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POLICY PERSPECTIVE

Connectivity Conservation and Endangered Species Recovery: A Study in the Challenges of Defining Conservation-Reliant Species

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Abstract

Many species listed under the US Endangered Species Act (ESA) face continuing threats and will require intervention to address those threats for decades. These species, which have been termed conservation-reliant, pose a challenge to the ESA's mandate for recovery of self-sustaining populations. Most references to conservation-reliant species by federal agencies involve the restoration of population connectivity. However, the diverse threats to connectivity faced by different species have contrasting implications in the context of the ESA's mandate. For species facing long-term threats from invasive species or climate change, restoration of natural dispersal may not be technically feasible in the foreseeable future. For other species, restoration of natural dispersal is feasible, but carries economic and political cost. Federal agencies have used a broad definition of conservation reliance to justify delisting of species in the latter group even if they remain dependent on artificial translocation. Distinguishing the two groups better informs policy by distinguishing the technical challenges posed by novel ecological stressors from normative questions such as the price society is willing to pay to protect biodiversity, and the degree to which we should grow accustomed to direct human intervention in species' life cycles as a component of conservation in the Anthropocene Epoch.

Introduction

The US Endangered Species Act (ESA) is among the world's most far-reaching and influential biodiversity protection statutes (Taylor *et al.* 2005). Listing of species as threatened or endangered under the ESA is designed to trigger an array of federal regulatory provisions that protect both the species and its habitat. Congress intended that these legal tools would reduce threats and allow a species' status to improve "to the point at which the measures provided pursuant to this Act are no longer necessary" (16 U.S.C. §1532 [3]). The species would then be removed from the ESA's list of threatened and endangered species (delisted) and primary management responsibility returned to the states.

Many of the first species to be delisted, such as the peregrine falcon (*Falco peregrinus*) and brown pelican (*Pelecanus occidentalis*), fit this pattern. These species were primarily threatened by pesticide pollutants that could be comprehensively addressed by new federal regulations. In contrast, many currently listed species face ecologically complex threats that are less amenable to regulatory remedy (Doremus & Pagel 2001). For example, as human landuse fragments natural habitats, many species have experienced a reduction in population connectivity (Soulé & Terborgh 1999). Connectivity is important to recovery because it may enhance demographic and genetic flows that support persistence of peripheral populations and long-term maintenance of a species' evolutionary potential (Lowe & Allendorf 2010).

Recovery efforts often seek to restore connectivity between core habitat areas by means of habitat restoration or restrictions on overexploitation in areas used for dispersal. This approach, because it can result in long-term amelioration in threats, is analogous to the falcon and pelican examples in fitting within the delisting framework envisioned under the ESA. Alternately, translocation (capture, transport, and release of individuals) offers an option for avoiding the socioeconomic costs of restoring connectivity in the landscape matrix where wildlife must coexist with human landuses. Such a translocation-based strategy does not create self-sustaining populations but rather relies on long-term intensive management to counteract the effect of connectivity loss on species viability. Such intensive management is a common approach for species, while they are listed as endangered or threatened (USFWS 2003, 2010). The question of whether a species can be delisted, while still dependent on such intensive management has proved more controversial.

Recent reviews have posited that most listed taxa are “conservation-reliant species” (CRS) because “preventing delisted species from again being at risk of extinction may require continuing, species-specific management” into the future (Scott *et al.* 2005, see also Scott *et al.* 2010 and Goble *et al.* 2012). The U.S. Fish and Wildlife Service (FWS) has employed the concept of CRS to justify delisting of species that still require direct manipulation of their populations to maintain a biologically secure status. This issue has most often arisen in the context of population connectivity; four of the five references to CRS in recovery planning and delisting documents have invoked CRS to justify delisting species that still require artificial translocation to maintain connectivity (Supplementary Information S3).

