly, Pimm *et al.* (2006) compare the survival and reproduction of purebred and hybrid panthers. They conclude that there is 'a strong presumption that purebred cats suffer a variety of unfortunate demographic consequences that hybrid cats do not'. While I tend to agree that a reduction in inbreeding depression has probably played a role in the recovery, I am not certain. One obvious problem is that the demographic data from hybrids and purebreds come from different (although overlapping) periods, and carnivore populations (particularly small ones) often show marked temporal variation in survival and reproduction. A second problem is that differences in the age distribution of hybrids and purebreds are not considered in the analysis of adult survival.

Of greater concern to me is the equivocal evidence that reproduction and survival differ for adult hybrids and purebreds. Pimm *et al*.'s (2006) conclusion quoted above focuses on the observations that hybrids survive better among kittens and females, but it is important to recall that reproduction and adult male survival showed no benefit of hybridization. Consider the analysis of adult survival. The simple fact is that a model allowing for differences between purebreds and hybrids is no better than a model that ignores genetic differences. Pimm *et al*. (2006) state: 'Splitting by origin, purebreds have higher mortalities than hybrids.' But the data give no support to this statement, because models including and ignoring genetic differences are identically 11 Akaike's information criterion (AICc) units worse than the best model. Sex, on the other hand, is a good predictor of annual survival (11 AICc units better than the model accounting for genetic origin). A model that allows genetic origin to modify sex differences is not demonstrably worse than one allowing only for sex differences (1 AICc unit worse, where $\Delta AICc = 2$ would indicate that genetic origin contributes no additional information; restricted to natural deaths, adding genetic origin substantially weakens the model allowing for sex differences: $\Delta AICc = 3$). If these data had been presented as a factorial ANOVA, it would show that the main effect of genetic origin on survival was very weak. The information presented does not allow me to say whether the interaction of sex by origin would be significant, because no test statistics were reported and their fig. 2 does not include estimates of error for mean survival rates. At best, Pimm *et al*. (2006) are treating a significant interaction as though it was a significant main effect.

This precludes clean inferences about the effect of genetic rescue on adult survival. If we had data only for females, we would conclude that hybrids survive better. If we had data only for males, we would conclude the opposite. It seems unlikely that this pattern would have been predicted a priori in formulating hypotheses about genetic rescue. Comparing data on natural deaths and deaths of all causes (their fig. 2a and b), we see another change in the sign of the effect (for males in this case). When the sign of an effect flip-flops repeatedly and unpredictably, cautious conclusions are in order.

With equivocal effects on reproduction and adult survival, but relatively clear effects on juvenile survival, it seems likely that reduced inbreeding has helped the population recover. The recovery itself is clear, but I do not think that the relative strengths of demographic and genetic rescue have been resolved. From the perspective of local ecology, increasing panther density and range expansion are clear successes. From the perspective of maintaining evolutionarily unique populations, this success comes at the cost of genetic swamping.

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