Westslope Cutthroat Trout, Hybridization, and the U.S. Endangered Species Act

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Allendorf et al. (2004) describe introgressive hybridization and the potential "listing" of westslope cutthroat trout (WCT, *Oncorhynchus clarki lewisi*) under the U.S. Endangered Species Act (ESA). This issue is complicated because many natural populations have experienced small amounts of introgression detectable only by molecular genetic methods. The issue is further complicated because portions of the native geographic ranges of WCT and rainbow trout (RT, *O. mykiss*), the principal hybridizing species, naturally overlap.

Allendorf et al. recommend only "nonhybridized" populations be considered WCT under the ESA. If this recommendation is followed, then populations with *any* detectable introgression would be excluded from the subspecies and would be eligible for eradication under an ESA listing. Thus, for situations like WCT, a biological dichotomy exists between (1) the need to conserve the genetic resources of an imperiled species in which introgression has occurred and (2) the need to eliminate hybridization threats posed by introduced taxa.

The U.S. Fish and Wildlife Service (USFWS) has thoroughly examined this issue in response to a court order (USFWS 2003) and has reached conclusions that differ from those of Allendorf et al. We comment here on their perspectives and provide alternative viewpoints. Details of the USFWS'conclusions are described elsewhere (USFWS 2003).

Allendorf et al. note (abstract), "There are currently no policy guidelines for treating hybrids under the U.S. Endangered Species Act." This is partially true. A proposed "intercross policy" (USFWS 1996) was developed but never finalized because the range of possible hybridization situations precluded a single policy. Instead, policy guidelines will be developed for each species on a case-by-case basis, as occurred for WCT (USFWS 2003).

Allendorf et al., citing Leary et al. (1995), suggest that natural hybridization between WCT and RT in regions of natural sympatry has been "extremely rare." More recent studies suggest otherwise (Weigel et al. 2002, 2003; Howell & Spruell 2003; Brown et al. 2004). As noted by Howell and Spruell (2003), "It is apparent that WSCT [WCT] × RB [rainbow trout] hybridization can be extensive in areas . . . where both taxa are native and there have been little to no introductions of hatchery RB."

Allendorf et al. may have misinterpreted Weigel et al. (2002) in the following statement (p. 1207): "They concluded that a hybridized population has to contain at least 50% admixture from RT to be identified reliably in the field." However, Weigel et al. (2002) did not estimate admixture proportions (i.e., percent RT genes) because they used dominantly expressed markers. In that study, the presence of at least one RT allele at one of eight DNA loci, among 20 individuals tested, was accepted as evidence of introgression. Based on those criteria, Weigel et al. (2002) detected introgression morphologically with 100% accuracy when 50% or more of the *fish* at a site expressed at least one RT allele. This latter percentage occurs for dominant DNA markers at substantially less than "50% admixture."

Allendorf et al. (2004:1209) conclude (p. 1209) that F1 hybrids of WCT and RT "had significantly reduced survival" under laboratory conditions. Those conclusions are based on unpublished work they reiterate (pp. 1207–1209) for a third time (Allendorf & Leary 1988; Leary et al. 1995). Allendorf et al., however, do not cite published work from their laboratory that leads to a different conclusion (Ferguson et al. 1985). In this latter experiment, F1 hybrids did not show decreased survival or any developmental incompatibility, suggesting "an absence of postmating isolating mechanisms between these taxa" (Ferguson et al. 1985:566).

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Rubidge et al. (2001) and Hitt et al. (2003) report temporal increases in RT introgression in natural populations of WCT. Rubidge et al. (2001) note that the increased introgression is most likely due to continued stocking of RT in a downstream reservoir. In Hitt et al. (2003), the maximum increase in introgression at any one site was only 7% (0% to 7% between 1984 and 1998), and the most probable source of the increased introgression throughout the watershed was a naturalized population of RT (with 2–11% WCT introgression) in the mainstem Flathead River (see Fig. 1 of Hitt et al. 2003). As a result, one need not hypothesize increased migratory behavior of WCT in introgressed populations versus nonintrogressed populations, as suggested by Allendorf et al., to explain temporal increases in genetic introgression. Instead, a simple stepping stone or diffusion model of gene flow from the naturalized rainbow trout population is sufficient to explain those increases.

