

Maternal effects can inflate rate of adaptation to captivity

An important concern of ex situ conservation programs is how maintenance of populations for several generations in a captive environment affects their performance when these populations are reintroduced to the wild. Although there is some evidence that adaptation to captivity entails a drop in fitness in the wild (1), how important this effect is and how quickly it arises remain elusive questions. In particular, it has been shown that the rate of adaptation to captivity may be quite variable, even in the same species, among populations facing similar captive environments (2). Recently in PNAS, Christie et al. (3) inferred evolutionary change in a single generation of maintenance in captivity of a wild steelhead (*Oncorhynchus mykiss*) population. The authors used a multigenerational pedigree analysis to “demonstrate that domestication selection can explain the precipitous decline in fitness observed in hatchery steelhead released into the Hood River in Oregon.” They compared the performance of first generation (F1) hatchery fish with that of wild fish spawned under identical conditions, reporting that the former had nearly double the lifetime reproductive success, and interpreting this as a clear demonstration of adaptation to captivity. They also observed that wild-born broodstock that had higher fitness in the captive environment had offspring with lower performance in the wild, which they interpreted as evidence of a tradeoff between the captive environment and the wild.

The problem is that it is not possible to disentangle environmental maternal effects from genetic effects in the comparisons of first-generation fish developed in the hatchery with their wild parents, whose mothers developed in the wild (4). Such maternal effects might explain the higher performance of the F1 hatchery broodstock relative to the wild broodstock, rather than genetic adaptation to captivity. To avoid such effects, an improved experimental design would compare two more advanced

generations in captivity [e.g., the fourth (or later) and third generations]. This would allow an estimate of the rate of adaptation to captivity without confounding maternal effects attributable to development of the parents of the earlier generation in the wild. Moreover, the tradeoff reported between the reproductive success of fish in captivity and that of their offspring in the wild may be partially caused by environmental costs of reproduction (e.g., females laying more eggs may have offspring with lower success), which is, again, a maternal effect and not a genetic tradeoff across environments. Such a negative covariance was reported between mother and daughter egg numbers in pink salmon (5). Although a similar effect is not expected with males, it might be that the environmental quality of bigger clutches affects later performance. A better experimental design would be to estimate the genetic tradeoff across environments using families of the same generation (e.g., a half-sib design).

Although the data reported are still of interest for revealing the impact that a single generation of captivity may have on the performance of a population when reintroduced in the wild, it is not legitimate to assign a genetic interpretation to the differences observed. Analysis removing maternal effects may complete the story.

Margarida Matos¹

Centro de Biologia Ambiental, Faculdade de Ciências da Universidade de Lisboa, Campo Grande, 1749-016 Lisbon, Portugal

1. Araki H, Cooper B, Blouin MS (2007) Genetic effects of captive breeding cause a rapid, cumulative fitness decline in the wild. *Science* 318:100–103.
2. Simões P, et al. (2008) How repeatable is adaptive evolution? The role of geographical origin and founder effects in laboratory adaptation. *Evolution* 62:1817–1829.
3. Christie MR, Marine ML, French RA, Blouin MS (2012) Genetic adaptation to captivity can occur in a single generation. *Proc Natl Acad Sci USA* 109:238–242.
4. Wolf JB, Wade MJ (2009) What are maternal effects (and what are they not)? *Philos Trans R Soc Lond B Biol Sci* 364:1107–1115.
5. Funk WC, Tyburczy JA, Knudsen KL, Lindner KR, Allendorf FW (2005) Genetic basis of variation in morphological and life-history traits of a wild population of pink salmon. *J Hered* 96(1):24–31.

Author contributions: M.M. wrote the paper.

The author declares no conflict of interest.

¹E-mail: mmatos@fc.ul.pt.