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***By Email and FedEx***

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Re: Notice of Violation of the Endangered Species Act: 2020 Gray Wolf Delisting Rule, 85 Fed. Reg. 69,778 (Nov. 3, 2020)

Greetings:

On behalf of Defenders of Wildlife, Center for Biological Diversity, Sierra Club, Oregon Wild, National Parks Conservation Association, and The Humane Society of the United States,<sup>1</sup> we write to provide you notice, pursuant to 16 U.S.C. § 1540(g), that the U.S. Fish and Wildlife Service's ("FWS") decision to remove gray wolves in the lower-48 states from the list of endangered species violates the Endangered Species Act ("ESA").

FWS issued the Final Wolf Delisting Rule on October 29, 2020, with publication in the Federal Register on November 3, 2020, under the title "Endangered and Threatened Wildlife and Plants; Removal of the Gray Wolf (*Canis lupus*) From the List of Endangered and Threatened Wildlife." 85 Fed. Reg. 69,778 (Nov. 3, 2020). The Delisting Rule will become effective 60 days following Federal Register publication on January 2, 2021. Unless FWS withdraws the Final Wolf Delisting Rule and remedies the ESA violations, at the end of 60-days' time, we will commence litigation to challenge and vacate the Rule.

Hunted, trapped, and poisoned with the approval of the predecessor of the FWS, by 1967 there were fewer than 1,000 gray wolves remaining in one small part of northeastern Minnesota with an isolated population on Isle Royale National Park in Lake Superior. FWS protected gray wolves, *Canis lupus*, throughout the United States under the ESA in 1978 as two groups, a

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<sup>1</sup> We have attached a list of these organizations' business addresses to the end of this letter.

threatened population in Minnesota and an endangered population in the rest of the lower-48 states. Final Wolf Delisting Rule, 85 Fed. Reg. at 69,780, Table 1. Today, there are recovering wolf populations in Minnesota, Wisconsin, Michigan, and the Northern Rocky Mountains; wolves have begun to inhabit the Pacific Northwest and California; and wolf habitat remains explored but largely unclaimed in states like the Dakotas, Maine, Colorado, and Utah. Slowly, with the ESA's protections, nationwide wolf recovery is moving forward.

Yet for more than a decade, FWS has proposed increasingly more tenuous delisting rules that federal courts have consistently rejected as invalid. In this series of prior delisting rules, FWS sought to remove ESA protections from gray wolves by splitting the population into small segments in order to declare each of those smaller segments recovered. Every time, federal courts struck down FWS wolf delisting rules for not only ignoring the vast amount of available wolf habitat still largely unoccupied, but also for purposefully leaving out "remnant" populations outside of the delisting area. *See* Final Wolf Delisting Rule, 85 Fed. Reg. at 69,780-81, Table 1—Key Federal Regulatory Actions under the Act and Predecessor Legislation pertaining to Gray Wolf and, Where Applicable, Outcomes of Court Challenges to these Actions.

Undaunted by this history of repeated unlawful actions, FWS has now finalized a nationwide delisting rule, once again eliminating all federal protections for these wolves. FWS justifies delisting by combining populations, ignoring available historical wolf habitat, and discarding relatively new wolf populations outside the Midwest as "colonizers" unnecessary to the survival and recovery of wolves in the Midwest.

Gray wolves still meet the ESA's definition of an endangered species, one that is "in danger of extinction throughout all or a significant portion of its range." 16 U.S.C. § 1532(6). FWS's Final Wolf Delisting Rule does not satisfy the ESA requirements that FWS may only delist species that are fully recovered and protected by adequate regulatory mechanisms, as well as the Administrative Procedure Act ("APA") requirement that agency decisions must show a rational connection between the facts found and the choices made. Specifically, in delisting gray wolves nationwide, FWS

- ignored the ESA's requirement that any delisting decision concerning wolves listed in the lower-48 states must consider the entire population, not merely wolves in the Midwest;
- failed to provide for a sustainable wolf population after delisting;
- failed to analyze and address the importance of lost historical habitat;
- did not rationally assess the status of gray wolves within significant portions of their current range;
- failed to use the best available science; and
- invalidly measured recovery using an out-of-date and geographically restricted recovery plan.

I. FWS FAILED TO EVALUATE THE DELISTING FACTORS FOR THE ENTIRE LOWER-48 GRAY WOLF POPULATION.

The ESA seeks to protect and recover imperiled species and populations by listing them as threatened or endangered based on enumerated statutory factors, 16 U.S.C. § 1533(a)(1)(A)-(E), using the “best scientific and commercial data available. 16 U.S.C. § 1533(b). The listing provisions are contained in section 4 of the ESA—the section Congress labeled the “cornerstone of effective implementation” of the Act. S. Rep. No. 97-418, at 10 (1982).

The ESA requires FWS to analyze the five listing/delisting factors of section 4(a), 16 U.S.C. § 1533(a)(1), as they apply to the protected entities. These factors are:

- (A) the present or threatened destruction, modification, or curtailment of its habitat or range;
- (B) overutilization for commercial, recreational, scientific, or educational purposes;
- (C) disease or predation;
- (D) the inadequacy of existing regulatory mechanisms; or
- (E) other natural or manmade factors affecting its continued existence.

FWS must use the best available science in its analysis. 16 U.S.C. § 1533(a)(1), (b)(1)(A).

On the basis of these factors, for delisting, FWS must determine whether a species has recovered and no longer meets the listing factors. The delisting evaluation must focus on the relevant species that was originally listed. Here, the relevant “species” are the Minnesota and lower-48 states’ wolf populations. *See* 43 Fed. Reg. 9607 (March 9, 1978) (listing wolves in Minnesota as threatened and wolves in the lower-48 U.S. states and Mexico as endangered).

Yet in the Final Wolf Delisting Rule, FWS’s analysis of the section 4(a) listing/delisting factors focused nearly exclusively on the wolf population in Minnesota, Michigan, and Wisconsin. FWS analyzed some of the factors for wolves in Washington, Oregon, and California, but only to determine how those populations affected wolves in the Midwest. FWS provided no section 4(a) analysis for significant portions of the wolf’s range, such as the Northeast or the southern Rocky Mountains. The ESA prohibits limiting analysis of the section 4(a) factors to only a portion of the listed entity. “The Endangered Species Act’s text requires the Service, when reviewing and redetermining the status of a species, to look at the whole picture of the listed species, not just a segment of it.” *Humane Soc’y v. Zinke*, 865 F.3d 585, 601 (D.C. Cir. 2017) (rejecting FWS attempt to designate and delist a gray wolf Western Great Lakes DPS).

The appellate court in *Humane Society* was particularly concerned about the fate of a “remnant” population—such as the wolves in the Pacific Northwest, a portion of a listed entity left out of importance through redefinition or delisting. Without assurances that the remnant population would remain a protectable species, FWS could later attempt to delist those wolves on the theory that they no longer comprise a listable entity. 865 F.3d at 601-03. This outcome

would violate the ESA. *Id.* (FWS’s “disregard of the remnant’s status would turn ... [the DPS] process into a backdoor route to the *de facto* delisting of already listed species, in open defiance of the Endangered Species Act’s specifically enumerated requirements for delisting”). To guard against that result, the D.C. Circuit held that FWS “must make it part and parcel of its segment analysis to ensure that the remnant, if still endangered or threatened, remains protectable under the Endangered Species Act.” *Id.* at 602. That is precisely what FWS has failed to do here.

FWS has tried this before, with the 2003 rule that attempted to create three new wolf DPSs and downlist two of them. *See Defenders of Wildlife v. Norton*, 354 F. Supp. 2d 1156, 1170-72 (D. Or. 2005) and *Nat’l Wildlife Fed’n v. Norton*, 386 F. Supp. 2d 553, 564-65 (D. Vt. 2005). The courts invalidated FWS’s attempt because it only assessed the status of core population portions of the new DPSs and did not apply the statutory listing factors outside of those areas. *Defenders of Wildlife*, 354 F. Supp. 2d at 1172 (“The Final Rule is arbitrary and capricious because FWS downlisted major geographic areas without assessing the threats to the wolf by applying the statutorily mandated listing factors.”); *Nat’l Wildlife Fed’n*, 386 F. Supp. 2d at 565 (“The FWS simply cannot downlist or delist an area that it previously determined warrants an endangered listing because it ‘lumps together’ a core population with low to non-existent populations outside of the core area.”).

