

The Service also recognizes special cases where all individuals of a “species” are considered hybrids. For example, the Service recognizes that deliberate hybridization may be necessary in extreme cases to prevent extinction of the genetic resources associated with a highly endangered species, as was the case for the Florida panther (*Felis concolor coryi*) (Hedrick 1995). Similarly, the Service continues to protect red wolves (*Canis rufus*) under the Act despite ongoing controversies regarding their possible hybrid origin (Nowak and Federoff 1998). In both of those cases, extending the Act’s jurisdictions and protections to “hybrids” may contribute to the conservation of the genetic resources of those taxa, consistent with the intent and purpose of the Act.

A potential dichotomy thus exists under the Act between: (a) The need to protect the genetic resources of a species in which introgression has occurred and (b) the need to minimize or eliminate the threat of hybridization posed by another taxon. Implementing actions under the Act that distinguish between these two alternatives is difficult when imperiled species are involved because a large number of populations may have experienced small amounts of genetic introgression from another taxon. These decisions are further complicated for WCT because the native geographic ranges of WCT and rainbow (redband) trout overlap in portions of the Columbia River drainage. For example, as noted by Howell and Spruell (2003), “It is apparent that WSCT [WCT] × RB [rainbow trout] hybridization can be extensive in areas, such as the John Day [River] subbasin, where both taxa are native and there have been little to no introductions of hatchery RB.”

For the purpose of providing conservation guidelines, Allendorf *et al.* (2001) have suggested that hybridization be categorized as either anthropogenic or “natural.” They further suggest that “hybrid” populations or taxa resulting from natural causes would be eligible for conservation protection, whereas genetically introgressed individuals or populations resulting from anthropogenic causes would generally not be protected unless “hybrids” were the last remaining genetic representatives of a hybridized species (their “Type 6” hybridization). Such criteria may be useful for prioritizing management options for populations or species that are not eligible for listing under the Act. However, the issue for species under potential jurisdiction of the Act is the extent to which hybridization poses a threat to the continued existence of the “species”

regardless of whether the cause is anthropogenic or “natural.” Both natural evolutionary processes, including catastrophic environmental events (e.g., floods, earthquakes), and anthropogenic factors can lead to secondary contact and hybridization between species. Also, distinguishing between anthropogenic and natural causes of hybridization, particularly for species with naturally overlapping geographic ranges, may be extremely difficult (e.g., Campton and Utter 1985; Young *et al.* 2001; Baker *et al.* 2002). A complicating issue in these determinations is the degree to which “natural” hybridization may have compromised the identity of a distinct species prior to anthropogenic influences (e.g., Weigel *et al.* 2002). The principal issues here under the Act are the threats and potential outcomes of hybridization, including other potential risks associated with the five statutory listing factors (e.g., habitat loss, disease), and not necessarily the mechanistic causes (natural or anthropogenic) of those threats. In this context, the Act does not distinguish between natural and “manmade” factors that may threaten the continued existence of a species (section 4(a)(1)).

Several studies have demonstrated that natural populations, and individual fish, conforming morphologically to the scientific taxonomic description of WCT may contain genes derived from rainbow trout or YCT as the result of a past hybridization event (Leary *et al.* 1984; Marnell *et al.* 1987; Forbes and Allendorf 1991a, b; Leary *et al.* 1996; Weigel *et al.* 2002, 2003). For example, Leary *et al.* (1984) reported that an introgressed population of WCT, with an estimated 20 percent of its nuclear genes derived from rainbow trout, was indistinguishable morphologically from nonintrogressed WCT populations. A subsequent study revealed a strong, positive correlation between percent rainbow trout genes in natural populations of WCT and the percent of individuals without basibranchial teeth in those populations (Table 1 in Leary *et al.* 1996). Indeed, based on this latter study, the percent of individuals without basibranchial teeth appears to be a fairly accurate predictor of the percent rainbow trout genes in natural populations where WCT are native. However, this correlation collapses in nonintrogressed populations of WCT where up to 18 percent of the individuals may not have any basibranchial teeth (Leary *et al.* 1996).

Weigel *et al.* (2002) recently conducted the most extensive study to date comparing variation in morphological characters to levels of

genetic introgression in natural populations of WCT. In that study, Weigel *et al.* (2002) compared variation in morphological characters to nuclear DNA genotypes at 16 dominant marker loci (Spruell *et al.* 1999, 2001) in random samples of 20 trout from each of 100 sites in the Clearwater and Lochsa River drainages in Idaho. In that study, the presence of at least 1 rainbow trout DNA marker among the 20 individuals tested at a particular site was accepted as evidence that genetic introgression had occurred in the native WCT population inhabiting that site. According to the authors, their DNA methods and sample sizes ( $n = 20$ ) allowed them to achieve 95 percent confidence (probability) of detecting genetic introgression in WCT populations with as little as 1 percent rainbow (or redband) trout genes. However, because those authors used “dominant” genetic markers, they could not distinguish heterozygotes from homozygotes, thus precluding calculations of allele frequencies and true estimation of admixture proportions (*i.e.*, percent rainbow trout genes) in each sample or population evaluated.

Despite those limitations, three main results pertinent to this status review can be gleaned from the paper by Weigel *et al.* (2002): (1) The percent of fish at each sample site with at least 1 rainbow trout marker was bimodally distributed among the 100 sample sites examined (see Figure 2 in Weigel *et al.* 2002); approximately 62 percent of the sites yielded population samples where zero to 30 percent of the fish showed evidence of introgression, while approximately 36 percent of the sample sites had 50 to 100 percent of the individuals showing evidence of introgression. (2) Variation in the mean values of four morphological characters among natural populations of WCT (*i.e.*, the presence or absence of red or orange slash marks, the number of basibranchial teeth, the shape of individual spots on the body, and the ratio of head length to total body length) was correlated with the amount of rainbow trout genetic introgression in those populations. (3) By employing a dichotomous morphology key, field observers attained 93 percent accuracy in morphologically detecting genetic introgression in natural populations of WCT where 50 percent or more of the fish in those populations had at least one rainbow trout DNA marker; however, those same observers were unable to accurately distinguish WCT populations with no DNA evidence of introgression from populations with low