The question of whether delisting such species is appropriate as a legal and policy matter has received little scrutiny. In aggregate, decisions on when to delist species have far-reaching implications for the ultimate status of biodiversity. Such decisions also touch on the broader issue of whether society should grow accustomed to direct human intervention in ecosystems and species’ life cycles as a necessary component of conservation in what has been termed the Anthropocene Epoch (Kareiva *et al.* 2012). The relevance of this broader question is not limited to the U.S. context. For example, Australia’s endangered species listing framework follows that of the International Union for Conservation of Nature (IUCN) in defining a “conservation dependent species” as one which is the focus of a species-specific conservation measures, the cessation of which would result in the species becoming vulnerable, endangered or critically endangered within a period of 5 years (IUCN 2013).

In this article, we first review the limited guidance provided by the ESA and subsequent case law on the question of what level of connectivity restoration is appropriate before a species is delisted. We then consider examples from a range of listed species to discover commonalities that can clarify key policy questions regarding connectivity restoration for endangered species.

The legal context of conservation reliance and connectivity

The language of the ESA and much subsequent agency practice emphasize an overarching goal of recovery of species and ecosystems in the wild (16 U.S.C. §1531 [a][3], see Supporting Information S1 for references to a goal of self-sustaining populations in recovery plans). In the 2009 case *Trout Unlimited v. Lohn* (559 F.3d 946, 9th Cir. 2009), the court cited both the ESA’s preamble and the act’s legislative history in concluding that “the ESA’s primary goal is to preserve the ability of natural populations to survive in the wild.” However, the relatively few court cases that have addressed this issue have not established clear precedent as to if and when exceptions can be made so that species can be delisted while still dependent on translocation. The most relevant case involves a 2007 U.S. FWS proposal to delist the Yellowstone grizzly bear (*Ursus arctos*), a carnivore with relatively limited dispersal range (Proctor *et al.* 2004; see Supporting Information S2 for additional information on species referenced in the text). FWS asserted that the Yellowstone grizzly bear is a conservation-reliant species because it requires active management (72 FR [Federal Register] 14987; see also Supporting Information S3 for a list of uses of “conservation-reliant species” in agency documents). FWS then relied on the CRS label to justify translocation of bears if efforts to reestablish natural connectivity between Yellowstone and more northerly bear populations were unsuccessful (72 FR 14896). The delisting rule was challenged in part over its potential future dependence on translocation. Although the rule was vacated on other grounds, the Montana District Court noted that “the concerns about long-term genetic diversity” (i.e., the need for translocation) did not warrant continued listing. It is unclear whether the court reached this conclusion because genetic concerns could be satisfactorily resolved by translocation following delisting, or simply because genetic concerns would not manifest within the “foreseeable future.” The Services’ (FWS and National Marine Fisheries Service) currently define the “foreseeable future” as extending as far into the future as predictions based on best available data can provide a reasonable degree of confidence (USDI 2009).

This definition, although not excluding consideration of long-term genetic threats, in practice allows wide latitude to the Services on whether to address such issues.

Unlike the grizzly bear, the gray wolf (*Canis lupus*) can disperse long distances (>800 km; Boyd *et al.* 1995). Although successful reintroductions in the mid-1990s led by 2005 to abundant wolf populations in the northern Rocky Mountains, delisting of the species was delayed in Wyoming, in part because the state's wolf management plan provided the species protection from overexploitation in only a small portion of the state. To ensure adequate dispersal between Yellowstone and other wolf populations, Wyoming subsequently agreed that wolves would receive more protection during peak dispersal season in limited areas. However, environmental groups sued to block the wolf delisting rule, in part because the state could resort to translocation if sufficient natural dispersal does not occur (77 FR 55530).

FWS referenced conservation reliance several times in rulemaking processes regarding wolves (Supplementary Information S3). Initially, the proposed delisting rule for wolves in the northern Rocky Mountains asserted that “[h]uman intervention in maintaining recovered populations is necessary for many conservation-reliant species and a well-accepted practice in dealing with population concerns (Scott *et al.* 2005)” (74 FR 15178, 76 FR 61816). In response to critical public comments, the FWS qualified and seemingly contradicted its earlier assertion by stating that the northern Rocky Mountain wolf population is “not expected to need or rely on human-assisted migration often, if ever, and these populations will not become “conservation-reliant” as defined by Scott *et al.* (2005, entire)” (77 FR 55565).