Here, instead of carving out a DPS from the larger entity to delist (as in 2011) or dividing the larger entity into multiple DPSs to downgrade or delist (as in 2003), FWS has delisted a combined entity. But, as before, FWS failed to assess the currently listed entities, separately or combined, under the statutory listing factors and instead relied on the status of core populations (in the Midwest) to justify delisting a much larger area. Large swaths of the lower-48 gray wolf population will lose ESA protections even though FWS failed to assess the status of those wolves under the statutory listing factors. FWS’s approach violated the plain language of the ESA and contradicted the reasoning behind the decisions in *Humane Society*, *Defenders of Wildlife*, and *National Wildlife Federation*.

In fact, FWS considered these combined populations together and delisted “the gray wolf entity” in part because “neither of the listed entities [Minnesota or the lower-48 population] is a DPS.” 85 Fed. Reg. at 69,784. But regardless of whether the Minnesota and Lower-48 listings would be lawful under the subsequently enacted DPS Policy, it is not a lawful solution to create yet another violation of the Endangered Species Act. FWS cannot validly consider a new ‘combined’ population for delisting; the analysis must be of “species included in a list.” 16 U.S.C. § 1533(c)(2).

## II. FWS’S DELISTING RULE DOES NOT PROVIDE FOR A SUSTAINABLE WOLF POPULATION AFTER DELISTING.

Under the ESA, FWS must determine whether the lower-48 gray wolf entity remains endangered or threatened because of any of five factors, including “the inadequacy of existing regulatory mechanisms.” 16 U.S.C. § 1533(a)(1)(D). If delisting is finalized, each individual

state would handle wolf management. While some states have welcomed wolves, some are hostile to wolf recovery, some favor trophy hunting over sustainable populations, and some have no plans at all. In Minnesota, without federal protection, landowners within approximately 60 percent of the state could kill wolves to protect livestock or pets even when there is no immediate threat. State management of wolves following delisting does not have a pretty history; in Montana and Idaho – where Congress ordered wolf delisting over scientific and legal objection – state wildlife agencies are managing wolves to drive down the population numbers and put wolf hunting ahead of other concerns.

FWS’s review of state wolf management plans in Washington, Oregon, and California is inadequate. *See* 85 Fed. Reg. at 69,835-37. California only recently adopted its wolf management plan, and its effectiveness is uncertain. All three West Coast states opposed federal delisting.<sup>2</sup> Oregon recently adopted a new wolf management plan, and Oregon has already removed gray wolves from its state endangered species list without sufficient scientific justification as well as legislatively blocked judicial review of this decision. Washington’s state wolf management plan has been controversial, has led to multiple years of state lethal control actions, and may not be robust enough to ensure permanent recovery. Following delisting, Washington will need to promulgate rules, for the first time, to govern wolf management. Other states, such as Wisconsin, have indicated that they intend to manage gray wolves to the minimum population level needed to prevent them from again warranting ESA protections, which is not the path to nationwide recovery.

Only eight states protect wolves as a state endangered or threatened species.<sup>3</sup> The majority of states within the lower 48 have no protections in place for gray wolves;<sup>4</sup> several of these states lack any plans or protections for wolves, even though wolves have dispersed into those states, including Indiana, Kentucky, Massachusetts, Maine, Missouri, Ohio, Utah and Vermont. *See* 78 Fed. Reg. at 35,675 (noting in the 2013 proposed nationwide delisting that wolves have been seen in Missouri and Indiana but no regulatory mechanisms relating to wolves exist in those states). Other states seek to actively prevent recovery of the species. For example, Utah requires state wildlife officials to capture and kill any wolf that comes into the state to prevent the establishment of a viable wolf pack. Utah Code § 23-29-201. South Dakota in 2013 passed legislation designating wolves in the eastern half of the state as “varmints” that can be

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<sup>2</sup> As did Minnesota and Michigan.

<sup>3</sup> California, Colorado, Illinois, Nebraska, New Hampshire, New York, Texas, Virginia, and Washington. In Colorado, although results are not yet official, voters appear to have passed a ballot initiative to require the Colorado Parks and Wildlife Commission to create and implement a plan to reintroduce gray wolves into Colorado west of the Continental Divide by December 2023. 85 Fed. Reg. at 69,837.

<sup>4</sup> Alabama, Arkansas, Arizona (portion outside of Mexican wolf range), Connecticut, Delaware, Florida, Georgia, Indiana, Kentucky, Louisiana, Massachusetts, Maryland, Maine, Missouri, Mississippi, North Carolina, New Jersey, Ohio, Oklahoma, Pennsylvania, Rhode Island, South Carolina, Tennessee, Utah, Vermont, and West Virginia.

shot on sight. S.D. Codified Laws § 41-1-1. Other states with wolves within their borders have classified wolves as furbearers or game animals and would likely allow regulated hunting and trapping and livestock predation control upon removal of federal protections, including Iowa, Kansas, Michigan, Minnesota, Nevada, North Dakota, Oregon, South Dakota, Washington, and Wisconsin. Several of these states have committed to managing wolves for an aggressive population decline following delisting, on the basis of inadequate and out-of-date management plans that do not reflect the best available science regarding the super-additive effects of hunting mortality on wolf populations or the population sizes necessary to maintain wolves' genetic viability over the short and long term. Such management measures constitute inadequate regulatory mechanisms that continue to threaten wolves.

### III. FWS FAILED TO ANALYZE THE IMPORTANCE OF LOST HISTORICAL RANGE FOR THE LISTED LOWER-48 WOLVES.

FWS's delisting rule is also flawed in its treatment of historical range. The ESA defines endangered and threatened species as "any species which is in danger of extinction or is likely to become an endangered species within the foreseeable future throughout all or a significant portion of its range..." 16 U.S.C. § 1532(6), (20) (emphasis added). The ESA does not define the phrase "significant portion of its range"; nor does it define the words "significant" or "range" as they are used in that phrase. In *Defenders of Wildlife v. Norton*, 258 F.3d 1136, 1145 (9th Cir. 2001), the Ninth Circuit held that "a species can be extinct 'throughout ... a significant portion of its range' if there are major geographical areas in which it is no longer viable but once was." (emphasis added). In *Tucson Herpetological Soc'y v. Salazar*, 566 F.3d 870, 876-77 (9th Cir. 2009), the court held that while the criteria for "significance" was undefined, FWS must "develop some rational explanation for why the lost and threatened portions of a species' range are insignificant before deciding not to designate the species for protection." *See also id.* at 878 (upholding FWS's flat-tailed horned lizard's lost historical range analysis).

This interpretation of "range" to include historical range came before the adoption of FWS's final policy on the interpretation of this phrase ("SPR Policy"), 79 Fed. Reg. 37,578 (July 1, 2014). Since adoption of the SPR Policy, two appellate courts upheld FWS's SPR Policy interpretation of "range" to mean "current range." *See Humane Soc'y v. Zinke*, 865 F.3d 585 (D.C. Cir. 2017) and *Center for Biological Diversity v. Zinke*, 900 F.3d 1053 (9th Cir. 2018). Both courts, however, stressed that the ESA required FWS to consider lost historical range:

The SPR policy still requires that FWS consider the historical range of a species in evaluating other aspects of the agency's listing decision, including habitat degradation. The SPR policy recognizes that loss of historical range can lead to reduced abundance, inhibited gene flow, and increased susceptibility to extinction.

*CBD v. Zinke*, 900 F.3d at 1067 (citations omitted). The D.C. Circuit was even clearer that FWS must account for lost historical range in its listing and delisting decisions, in particular because FWS's SPR Policy interprets range as current range only:

We hold that [FWS's] analysis of the status of the Western Great Lakes segment [of gray wolves] within its current range wrongly omitted all consideration of lost historical range. Just because the Endangered Species Act does not compel the Service to interpret "range" to mean historical range, that does not mean that the Service can brush off a substantial loss of historical range as irrelevant to the species' endangered or threatened status.