Allendorf et al. speculate (p. 1210) that loss of adaptations from genetic introgression will be "difficult to detect because some local adaptations of native populations might only be essential during periodic episodes of extreme environmental conditions, such as winter storms, drought, or fire." From our reviews of the scientific literature, we are unaware of any data on WCT that support the notion that they are locally adapted to winter storms, drought, fire, or other episodic environmental events to a greater or lesser extent than RT, Yellowstone cutthroat trout (*O. c. bovieri*), or introgressed populations. Indeed, upper thermal tolerances for RT, cutthroat trout, and their hybrids are very similar ($\approx$ 24–26° C; Johnstone & Rahel 2003; Table 4 of Selong et al. 2001 and references therein), although some populations of RT appear to have significantly higher temperature tolerances (Behnke 1992). Consequently, we believe the aforementioned speculation of Allendorf et al. is unsupported scientifically and, thus, unwarranted.

Allendorf et al. state (p. 1205, see also abstract), "The WCT are threatened by widespread genomic extinction." They also note (p. 1207, see also abstract) "all of the progeny of a hybrid will be hybrids," where they define ***hybrid*** as (p. 1204) "any individual that is either a first-generation hybrid or whose recent ancestry (within the last 100 years or so) includes at least one first-generation hybrid individual." (To put this definition in proper perspective, assume an F1 hybridization event [WCT x RT] occurred 100 years ago. After 100 years [approximately 20 generations] of repeated backcrossing with WCT, the predicted proportion of a descendant's genes derived from RT would be approximately $[0.5]^{20}$, or $< 0.0001\%$. Such an individual would be considered a hybrid, according to Allendorf et al. [2004]). The implicit interpretation is that any genetic introgression will result in "genomic extinction." Those perspectives are overly simplistic because they fail to recognize the phenotypic effects (e.g., morphological, behavioral, physiological), or lack thereof, of varying levels of introgression (e.g., 1% versus 50%). Understanding those effects is especially critical under the ESA because many populations, representing the ancestral genetic resources of an imperiled taxon, may have experienced small amounts of introgression (natural or anthropogenic) detectable only by molecular genetic methods (e.g., Dowling & Childs 1992; Peacock & Kirchoff 2004).

If the recommendations of Allendorf et al. are followed, then natural populations of WCT with any detectable introgression would be eligible for eradication under an ESA listing. For example, RT introgression was detected in 22 of 40 WCT populations in the middle and north forks of the Flathead River, although < 10% introgression was detected in 14 of those populations (Hitt et al. 2003). Suppose those 22 introgressed populations are eradicated to protect the other 18 nonintrogressed populations. What if the eradication is not completely successful, and 1-10% introgression is detected in 16 of the remaining 18 populations 50 years from now? Should those 16 introgressed populations be eradicated to protect the remaining two nonintrogressed populations? Such a course could eliminate more genetic resources of WCT than it protects. Consequently, we do not believe this latter approach is consistent with the intent and purpose of the ESA or with the conservation interests of the subspecies. Such a strategy overlooks the real hybridization threat to WCT: a naturalized population of RT in the mainstem Flathead River (Hitt et al. 2003).

In response to a court order, the USFWS developed a holistic strategy for including potentially introgressed populations of WCT with the WCT subspecies under the ESA (USFWS 2003). The USFWS concludes that an introgressed population should be considered WCT under the ESA if that population conforms phenotypically to the scientific, taxonomic description of the subspecies. Conversely, populations conforming phenotypically to the scientific, taxonomic description of WCT are not considered a hybridization threat to the subspecies. The USFWS also provides molecular genetic criteria consistent with those phenotypic criteria (USFWS 2003). In many cases, locally adapted populations, representing a significant proportion of the ancestral genetic resources of an imperiled species, may have experienced small amounts of introgression detectable only by molecular genetic methods. Such populations can be protected under the USFWS' strategy, whereas nonintrogressed populations can be given the highest priority for protection, either as part of a state management plan or ESA recovery plan if a listing occurs.

Allendorf et al.'s recommended approach, if implemented, could result in the eradication of numerous, slightly introgressed populations of WCT under an ESA listing. We believe such an approach is inconsistent with the intent and purpose of the ESA (USFWS 2003). Similar viewpoints have been expressed elsewhere (O'Brien & Mayr 1991; Dowling & Childs 1992; Avise 1994).

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