FWS's treatment of connectivity requirements in wolf populations contrasts with its consideration of connectivity for the wolverine (*Gulo gulo*), a carnivore species inhabiting the northern Rocky Mountains with dispersal abilities similar to the wolf (>500 km, Flagstad *et al.* 2004). In a recent draft proposal to list the wolverine as a threatened species, FWS found loss of natural connectivity a primary reason the species merited listing (78 FR 7886). Whereas for wolves, translocation was judged as consistent with delisted status, FWS found the need for such action warrants listing of wolverines as threatened.

The influence of ecological factors on a species' connectivity requirements

Ecological factors such as a species' mating system, magnitude of population fluctuations, and migratory behavior (Table 1) affect the level of connectivity required for re-

covery. The most commonly proposed rule of thumb for connectivity suggests that at least one genetically effective migrant (but in some cases >10 migrants; Vucetich & Waite 2000) per generation into a population is necessary to minimize loss of polymorphism and heterozygosity (Allendorf 1983; Table 1, column 1). If the species' mating system causes individuals to have widely varying reproductive contributions, many individual “census migrants” are required to ensure that one migrant is genetically effective (produces at least one offspring in the recipient population) (Table 1, column 2). For example, among gray wolves, only a single pair of dominant individuals typically breeds within each pack.

The magnitude of population fluctuations experienced by a population also affects the role of connectivity in ensuring persistence. Invertebrates, such as the Karner blue (*Lycaeides melissa samuelis*) and Fender's blue butterfly (*Icaricia icaroides fenderi*), typically have short generation times and highly variable population sizes (US-FWS 2003, 2010). This causes population connectivity in the form of demographic rescue (Brown & Kodric-Brown 1977) to be critical if the overall metapopulation is to persist in a dynamic natural environment (Table 1, column 3). Lastly, a species' migratory behavior may imply that a large proportion of population must successfully move between areas on an annual or generational basis (Table 1, column 4). For example, Pacific salmon from the Columbia River spend 3–4 years in the ocean, so up to a third of the adult cohort must return to the natal river each year.

We classified species (Table 1) by these three ecological factors and by whether connectivity restoration could be achieved by one-time measures (e.g., dam removal or operational changes) or necessitated continued intervention (e.g., invasive species control). Species affected by more than one factor (e.g., species with varying reproductive contributions inhabiting fluctuating environments) are categorized based on the factor imposing the highest connectivity requirements.

Lack of connectivity is an immediate demographic threat to migratory species such as Columbia River Pacific salmon. Recovery plans for species in this group (cell with horizontal line background; Table 1) propose translocation as necessary both before and after delisting, and do not include recovery actions that would restore natural migration. Although it is technically feasible to remove or mitigate barriers to migration such as hydroelectric dams, there are often enormous economic and legal impediments to doing so. Proposals to delist such species as dependent on translocation in perpetuity are in effect proposals to reconsider the ESA's normative assumption concerning the value society places on recovery of wild, self-sustaining populations.

Table 1 Categorization of species discussed in text in terms of degree of population connectivity (i.e., dispersal rate) required for recovery and socioeconomic cost required to restore connectivity. Species affected by more than one ecological factor are categorized based on the factor imposing the highest connectivity requirements

Type of intervention necessary to restore connectivity	Degree of connectivity required for recovery, due to life history or ecological factors			
	1. Lowest—One to several genetically effective migrants per generation	2. Low—Genetically effective migration where individuals have highly varying reproductive contribution	3. Medium—Demographic rescue due to variable population size	4. High—Migratory populations
One-time intervention (dam removal, habitat restoration, and regulatory remedy)	Grizzly bear Concho water snake	Gray wolf Red-cockaded woodpecker	Fender's blue butterfly Karner blue butterfly	Columbia river salmon
Continuing intervention (augmentation, translocation, control of invasive species)	Wolverine Many species due to climate change	Southern Idaho ground squirrel Greater sage grouse	Black-footed ferret	Peary caribou