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[A]n adequate evaluation of the threats confronting the survival of a species within its current range requires looking at more than just the current moment in time. The Service, consistent with its own Range Policy, also needs to consider the scope of the species' historical range, and the impact that material contraction or relocation might indicate for survival within a currently constricted or confined range.

*Humane Soc'y v. Zinke*, 865 F.3d at 605-06 (vacating FWS rule designating gray wolves in eight Midwestern states as the Western Great DPS and delisting that newly designated DPS).

The facts before FWS with respect to gray wolf historical habitat have not changed since the *Humane Soc'y* ruling: "[G]ray wolves have been extirpated from most of the southern portions of their historical North American range," with undisputed estimates that "95% of the gray wolf's historical range has disappeared." *Id.* at 606. And as before, FWS has failed to analyze the impact of that loss of historical range on the survival of the gray wolves as a whole or in various segments. FWS's delisting rule discussed historical range and abundance of gray wolves (85 Fed. Reg. at 69,786 and Figure. 2) and contained a section entitled historical context (85 Fed. Reg. at 69,792). Yet FWS actively omitted lost historical range in its actual delisting analysis. *Id.* at 69,853 ("In other words, we interpret 'range' in these definitions to be current range, i.e., range at the time of our analysis."). This omission is particularly problematic with respect to areas in the Northeast as there is no analysis at all of how that lost range affects the viability of wolf populations in other areas.

#### IV. FWS DID NOT RATIONALLY ASSESS THE STATUS OF GRAY WOLVES WITHIN SIGNIFICANT PORTIONS OF THEIR CURRENT RANGE.

While failing to consider the impact to gray wolves of their lost historical range, FWS also arbitrarily failed to assess the gray wolf's status within "significant portion[s] of its range," 16 U.S.C. § 1532(6), which FWS defines as current range.

A. Current Range Cannot Be Limited to Identified Wolf Populations.

FWS dismissed threats to wolves in significant portions of their range by improperly constricting its definition of “current range.” FWS has acknowledged documented wolves in Vermont, Massachusetts, New York, Indiana, Illinois, Iowa, Missouri, North Dakota, South Dakota, Nebraska, Kansas, Colorado, Utah, Arizona, and Nevada over the last twenty years. 85 Fed. Reg. at 69,789. Independent reviews have documented wolves in many more states. See Petition to Maintain Protections for Gray Wolves (*Canis lupus*) in the Lower 48 States as Endangered or Threatened “Distinct Population Segments” Under the Endangered Species Act at 30 (December 17, 2018), [https://www.biologicaldiversity.org/campaigns/gray\\_wolves/pdfs/Wolf-Petition-12-17-2018.pdf](https://www.biologicaldiversity.org/campaigns/gray_wolves/pdfs/Wolf-Petition-12-17-2018.pdf).<sup>5</sup> FWS, however, did not consider these areas to be part of the gray wolf’s current range because they exist outside of established wolf packs or breeding pairs in the Midwest and Pacific Northwest. 85 Fed. Reg. at 69,789 (“In sum, gray wolves in the lower 48 United States today exist primarily as two large metapopulations: one spread across northern Minnesota, Michigan, and Wisconsin, and the other consisting of the recovered and delisted NRM DPS wolf population that is biologically connected to a small number of colonizing wolves in western Washington, western Oregon, northern California, and, most likely, Colorado.”).

The Service has failed to offer a rational explanation for why the gray wolf’s current range should exclude other areas where wolves recently have been documented and could repopulate with continued protections under the ESA. Limiting current range in such a way is not consistent with the FWS’s own policy that defines range to encompass the “general geographical area within which the species is currently found, including those areas used throughout all or part of the species’ life cycle, even if not used on a regular basis.” SPR Policy, 79 Fed. Reg at 37583 (emphasis added).

B. The Delisting Rule Lacks Adequate (or Any) Discussion of Suitable Wolf Habitat in the Southern Rockies and the Northeast.

Although earlier delisting attempts more thoroughly surveyed suitable wolf habitat in Colorado, Utah, and the northeast United States, the delisting rule is virtually silent on wolves and wolf habitat in these areas. The lack of established wolf packs in Colorado, Utah, and New Mexico is instead used as an excuse to avoid consideration of suitable wolf habitat there, a formulation that turns ESA decisions upside-down. Prior habitat modeling has suggested that Colorado alone could support a population of over 1,000 wolves (Carroll et al. 2006), yet the delisting rule only notes that individual wolves have been confirmed in Colorado and other states.

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<sup>5</sup> In the Delisting Rule, FWS also denied this Petition without rational justification, summarily and unjustifiably finding that the petition did not present substantial scientific or commercial information indicating that the petitioned actions were warranted. 85 Fed. Reg. at 69,778, 69,878-79.

The delisting rule also ignores northeast wolves and suitable wolf habitat in the northeast entirely, contrary to the 2013 proposed wolf delisting rule and other prior wolf planning documents. FWS defended this analysis gap by again asserting that any wolf populations outside the Great Lakes region are unnecessary for gray wolf recovery.

C. Wolves in the Lower-48 Remain Imperiled Throughout a Significant Portion of their Range.

In addition to misapplying the term “range” to exclude occupied portions of the gray wolf’s current range, FWS arbitrarily assessed whether portions of the gray wolf’s range are “significant.” 16 U.S.C. § 1532(6). In the delisting rule, FWS repeated its circular definition of significant that had already been rejected by courts. *See Desert Survivors v. U.S. Dep’t of Interior*, 321 F. Supp. 3d 1011 (N.D. Cal. 2018); *see also Center for Biological Diversity v. Jewell*, 248 F. Supp. 3d 946 (D. Ariz. 2017). Under FWS’s SPR Policy, listing a species based on threats in a significant portion of its range would be considered warranted only if three conditions were satisfied: (1) the species was neither endangered nor threatened throughout all of its range, (2) the portion’s contribution to the viability of the species was so important that, without the members in that portion, the species would be endangered or threatened throughout all of its range, and (3) the species was endangered or threatened in that portion of its range. *See* 79 Fed. Reg. at 37,582-83. The courts rejected FWS’s position as “illusory,” because “if a portion of a species’ range is so vital that its loss would render the entire species endangered or threatened, and the species is endangered or threatened in that portion, then the entire species is necessarily endangered or threatened. Threats that render a species endangered or threatened in such a vital portion of its range should necessarily be imputed to the species overall.” *Center for Biological Diversity v. Jewell*, 248 F. Supp. 3d at 956 (emphasis added). The district court in *Desert Survivors* vacated the “significant portion” part of the SPR Policy nationwide. *Desert Survivors*, 336 F. Supp. 3d 1131, 1134-37 (N.D. Cal. 2018). While the Proposed Delisting Rule acknowledged the nationwide injunction against applying the SPR significance definition, 84 Fed. Reg. at 9684, the Final Delisting Rule does not mention the nationwide injunction at all.<sup>6</sup>

FWS asserted that for the delisting rule, it would ask “whether any portions of the range may be biologically meaningful in terms of resiliency, redundancy, or representation of the entity being evaluated.” 85 Fed. Reg. at 69,878. And yet, FWS then turned to precisely the disallowed standard from *Desert Survivors*, asserting that, for each of the combinations of wolf populations considered “these portions are not “‘significant’ under any reasonable definition of that term because they are not biologically meaningful to the [listed] entity in terms of its resiliency, redundancy, or representation.” *Id.* at 69,882, 69,885, 69,888, 69,889, 69,892, 69,893.

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<sup>6</sup> Because FWS relied on the SPR Policy, 79 Fed. Reg. 37,578 (July 1, 2014), to justify in part its Delisting Rule, Defenders of Wildlife *et al.* will also challenge that policy, and the SPR significance definition as applied here because the SPR policy is unlawful on the same basis as found in *Desert Survivors*.

