



The Role of Culture in Conservation Planning for Small or Endangered Populations

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Introduction

The role of culture in population structuring has received much recent attention (e.g., Slabbekoorn & Smith 2002; Freeberg 2004); for example, the 2005 International Mammal Congress (<http://www.imc9.jp/>) had a full symposium on the topic. The idea that culturally significant units (CSUs) should be considered in conservation planning is recent (Whitehead et al. 2004). But how generalizable is this idea? To what extent is culture measurable? Where does it fit in the current language of conservation planning? I address some of these questions and provide suggestions for accommodating culture in current conservation rubrics.

The ESA, ESUs, and Distinct Population Segments

In the conservation literature of the 1990s, the concept of evolutionarily significant units (ESUs) was hotly debated (DeWeerd 2002). The goal was to define unique population segments that may not conform to species concepts (Waples 1991; Dizon et al. 1992; Moritz 1994; Dimmick et al. 1999) in part to address a 1978 amendment to the U.S. Endangered Species Act that permitted listing “distinct population segments” as threatened or endangered. The axes for defining ESUs that evolved from this debate are adaptive variation (Crandall et al. 2000), emphasizing retention of genetic and phenotypic diversity, and vicariant evolutionary divergence, arising through historic or geographic isolation (Dizon et al. 1992; Moritz 1994, 2002). In the context of listing, Waples’ (1991) work on Pacific salmon emphasizes not only isolation but also uniqueness of population segments, contributing to the “evolutionary legacy of the species.”

Culture can also provide a significant mechanism of isolation. Identification of culturally distinct population segments is becoming prevalent in studies of small or endangered populations, but it is unclear how this translates into conservation plans. Although there has been contention over the definition of *culture*, the definition I use here is a behavior or skill acquired through horizontal transmission: social learning (Cavalli-Sforza & Feldman 1981; Boyd & Richerson 1985). Its extrapolation from the human social and anthropological literature to non-human species is not novel, but analysis of this form of population structure as a biological construct is (Mace & Holden 2005). Quantifying culture in nonhuman species and demonstrating its role in population structuring is complicated, both in determining horizontal transmission and recognizing the adaptive advantage it may confer.

Language Barriers

Learned songs are barriers to dispersal in birds, where individuals with unrecognized songs are excluded from groups (Petrinovich et al. 1981), and Slabbekoorn and Smith (2002) even cited learned song exclusion as a potential cause of speciation. Amazonian parrot dialects maintain regional diversity (Wright & Wilkinson 2001), and song dialects in White-crowned Sparrows (*Zonotrichia leucophrys oriantha*) are associated with reductions in regional gene flow (MacDougall-Shackleton & MacDougall-Shackleton 2001). Identification of dialects in mammals is also coming to light (e.g., vocal patterns in elephants and vocal clans in whales and dolphins [Rendell & Whitehead 2003; Whitehead et al. 2004]). Whitehead et al. (2004) discuss the emerging recognition of culture in population structuring of cetaceans and its possible role

in conservation and introduce the term *CSU*. Vocal cultural transmission is clearly analogous to ethnolinguistic groups in humans. Mace and Holden (2005) draw parallels between classic phylogenetic evolution and human cultural evolution, showing that population structure arises at the level of language and that cultural groups have gone extinct. Indeed, there have been several articles (Abrams & Strogatz 2003; Sutherland 2003) mourning the extinction of human languages and ethnolinguistic groups.

Additional examples of culture in birds include learned courtship and mating patterns influencing female mate choice and population structure in cowbirds (Freeberg et al. 1999; Freeberg 2004) and tool use and technological evolution in crows (Hunt & Gray 2003). Authors have also noted the conservation implications of the diversity of complicated cultures arising through tool use, gestures, and other learned behaviors in chimpanzees (Whiten & Boesch 2001) and orangutans (*Pongo pygmaeus*; van Schaik et al. 2003). Another well-studied cultural phenomenon is potato washing behavior of Japanese snow monkeys (*Macaca fuscata*; Matsuzawa 2003). The advantage of learning socially transmitted behaviors may benefit the group whose members have the behavior over those that do not. Moreover, building a suite of behaviors from conspecifics—cultural exchange—may be important to population persistence. The 2004 update on the status of southern resident killer whales (*Orcinus orca*) explicitly includes behavioral and cultural considerations for population persistence of North Pacific killer whales (Krahn et al. 2004). They argue that behaviors such as depredating long-line caught fish may be behaviorally transmitted from the southern residents to other segments of the North Pacific subspecies.

Culture and the Evolutionary Landscape

Odling-Smee et al. (2003) argue that evolution occurs in part because of niche modification by individuals. By changing the landscape on which adaptation acts, organisms guide their own evolution. In this monograph, Odling-Smee et al. demonstrate behavioral niche modification for a wide taxonomic array. Demonstrations of the potential population structuring effects of niche modification have been explored at the gene level by Laland et al. (1999) and at a demographic level by Ihara and Feldman (2004).

Learned behaviors that lead to population structuring can take on many forms, from dialects to tool use to learned niche modification. The degree to which these are recognizable and quantifiable as culture is highly variable and even contentious, but what is emerging is a need to understand them for conservation purposes. An obvious question to ask is when cultural population structuring will matter to conservation plans.

When reproductive success is restricted by cultural lines, identifying groups to retain sufficient numbers for

persistence may become the most important component of a conservation plan. The timescale over which culture alone could affect a distinct population segment may differ from simultaneous ongoing mechanisms of isolation (e.g., geographic and phenotypic adaptation). Identifying the process of cultural isolation is complicated, meaning that we tend to see only documentation of the result. We cannot know a priori which mechanism of isolation is driving a population toward genetic distinction. Thus, I propose that cultural isolation represents a third axis in the ESU framework (Fig. 1), making “distinct population segments” a combination of three factors. The degree to which a population segment has become culturally isolated will ultimately give rise to genetic distinction and similarly to geographic and historic isolation.