A second group of species (cells with vertical line background; Table 1) may be nonmigratory, but nonetheless face long-term genetic threats from loss of connectivity. With the exception of reintroductions needed to restore extirpated populations, recovery plans for these species typically do not specify translocation prior to delisting but acknowledge that translocation may be necessary in the future if adequate genetic diversity is not present. Recovery plans may choose not to include recovery actions designed to reestablish natural dispersal because of significant societal opposition to the species' presence in dispersal zones (wolves and grizzly bears) or because of the economic costs of removing barriers to natural dispersal (Concho water snake [*Nerodia paucimaculata*]; USFWS 1993).

In the examples discussed above, connectivity restoration can be achieved via controversial or costly—but technically feasible—actions such as dam modification or removal, or via restrictions on overexploitation in habitat important for natural migration. For a final category of species (cells with gray background; Table 1), loss of historic levels of population connectivity is due to threats (e.g., invasive species, altered disturbance regimes, or climate change) that are extraordinarily challenging or impossible to fully remedy given current technical knowledge. For example, invasive species may operate synergistically with altered disturbance regimes to degrade an ecosystem to the point where restoration to the previous state may become difficult or impossible (Suding et al. 2004). In large portions of the western United States, sagebrush (*Artemisia* spp.) has been replaced by cheat

grass (*Bromus tectorum*), an exotic annual bunchgrass. This trend, in turn, may trigger a shift toward more frequent fires that inhibit sagebrush recovery and limit dispersal of sagebrush-associated species such as the southern Idaho ground squirrel (*Spermophilus brunneus endemicus*) and greater sage grouse (*Centrocercus urophasianus*) (Knick et al. 2003). Climate change is projected to cause contraction or shifts in suitable habitat for a large proportion of the world's species (Thomas et al. 2004). For example, wolverines are threatened by loss of natural connectivity as climate change causes loss of their habitat, which is associated with snow-covered areas (78 FR 7886).

Discussion

Based on a review of recovery plans for a range of species (Table 1 and Table S2), we conclude that three contrasting types of challenges confront efforts to restore connectivity between populations of listed species: 1) threats that society avoids addressing because of the socioeconomic costs of doing so, 2) threats that society avoids addressing because they are not immediate, and 3) threats for which there is no permanent resolution at any cost given current technical knowledge. Distinguishing species affected by these three classes of threats is important because it allows us to distinguish normative questions from the technical obstacles to maintaining a self-sufficient population of a species that arise from the ecological attributes of a species and its stressors. These normative questions include both economic elements (what price society is willing to pay to protect biodiversity and how future risks are

weighed against current costs), and ethical elements such as whether humans have an obligation to prevent species extinction (Callicott 2009).

As the Services attempt recovery of controversial and formerly widely distributed species such as gray wolves (Bruskotter *et al.* 2013), the agencies have gradually decreased their focus on recovering self-sustaining populations, a shift justified in some instances by reference to a broad definition of conservation-reliant species (74 FR 15178). This is consistent with reviews that found that most (Scott *et al.* 2010) or all (Goble *et al.* 2012) listed species fit the definition of conservation-reliant. Scott *et al.* (2010) classified most listed species as conservation-reliant in part because they included species requiring any of several types of ongoing conservation action, including efforts to 1) control other species, 2) control pollutants, 3) manage habitat, 4) control exploitation or human access, or 5) augment populations. However, these five types of actions have contrasting implications as to whether a species' status is self-sustaining in light of the ESA's mandate. The ESA anticipated that new regulations would be necessary to remedy threats such as overexploitation and pollutants, even for otherwise self-sustaining populations (Rohlf *et al.* in press). Similarly, because the continued persistence of almost all species requires regulatory limitations on human actions that destroy their habitat, the need for such protections should not preclude considering a population as self-sustaining. In contrast, a species that requires repeated population augmentation or intensive control of invasive competitor or predator species or disease does conflict with the paradigm of listing as a temporary stage followed by recovery of self-sustaining populations.