Whatever the appropriate definition of significant portion of range may be, it cannot be the same illusory definition rejected by the federal courts.

FWS relied on the metric of representation, redundancy, and resiliency (the “3Rs”) to assess whether an area is significant, focusing on how the current population in a particular portion contributes to the 3Rs. But FWS’s use of the 3Rs metric was unreasonable and contrary to the conservation purpose of the ESA because it bars any area that lacked a recovered population from being considered a “significant” portion.

For example, FWS dismissed wolves on the west coast because only a small number of animals currently live there. Yet this position means that a species would never need to be recovered in any portion of its historical range because a tiny population could never meaningfully contribute to the 3Rs. FWS’s interpretation eviscerates the ESA’s conservation purpose. 16 U.S.C. §1531(b).

FWS also denigrates Pacific wolves as “colonizing wolves” from the Northern Rocky Mountains whose presence is unnecessary for wolf recovery. “In sum, gray wolves in the lower 48 United States today exist primarily as two large metapopulations: One spread across northern Minnesota, Michigan, and Wisconsin, and the other consisting of the recovered and delisted NRM DPS wolf population that is biologically connected to a small number of colonizing wolves in western Washington, western Oregon, northern California.” 85 Fed. Reg. at 69,789; *id.* at 69,894 (these wolves “are part of the recovered and delisted population of gray wolves in the NRM DPS.”).

Yet when the Northern Rocky Mountain DPS was carved from the lower-48 listing, FWS found that it was discrete from any wolves that could repopulate the west coast states due to the stretches of unsuitable habitat between them. 73 Fed. Reg. 10,518, 10,519 (Feb. 27, 2008). FWS’s new position (that the coastal wolves are not discrete from the Northern Rocky Mountain DPS) raises red flags, as a prime example of the disappearing remnant population that the *Humane Society* court cautioned against—carving a DPS out of a larger listing only to turn around and declare that the remnant is no longer a valid DPS and therefore unlistable. *Humane Soc’y*, 865 F.3d at 603 (“The Service cannot circumvent the Endangered Species Act’s explicit delisting standards by riving an existing listing into a recovered sub-group and a leftover group that becomes an orphan to the law.”).

Finally, FWS determined that there are no significant portions of the gray wolf’s range because the single gray wolf population that resides in the three Western Great Lakes states—Minnesota, Michigan and Wisconsin—is neither threatened nor endangered. This analysis flies in the face of years of court decisions. In litigation challenging a rule very similar to the proposed delisting Rule here, two federal courts invalidated FWS’s decision to downlist gray wolves in large portions of the species’ range where it had not recovered based on the viability of two core populations. *See Defenders of Wildlife v. Norton*, 354 F. Supp. 2d 1156, 1168 (D. Or. 2005) (“The Secretary’s conclusion that the viability of two core populations in the Eastern and

Western DPSs makes all other portions of the wolf's historical or current range insignificant and unworthy of stringent protection is contrary to Ninth Circuit precedent and the ESA.”) and *Nat'l Wildlife Fed'n v. Norton*, 386 F. Supp. 2d 553, 565 (D. Vt. 2005) (“The FWS simply cannot downlist or delist an area that it previously determined warrants an endangered listing because it ‘lumps together’ a core population with a low to non-existent population outside of the core area.”).

#### V. THE DELISTING RULE FAILS TO USE THE BEST AVAILABLE SCIENCE.

Under the ESA, FWS is required to make listing and delisting determinations “solely on the basis of the best scientific and commercial data available[.]” 16 U.S.C. §1533(b)(1)(A). In issuing the Gray Wolf Delisting Rule, FWS violated this requirement, disregarding science and otherwise acting arbitrarily. While FWS offered responses to the peer review critiques in the Final Delisting Rule, *see* 85 Fed. Reg. at 69,844-56 (Comment 1-46), the responses did not change FWS's decision to delist nor its reasoning in support of delisting.<sup>7</sup>

The independent peer reviewers chosen by FWS expressed serious concerns about the proposed delisting rule and its failure to use the best available science. Summary Report of Independent Peer Reviews for the U.S. Fish and Wildlife Service Gray Wolf Delisting Review (May 2019). All five reviewers identified unclear or missing information in the Draft Biological Report and Proposed Delisting Rule, particularly with the Service's “inadequate treatment of the [distinct population segment] structure of gray wolves in the lower 48 states.” Summary Report, App. C, Reviewer 1 – Dr. Fred W. Allendorf at 3.

Dr. Carlos Carroll criticized the proposed delisting rule for its failure to “build on the assembled scientific information [in the biological report] to provide coherent factual support or logical explanation for the agency's conclusions.” Summary Report, App. C, Reviewer 2 – Dr. Charles (Carlos) Carroll at 5. Dr. Carroll questioned the proposed rule's “lack of detail and rigor in the treatment of genetic issues,” *id.* at 6, as an “extreme oversimplification of the genetic structure of wolf metapopulations at regional and continental extents,” *id.* at 7. This concern was echoed by multiple public commenters, who noted that the best available science showed that genetic health remained a threat to wolves across the listed entity and criticized FWS's failure to adequately consider the minimum viable population and effective population sizes necessary to ensure long-term genetic viability. Dr. Carroll also highlighted how the proposed rule's central tenet – that the loss of all gray wolf populations outside the Great Lakes region in Minnesota and Wisconsin would not threaten the listed entity – depends on a truncated view of the ecological concept of range and the specifics of range dynamics. *Id.* at 8-9, 16. Neither does the proposed

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<sup>7</sup> The Final Delisting Rule also failed to consider a recent article published in BioScience authored by Dr. Carroll and others entitled “Wolf Delisting Challenges Demonstrate Need for an Improved Framework for Conserving Intraspecific Variation under the Endangered Species Act,” available at <https://academic.oup.com/bioscience/advance-article/doi/10.1093/biosci/biaa125/5941853> and attached to this letter.

rule use the ecological concepts of resiliency, redundancy, and representation correctly. *Id.* at 11-12.

Another area of deep concern from the independent scientists centered on the almost complete omission of information on suitable habitat in regions such as Utah, Colorado, and the northeast U.S. *See* Carroll at 18-22; Treves at 6. As Dr. Carroll noted, “in 2008, the FWS embarked on an effort to develop a National Wolf Strategy through the use of a ‘Structured Decision Making’ (SDM) process designed to develop a comprehensive strategy for gray wolf conservation by identifying appropriate wolf listing units within the broader continental distribution of the species as a whole.” Although the process was flawed, “this process at least provided a comprehensive analysis of what recovery efforts would be appropriate in the different regions which still held suitable habitat for the species. ... This current proposed rule, in contrast, omits substantive treatment of two regions which were previously considered to merit consideration because they hold substantial suitable habitat: the Colorado/Utah assessment unit and the area of the northeast US proposed in the SDM process to be occupied by the eastern wolf (putative *C. lycaon*).” *Id.* at 14.

Dr. Adrian Treves found that “the proposed rule does not address human-caused mortality or habitat suitability adequately,” Summary Report, App. C, Reviewer 4 – Dr. Adrian Treves at 1, 9-21, and that the “conclusions drawn about current range, vacant habitats, and northeastern USA gray wolves were not well substantiated. My scientific judgment is that the gray wolf entity’s current range is not defined well by scientific standards.” *Id.* at 4; *see also id.* at 5-9 (“The scientific basis of the gray wolf entity and its range seems questionable on scientific grounds because I found neither consistent terminology for subpopulations of current wolves, nor consistent handling of data on dispersal, discreteness, range, or status across the entity.”).

Dr. MacNulty disagreed with the proposed rule’s determination that western listed wolves were not discrete from eastern wolves. “I found no scientific information in the Proposed Rule or Draft Biological Report supportive of the Service’s interpretation that western listed wolves are not discrete from wolves in Minnesota, Wisconsin, and Michigan. Rather, the Proposed Rule and the Draft Biological Report supply scientific information that supports the opposite interpretation: that western listed wolves are discrete from wolves in Minnesota, Wisconsin, and Michigan.” Summary Report, App. C, Reviewer 5 – Dr. Daniel R. MacNulty at 5.<sup>8</sup> Dr. MacNulty also questioned the Service’s treatment of “current range” in contrast with “current distribution,” *id.* at 6-8, and critiqued as incomplete the Service’s review and analysis of human-caused mortality, *id.* at 9.