Identifying CSUs prior to enacting a conservation plan may be vital to a population’s persistence. For example, the Amazonian parrots (Wright & Wilkinson 2001), with clear dialectic lines, must be managed as separate units rather than one population. However, as may more often be the case, by the time a population is small or sufficiently fragmented to attract attention, identifying CSUs may be moot.

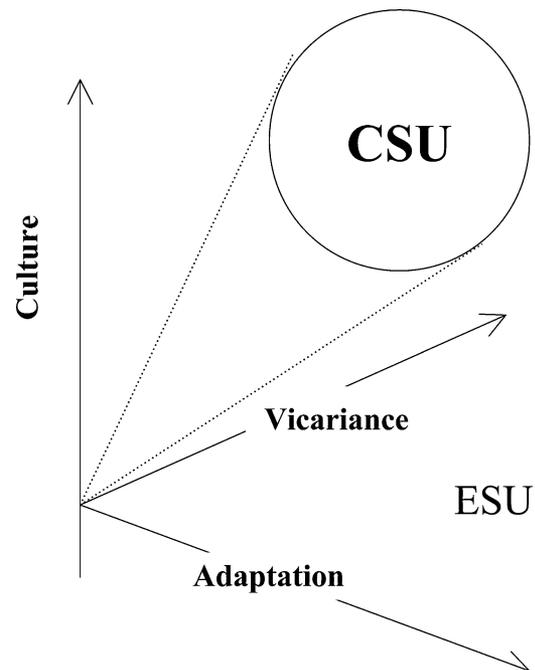


Figure 1. Mechanisms of isolation leading to speciation through population structuring (x-axis, process of adaptation via phenotypic variation; y-axis, vicariance arising through historic or geographic isolation; z-axis, culture; ESU, evolutionarily significant unit. The combination of these processes results in a culturally significant unit (CSU), a new definition of distinct population segment.

Table 1. Conservation strategies for small or endangered populations and the implications of culturally significant units (CSUs) under their rubrics.

<i>Conservation action</i>	<i>Strategy level*</i>	<i>CSU implication/objective</i>
Protect critical habitat	optimal triage	Identify and retain all habitat used and associated with CSUs. Identify priority CSU and specific habitat, particularly in the case of niche modification.
Translocation	optimal triage	Translocate a sufficient number of individuals to retain the entire suite of CSUs identified. Ensure that translocated individuals are from the same CSU if there is already sufficient population substructure. Alternately, if the CSU is still plastic, the goal may be to maximize the breadth of the trait. In this case, individuals of as many CSUs as possible should be translocated.
Captive breeding	optimal and triage	Similar to translocation, with the added caveat that if CSUs are evolving as a form of local adaptation and niche modification, the captive habitat must reflect that local selection landscape.
Reintroduction	optimal triage	In the optimal situation, a reintroduction will comprise sufficient numbers and allelic diversity to allow behavioral, phenotypic, and cultural plasticity in the face of an environment that may be different from that in which the species were raised. On the basis of the philosophy that one would want reintroduction to promote survival and reproduction, the individuals that can survive and reproduce together (same CSU) ought to be reintroduced together.

*The optimal strategy is what one would do given infinite time, resources, and information. The triage strategy is what one would do in a less than ideal situation but still consider CSUs.

Allocating Conservation Strategies

When and to what degree should we incorporate culture into conservation plans? Table 1 lists several broad conservation measures for preserving small/endangered populations and identifies the role of CSUs. Maintaining diversity while managing small populations, through translocations, captive breeding, and reintroduction, is often undertaken and measured at a genetic level (Earnhardt et al. 2001). The goal of these programs generally is to maintain as much of the original genetic variation as possible. To maintain cultural diversity, one could argue that preserving a group of individuals with the capacity to learn the behavior is sufficient (analogous to conserving evolutionary processes [Moritz 2002]). In this case, there may be a quantifiable threshold of individuals needed to provide the diversity of arising behaviors or niche modifications on which selection can act. We do not currently have the means to measure this number, so the focus of these programs should be identification and maintenance of cultural groups. If they preclude outbreeding at a local level, they must be preserved as distinct groups (because they reflect something akin to historic isolation) that have not evolved yet into a genetically distinct grouping.

Culturally significant units present the conundrum of opposing strategies: maximizing variation versus preserving uniqueness. When a population is so small that demographic goals override genetic consideration, cultural considerations must also fall by the wayside. However, particularly in captive populations, the role of learned social behavior in program success is striking. Captive fe-

male gorillas who had not been raised by their mothers or joined a social group after weaning were incapable of raising their own offspring, and in many cases could not reproduce owing to a lack of learned copulatory behavior (Ryan et al. 2002). This underscores the need to retain CSUs, if a trait has become influential on reproductive success. The need to identify reproductively isolating cultural traits also applies to fragmented populations, with added caution when initiating translocations or reintroductions. If the behavior is a strong local adaptation, admixtures might cause communication breakdowns among individuals, lack of mate recognition, and decreased fitness.

Simply raising the level of awareness of CSUs among conservation biologists is an important first step to establishing appropriate conservation plans. Although the logistical implementations of plans will be different for whales than for chimpanzees, the policy language is similar. Whether the conservation world needs another acronym to contend with is debatable, but to label the cultural phenomenon within a currently established context of ESUs and the U.S. Endangered Species Act is invaluable.

Acknowledgments

I thank C. Moritz, A. P. Dobson, A. G. Vaughan, and two reviewers for discussions, edit, and comments. Environmental Protection Agency (EPA) STAR Fellowship FP-916382 funds my research.

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