We agree with Scott *et al.* (2010) that conservation reliance is "a continuum encompassing different degrees of management," and acknowledge that some examples straddle the border between species that are or are not potentially self-sustaining in the wild. For example, although delisted populations of Karner blue and Fender's blue butterfly may not be dependent on translocation, they will require continued prescribed fire or fire surrogates to maintain suitable habitat. Because prescribed burning might not be necessary if conservation areas were sufficiently large to accommodate natural disturbance regimes (Pickett & Thompson 1978), such populations could become self-sustaining in the absence of humans. In most landscapes, however, disruption of natural disturbance processes can be remedied only by continued intervention to maintain fire-dependent ecosystems. Because prescribed fire is typically not a "species-specific" intervention (as specified in Scott *et al.* 2005's definition of CRS), but rather an ecosystem restoration tool, it is consistent with the ESA's mandate

for conserving the ecosystems upon which listed species depend.

When the Services interpret the ESA's mandate using a definition of conservation-reliant species that include most or all listed species, they presuppose that costly or politically difficult obstacles to a species' self-sufficiency need not be fully addressed to delist species if these species could be secure given continued intensive management. Removing self-sufficiency from the threshold for considering a species recovered has several undesirable consequences. If natural dispersal is achievable (e.g., for highly vagile species such as the gray wolf or wolverine), delisting of populations still dependent on translocation rather than natural dispersal lowers the likelihood that delisted populations will meet other common recovery standards such as resiliency, redundancy, and representation (Shaffer & Stein 2000). Populations that require intensive management actions such as translocation by definition have lower resilience than those that are self-sustaining without such measures (Redford *et al.* 2011). Conversely, broad-scale connectivity is likely to increase the resilience of species to climate change by increasing adaptive potential (Lowe & Allendorf 2010).

The ESA of 1973 went beyond previous versions of the act in extending legal protections to vertebrate species facing extinction in only a portion of their range (Carroll *et al.* 2010). This had the overall effect of raising the threshold for recovery away from the earlier focus on preserving relict populations toward a more ambitious goal of geographically widespread recovery of self-sustaining populations and the ecosystems on which species depend. Species that are well-distributed outside of core habitat (e.g., in dispersal corridors) are more likely to achieve the representation goals suggested by the ESA's protection for species imperiled in a "significant portion of [their] range" (Carroll *et al.* 2010).

We advocate use of a narrower and more explicit definition of conservation reliant species, which would be limited to those species that lack the ability to persist in the wild in the absence of direct and ongoing human manipulation of individuals or their environment (Rohlf *et al.* in press). This definition distinguishes those species which would persist and even thrive if humans were to vanish from the landscape (e.g., gray wolf) from those whose only hope of persistence lies in human intervention (e.g., black-footed ferret threatened by introduced plague).

The complex question of whether species permanently threatened by invasives, altered disturbance regimes, and climate change should be eventually delisted or remain under long-term federal management involves both normative and technical issues. Ultimately, resolution of the normative issues hinges on resolving contrasting

visions of the meaning of ecological recovery in the Anthropocene Epoch. A definition of conservation-reliant species that clearly distinguishes technical from values-based judgments will allow society to better address the normative debate over what cost should be borne to protect biodiversity, while separately addressing the urgent biological challenges that novel stressors such as climate change and invasive species pose for ecosystem and species restoration.

Supporting Information

Additional Supporting Information may be found in the online version of this article at the publisher's web site:

S1. Examples of references to the goal of self-sustaining populations in recovery planning documents.

S2. Table of attributes of species mentioned in text that provide examples of consideration of connectivity in recovery planning.

S3. Use of the term "conservation-reliant species" by the US Fish and Wildlife Service in recovery and delisting documents.

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