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<sup>8</sup> The Final Delisting Rule attempted to address this concern by noting that “[t]he intent was not to imply that all of those wolves were meaningfully connected as part of a single metapopulation; we agree that there are no data to show effective dispersal between those two larger areas.” 85 Fed. Reg. at 69,867-68.

The Final Rule explains that “Minnesota appears to be the western edge of a hybrid zone between gray wolves in the west and eastern wolves.” 85 Fed. Reg. at 69,787. Two of the peer reviewers raised similar concerns about the uncertain taxonomic status of gray wolves and eastern wolves. Summary Report, App. C, Reviewer 3 – Dr. Adrian P. Wydeven at 9; Summary Report, App. C, Reviewer 5 – Dr. Daniel R. MacNulty at 5. Despite this uncertainty, FWS concludes that “any eastern wolves within the geographic boundaries of the entities we evaluated [are] members of the species *C. lupus*.” 85 Fed. Reg. at 69,786. Dr. Wydeven criticizes that approach as “arbitrary.” Wydeven at 9.

It is important to remember that FWS’s 2013 delisting proposal was derailed because the agency failed to use the best available science with respect to species and sub-species wolf classifications in North America. As the independent peer reviews show, the genetics of the different wolf populations remain uncertain. Summary Report, App. C, Reviewer 3 – Adrian P. Wydeven at 1-2 (discussing eastern and gray wolf confusion); Summary Report, App. C, Reviewer 2 – Dr. Charles (Carlos) Carroll at 17-18 (discussing potential genetic uniqueness of west coast wolves). FWS has again failed to ensure that its proposed rule uses the best available science, as required by the ESA, 16 U.S.C. § 1533(b)(1)(A).

#### VI. FWS CANNOT VALIDLY MEASURE RECOVERY USING THE OUT-OF-DATE AND GEOGRAPHICALLY LIMITED 1992 RECOVERY PLAN.

The delisting rule mouths the language of recovery but looks only to a decades-old plan focused solely on the Midwest for its recovery standards. When FWS protected the gray wolf as a single species across the lower-48 states, it did not develop a nationwide recovery plan. Instead, for most of the lower-48 states (with the exception of the Northern Rocky Mountains gray wolf and Southwest Mexican wolf populations), FWS evaluated recovery efforts under its Western Great Lakes Recovery Plan, revised and renamed in 1992 as the Eastern Timber Wolf recovery plan. This limited and outdated recovery plan remains the planning document used by FWS to this day, despite pleas, petitions, and at least one lawsuit asking the agency to update it.

Reliance on such an outdated and geographically-restricted plan prevented FWS from facilitating nationwide wolf recovery, including in places such as the Pacific Northwest and the Northeast. Further, such a plan cannot provide “objective and measurable criteria” to support delisting outside of the plan’s geographic scope. 16 U.S.C. § 1533(f)(1)(B)(i)-(iii). Not only does the failure to develop a nationwide wolf recovery plan violate FWS’s duty under ESA § 4(f), but basing the delisting rule on the Eastern Timber Wolf Recovery Plan violates FWS’s duty to use the best available science in a delisting decision.

#### VII. CONCLUSION

FWS’s issuance of the Final Gray Wolf Delisting Rule violates the law and fails to use the best science. If FWS fails to withdraw the Rule within 60 days of receiving this letter, the

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named organizations intend to file legal claims for declaratory and injunctive relief. *See* 16 U.S.C. § 1540(g).

If you believe any of the foregoing is in error, have any questions, or would like to discuss this matter, please do not hesitate to contact us.

Sincerely,

A handwritten signature in blue ink that reads "Kristen L. Boyles". The signature is written in a cursive style.

Kristen L. Boyles  
Timothy J. Preso

*Attorneys for Defenders of Wildlife, Center for  
Biological Diversity, Sierra Club, Oregon Wild,  
National Parks Conservation Association, and The  
Humane Society of the United States*

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Business Addresses for Named Organizations:

**Defenders of Wildlife**

1130 17th Street NW  
Washington, D.C. 20036  
1-800-385-9712

**Center for Biological Diversity**

1212 Broadway Street, #800  
Oakland, CA 94612  
510-844-7100

**Sierra Club**

2101 Webster Street  
Suite 1300  
Oakland, CA 94612  
415-977-5500

**Oregon Wild**

5825 N. Greeley Ave.  
Portland, OR 97217  
503-283-6343

**National Parks Conservation Association**

777 Sixth Street NW  
Suite 700  
Washington, D.C.  
202-223-6722

**The Humane Society of the United States**

1255 23rd Street NW  
Suite 450  
Washington, D.C. 20037  
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Attachment

# Wolf Delisting Challenges Demonstrate Need for an Improved Framework for Conserving Intraspecific Variation under the Endangered Species Act.

CARLOS CARROLL, DANIEL J. ROHLF, BRIDGETT M. VONHOLDT, ADRIAN TREVES, AND SARAH A. HENDRICKS

*Recent advances in genomics have increased our understanding of geographic patterns of intraspecific variation and the importance of this variation in enhancing species' potential to adapt to novel threats. However, as part of an effort to limit the scope of the Endangered Species Act (ESA), the US government has proposed the removal of the gray wolf from the list of protected species on the basis of a claim that the statute permits a species to be declared recovered given the existence of a single presently secure population. We rebut this interpretation and propose a framework for the conservation of adaptive potential that builds on current agency practice in delineating subspecific recovery units and reconciles the definition of significance in the statute's "distinct population segment" and "significant portion of range" clauses. Such a coordinated policy would enhance the ESA's effectiveness in stemming loss of biodiversity in the face of climate change and other factors altering Earth's ecosystems.*

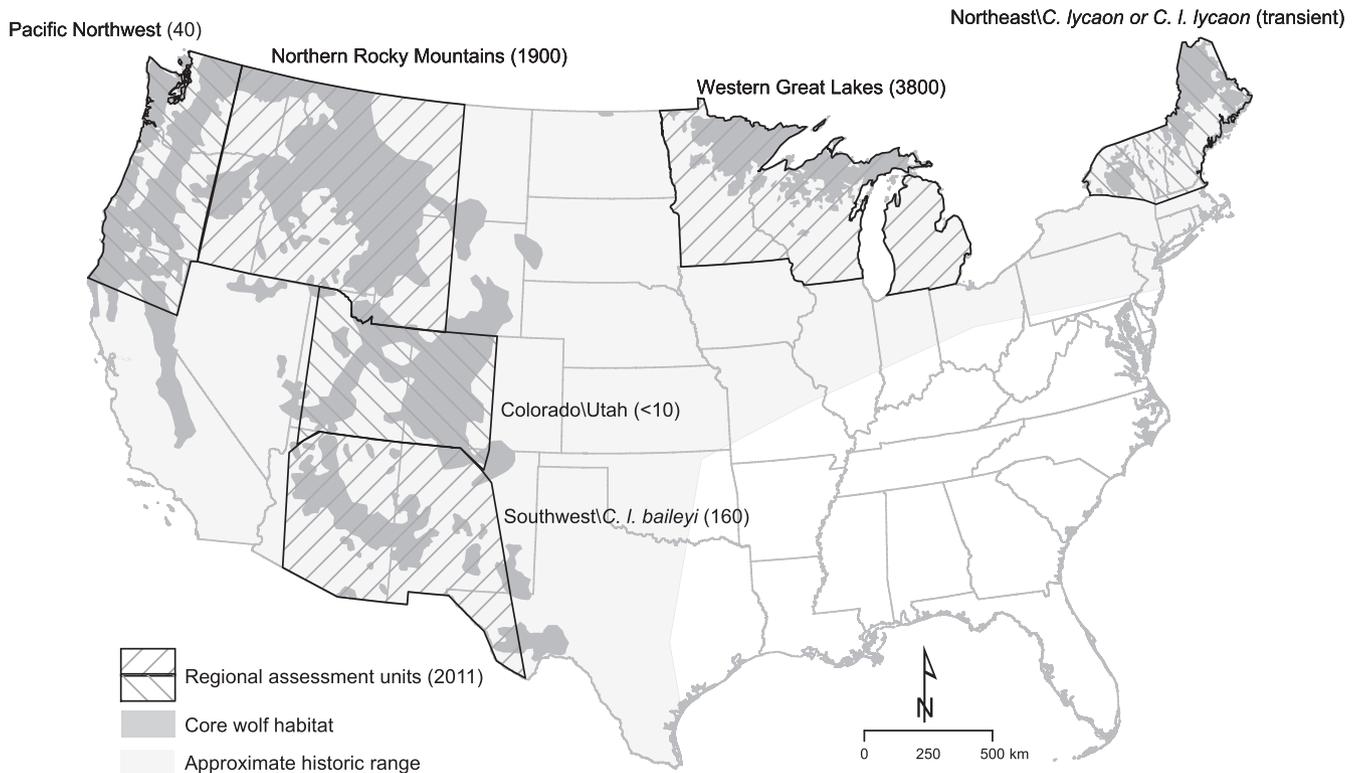
*Keywords: adaptive potential, Canis lupus, conservation genomics, distinct population segment, recovery planning*

**A**lthough the US Endangered Species Act (ESA; 16 U.S.C. §§ 1531–44) is among the world's most influential biodiversity protection statutes, key aspects of how the law should be implemented remain contested. A central issue involves the appropriate level of ambition for recovery of formerly widely distributed species such as the North American gray wolf (*Canis lupus*; figure 1; Enzler and Bruskotter 2009, Carroll et al. 2010). If the ESA aims only to prevent the complete extinction of a species, is the existence of a single secure population sufficient to declare a species recovered? Alternately, does a species need to achieve recovery in all or a majority of its historical range before it can be removed (delisted) from the list of protected species? If the purpose of the statute lies somewhere between these bounds, how can appropriate recovery goals be established? These questions resonate beyond the US context because they address how best to conserve variation below the level of the taxonomic groupings (species and subspecies) typically acknowledged in conservation statutes of other nations

(Laikre et al. 2016, vonHoldt et al. 2018, Hendricks et al. 2019a).

Although Congress and federal agencies have long recognized the importance of conserving intraspecific variation, recent agency actions, exemplified by a 2019 proposal to delist the gray wolf (84 FR 9648), suggest a shift away from biologically informed policy (Lambert 2019). In this Forum, we use the 2019 delisting proposal to demonstrate that recent inconsistent implementation of the ESA's mandate for the conservation of intraspecific variation undermines the conservation outcomes intended by Congress. We propose a more consistent and transparent framework that coordinates the two elements of the ESA that authorize the conservation of intraspecific variation: the distinct population segment (DPS; see supplemental table S1 for a definition of terms) and significant portion of range (SPR) clauses, while building on current agency guidance for delineating subspecific recovery units. Rather than representing a detailed policy proposal or a comprehensive review of case law in the present article, we synthesize

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**Figure 1.** Map of regional assessment units used in the 2008–2011 national wolf strategy process (Runge 2011). Current estimates of population numbers in each assessment unit (USFWS 2019) are given in parentheses and are approximate particularly in two units (Western Great Lakes and Northern Rocky Mountains) with recent changes in census methods. Wolf packs in Washington and Oregon are divided between the Pacific Northwest and Northern Rocky Mountain assessment units, with most falling within the latter unit. Distribution of potential core habitat is as delineated by CBD and HSUS (2018) based on published regional habitat models. Many areas of potential core habitat currently lack wolves, and many areas of historical range outside of core habitat could be inhabited by wolves given sufficiently low anthropogenic mortality.

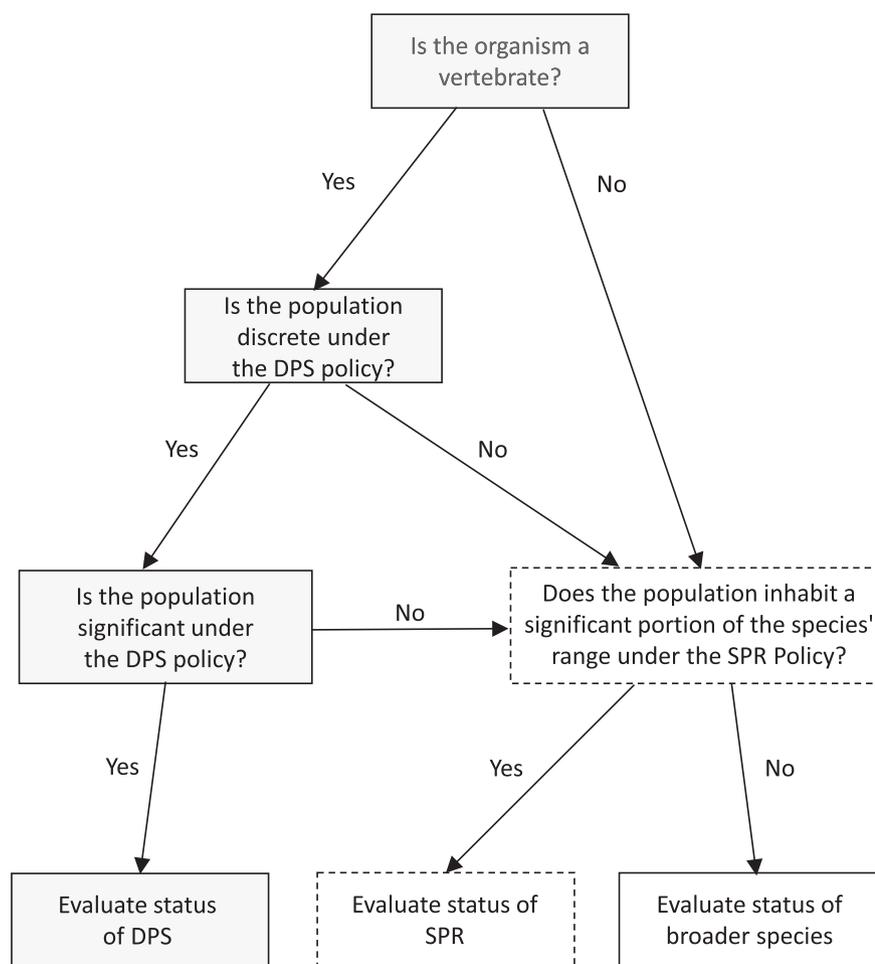
information from the fields of conservation genetics, wildlife ecology, and endangered species law to advance the discussion and resolution of conceptual issues regarding the conservation of intraspecific variation under the ESA.

### Why is conservation of intraspecific variation important?

Why would a statute designed to protect the nation's biodiversity, such as the ESA, mandate the conservation of multiple populations of widely distributed species rather than a museum piece approach (Vucetich and Nelson 2014) based on preserving a single narrowly distributed population? The ESA's preamble mentions an array of "esthetic, ecological, educational, historical, recreational, and scientific" benefits provided by maintaining a species presence throughout substantial proportions of its range (Carroll et al. 2010, Nelson et al. 2016). Science also increasingly supports the conclusion that preserving multiple populations furthers conservation efforts by enhancing adaptive potential, the genetic variability that allows species to adapt in the face of climate change and other factors altering Earth's ecosystems

(Funk et al. 2019). The conservation of multiple genetically distinct ecotypes (i.e., populations adapted to a particular habitat) in a metapopulation structure across a species's range enhances metapopulation connectivity and allows gene flow and the exchange of adaptive variants among populations, enhancing the adaptive potential of the metapopulation as a whole (Crandall et al. 2000, Hoffmann and Sgro 2011, Hamilton and Miller 2015, vonHoldt et al. 2018, Hendricks et al. 2019a).

Quantitative models have been developed to predict how gene flow among populations enhances adaptive potential and reduces extinction risk in species experiencing environmental shifts because of climate change or other factors (Funk et al. 2019, Razgour et al. 2019). In addition, the conservation of adaptive potential has long been recognized as forming part of "an ethical imperative to provide for the continuation of evolutionary processes" (Soulé 1985), with value extending beyond its immediate role in lowering extinction risk over the relatively short time horizons typically considered in population viability analyses (Wolf et al. 2015).



**Figure 2.** Flow diagram illustrating the proposed framework for designation of intraspecific conservation units under the US Endangered Species Act (ESA). Gray filled boxes represent decision steps currently taken when the Services evaluate whether a population constitutes a distinct population segment (DPS), a designation that the ESA limits to vertebrate species. Dashed boxes represented decision steps taken under the proposed “significant portion of range” (SPR) policy. Definitions of significance under the DPS and proposed SPR policy would be substantially similar but may diverge in emphasis as was described in the text.

### Conservation of intraspecific variation via the ESA’s distinct population segment clause

Although the ESA predates the modern genetics research described above, lawmakers indicated their support for conserving intraspecific variation via the act’s DPS and SPR clauses. Initially, almost all ESA listings were of entire species and subspecies, although the act did include language allowing listings of “any other group... in common spatial arrangement that interbreed when mature.” In 1978, Congress clarified the law to allow listing of “distinct population segments” (DPS) of vertebrate species (16 U.S.C. §1532(3.16)), although lawmakers directed that DPS designation be used “sparingly.”

In 1996, the Services (the US Fish and Wildlife Service [FWS] and its counterpart, the National Marine Fisheries

Service [NMFS]) finalized a policy that evaluates a population’s “discreteness” and “significance” to its taxon in order to decide whether the population qualifies for protection as a DPS (61 FR 4722; figure 2). Similar frameworks based on discreteness and significance were subsequently adopted outside of the United States, such as in Canada’s policy for identifying designatable units within species and subspecies (COSEWIC 2018).

The DPS policy’s factors for determining what constitutes a significant population include evidence that the population persists in a unique ecological setting, that the loss of the population would result in a significant gap in the range of the taxon, that the population represents the only surviving natural occurrence of a taxon that may exist as an introduced population outside its historical range, and that the population’s genetic characteristics differ markedly from those of other populations (Waples et al. 2018). Discreteness requires either marked separation from other populations of the same taxon as a consequence of physical, physiological, ecological, or behavioral factors or delimitation by international governmental boundaries with important differences in management or conservation status (61 FR 4722). Recognizing that population connectivity rates fall along a continuum, the DPS policy’s standard for a discrete population requires “marked” rather than complete separation (61 FR 4722). For example, NMFS identifies distinct populations for salmonid species even

though a small proportion of returning fish will reproduce within adjacent regions rather than the natal population (Waples 2006).

### Recolonizing species and hybridizing lineages pose challenges for delineating intraspecific conservation units

A large proportion of litigation concerning conservation of intraspecific variation under the ESA (table 1) relates to gray wolf delisting. This is due not only to the fraught politics surrounding this species but also to aspects of its distribution and systematics. Defining intraspecific conservation units for species such as the wolf that have been extirpated from the majority of their historical range is more complex than for species that are declining but remain extant across

**Table 1. A timeline of gray wolf listing and delisting related actions.**

Year	Action	Conservation unit	Reference
1967	<i>C. l. lycaon</i> listed.	Subspecies	32 FR 4001, 11 March 1967
1973	<i>C. l. irremotus</i> listed.	Subspecies	38 FR 14678, 4 June 1973
1974	<i>C. l. lycaon</i> listed.	Subspecies	39 FR 1171, 4 January 1974
1976	<i>C. l. baileyi</i> listed as Endangered.	Subspecies	41 FR 17736, 28 April 1976
1976	<i>C. l. monstabilis</i> listed as Endangered.	Subspecies	41 FR 24064, 14 June 1976
1978	<i>C. lupus</i> in lower 48 United States (except Minnesota) and Mexico reclassified as Endangered.	Species	43 FR 9607, 9 March 1978
1978	<i>C. lupus</i> in Minnesota reclassified as Threatened.	State population	43 FR 9607, 9 March 1978
2003	<i>C. lupus</i> Eastern, Western, and Southwestern DPS designated and reclassified.	DPS	68 FR 15804, 1 April 2003
2005	<i>C. lupus</i> DPS Rule vacated.	DPS	Defenders of Wildlife v. Norton, 354 F. Supp. 2d 1156 (D. Or. 2005); National Wildlife Federation v. Norton, 386 F. Supp. 2d 553 (D. Vt. 2005)
2007	<i>C. lupus</i> WGL DPS designated and delisted.	DPS	72 FR 6052, 8 February 2007
2008	<i>C. lupus</i> WGL delisting rule vacated.	DPS	Humane Society of the United States v. Kempthorne, 579 F. Supp. 2d 7 (D.D.C. 2008)
2008	<i>C. lupus</i> NRM DPS designated and delisted.	DPS	73 FR 10514, 27 February 2008
2008	<i>C. lupus</i> NRM Rule vacated.	DPS	Defenders of Wildlife v. Hall, 565 F. Supp. 2d 1160 (D. Mont. 2008)
2008	Protections for <i>C. lupus</i> WGL and NRM DPS reinstated.	DPS	73 FR 75356, 11 December 2008
2009	<i>C. lupus</i> WGL DPS designated and delisted.	DPS	74 FR 15070, 2 April 2009
2009	<i>C. lupus</i> WGL DPS delisting rule vacated.	DPS	Humane Society of the United States v. Salazar, 1:09-CV-1092-PLF (D.D.C. 2009)
2009	<i>C. lupus</i> NRM DPS (except Wyoming) designated and delisted.	DPS	74 FR 15123, 2 April 2009.
2009	Protections for <i>C. lupus</i> WGL DPS reinstated.	DPS	74 FR 47483, 16 September 2009
2010	<i>C. lupus</i> NRM DPS delisting rule vacated.	DPS	Defenders of Wildlife v. Salazar, 729 F. Supp. 2d 1207 (D. Mont. 2010)
2010	Protections for <i>C. lupus</i> NRM DPS reinstated.	DPS	75 FR 65574, 26 October 2010
2011	<i>C. lupus</i> NRM DPS delisted by Congress.	DPS	Public Law 112-10 and 76 FR 25590, May 5, 2011
2011	<i>C. lupus</i> WGL DPS designated and delisted.	DPS	76 FR 81666, 28 December 2011
2012	<i>C. lupus</i> in Wyoming delisted.	State population	77 FR 55530, 10 September 2012
2014	<i>C. lupus</i> WGL DPS delisting rule vacated.	DPS	Humane Society of the US v. Jewell, 76 F. Supp. 3d 69, 110 (D.D.C. 2014)
2014–2017	<i>C. lupus</i> Wyoming delisting rule vacated but reinstated on appeal.	State population	Defenders of Wildlife v. Jewell, 68 F. Supp. 3d 193 (D.D.C. 2014), Defenders of Wildlife v. Zinke, 849 F.3d 1077 (D.C. Cir. 2017)
2013	Delisting of <i>C. lupus</i> in lower 48 United States (except NRM and WGL DPS) and Mexico proposed.	Species	78 FR 35664, 13 June 2013
2015	<i>C. l. baileyi</i> listed as endangered.	Subspecies	80 FR 2488 and 80 FR 2512, 16 January 2015
2015	Protections for <i>C. lupus</i> WGL DPS and <i>C. lupus</i> in Wyoming reinstated.	State population	80 FR 9218, 20 February 2015
2017	Delisting of <i>C. lupus</i> in Wyoming reinstated.	State population	82 FR 20284, 1 May 2017
2019	<i>C. lupus</i> delisting in lower 48 United States (except NRM DPS and <i>C. l. baileyi</i> ) and Mexico proposed.	Species	84 FR 9648, 15 March 2019

Source: Adapted from 2019 proposed delisting rule (84 FR 9648). Abbreviations: DPS, Distinct Population Segment; NRM, Northern Rocky Mountains; WGL, Western Great Lakes.

their historical range. The range of a species is inherently difficult to define, being contingent on timeframe as well as spatial scale (Gaston and Fuller 2009). For example, when the FWS initially proposed to delist the gray wolf in 2013, no breeding pairs of wolves existed in California, and therefore, under the Services' definition, the state was not within

the species's range (78 FR 35664). However, by the time of the 2019 proposal, at least one breeding pair was known to inhabit California, and the FWS considered the state as within the species's range (84 FR 9653).

The conservation of such small recolonizing populations is important in part because their genetic composition can

diverge rapidly from that of the source population, given the small number of founders. This divergence provides a rapid mechanism for novel and potentially adaptive genetic variants to originate and be acted on by natural selection. An example in North American wolves is provided by the historic spread of the allele controlling black coat color, which correlates with enhanced fitness during canine disease outbreaks (Schweizer et al. 2018).

In addition, canids such as the gray wolf can hybridize and form extensive zones of intergradation, which poses challenges for policies that involve assigning subspecies and genetic groupings to disjunct geographic areas (Leonard et al. 2005, vonHoldt et al. 2011). For example, the Great Lakes wolf population—on which the 2019 delisting rule depends for its claim that the gray wolf is recovered—is an admixture with contributions from up to three canid species (*C. lupus*, *Canis latrans*, and putative *Canis lycaon*; Heppenheimer et al. 2018).

Although the conservation of intergradation zones is important for maintaining adaptive potential (Leonard et al. 2005), populations in these areas may not meet the DPS policy's standard for discreteness (i.e., marked geographic or genetic separation). Recent genetic research has concluded that evolutionary relationships in canids and some other taxa resemble a web of life because of historical and possibly ongoing genetic exchange, rather than a tree of life defined by reproductive isolation (vonHoldt et al. 2018), implying that the discreteness standards in the DPS policy may not be well suited for protecting admixed populations important to the overall taxon. Such genomic admixture can be a rich source of beneficial alleles, which quickly boost genetic variation in recently bottlenecked populations (vonHoldt et al. 2018).

### Conservation of intraspecific variation via the ESA's significant portion of range clause

Lawmakers also included within the ESA a second clause supporting the conservation of intraspecific variation, which has proved more challenging for the Services to implement than was the DPS clause. The ESA of 1973 differed from two previous versions of the law (P.L. 89–669 [1966], P.L. 91–135 [1969]) in recognizing that endangerment has a geographic component and in extending legal protections to species “at risk of extinction throughout all or a significant portion of its range” (16 U.S.C. §1532(3.6)). The SPR clause suggests that Congress intended that managers interpret the concept of endangerment more broadly than an entire species facing the risk of extinction (Wolf et al. 2015). From this perspective, recovery requires not only that a species exist but also that it be present across all “significant” portions of its range (Carroll et al. 2010).

The ambiguity of the ESA's SPR clause, coupled with ongoing controversy concerning the geographic component of recovery under the statute, have led to numerous legal challenges to delisting proposals (table 1). Two related themes have emerged from the series of SPR-related court

decisions, many of which involved the gray wolf. The first revolves around the meaning of the term *range* in the SPR clause. The courts, although deferring to the Services' desire to interpret the term *range* as indicating current rather than historical range, have nonetheless required the agency to consider loss of historical range when assessing a species's viability (Enzler and Bruskotter 2009, *Humane Society v. Zinke*, 865 F. 3d 585 [2017]).

Second, in several decisions stretching over two decades (from *Defenders of Wildlife v. Norton*, 258 F. 3d 1136 [2001] to *Center for Biological Diversity v. Everson*, 1:15-cv-00477 [2020]), the courts have concluded that the Services must interpret the term *significant* in the SPR clause in such a way that it is not rendered duplicative; that is, a species in peril throughout all of its range must somehow differ from a species in danger of extinction throughout just a significant portion of its range (Enzler and Bruskotter 2009). Although the Services have made multiple attempts to establish policy defining SPR, several court decisions have concluded that the most recent (2014) SPR policy (79 FR 37577), like previous efforts, runs counter to congressional intent (*Humane Society of the United States v. Jewell*, Case No. 13–186 [2014]), and the policy has been vacated nationwide (*Desert Survivors v. US Dept. of the Interior*, 231 F. Supp. 3d 368 [2017]). The courts concluded that the 2014 policy did not distinguish between a species at risk in a SPR and one at risk throughout its range, because it made SPR status contingent on a conclusion that extirpation of a regional population would place the entire species at risk of endangerment in the relatively short timeframe represented by the Services' definition of the “foreseeable future.”

### Recovery units as a tool for conserving intraspecific variation

The Services have also developed guidance for delineating “recovery units” as an additional tool for conserving intraspecific variation. A recovery unit is “a special unit of the listed entity that is geographically or otherwise identifiable and is essential to the recovery of the entire listed entity, i.e., recovery units are individually necessary to conserve genetic robustness, demographic robustness, important life history stages, or some other feature necessary for long-term sustainability of the entire listed entity” (NMFS 2018). The Services often evaluate whether a regional population merits recovery unit status on the basis of whether it contributes to a species's resiliency, redundancy, and representation (Evans et al. 2020 [preprint] doi:10.1101/2020.03.15.991174). These 3R criteria suggest that a species, to be considered recovered, should be present in many large populations arrayed across a range of ecological settings (Shaffer and Stein 2000). Recovery units are especially appropriate “for species occurring across wide ranges with multiple populations or varying ecological pressures in different parts of their range,” for “ensuring conservation of the breadth of a species's genetic variability... necessary to provide adaptive flexibility,” “reestablishing historical or maintaining current genetic flow,”

and “encompassing current and historical population and habitat distributions” (NMFS 2018). The clause “necessary for long-term sustainability” is not strictly defined in the context of recovery unit designation. Nonetheless, unlike the invalid definition of SPR used in the Services’ 2014 policy, it is clearly distinct from the threshold used to judge whether a species is at risk of extinction throughout its range.

Although the existing recovery unit guidance provides a tool for conserving intraspecific variation, several shortcomings in its current implementation limit its effectiveness. The delineation of recovery units is discretionary, representing only about 2% of ESA-listed species, and is biased toward specific taxonomic groups (Evans et al. 2020 [preprint] doi:10.1101/2020.03.15.991174). Although the recovery unit guidance for defining intraspecific variants is relevant to defining SPR, the Services have not linked recovery units to the courts’ requirement that the agencies consider SPR in listing and delisting decisions. Although the recovery unit guidance states that “some recovery units may qualify as a DPS,” there is no clear decision tree to help planners decide which option to select (NMFS 2018). In theory, recovery units should inform consultations under the ESA’s section 7 regarding whether an action by another federal agency places a species in jeopardy, but this frequently does not occur (Evans et al. 2020 [preprint] doi:10.1101/2020.03.15.991174).

The wolf example detailed below, in which the FWS proposed to delist a widely distributed species on the basis of the recovery of a single population (a proposal at odds with the practice for other species), reinforces the conclusion of Evans and colleagues ([preprint] doi:10.1101/2020.03.15.991174) as to the “need for standardized practice regarding the use of recovery units” (see box 1). We propose that explicitly linking the delineation of intraspecific conservation units to the ESA’s SPR mandate would increase consistency, limit the broad discretion (and consequent opportunity for inappropriate political influence) that characterizes the Services’ current approach, and provide the foundation of an SPR policy that could withstand judicial review.

### **Toward a consistent and effective framework for conserving intraspecific variation under the ESA**

The current implementation of the ESA falls short in protecting intraspecific variation when faced with ecological and genetic complexities such as those described above. A more integrated approach to evaluating potential DPS and SPR can help overcome these challenges and prevent species such as the gray wolf from falling through the cracks. At first glance, the context of how *significant* is used in the SPR clause differs from how the term is used in the DPS policy. In the case of SPR, *significance* refers to a geographic area inhabited by a population (i.e., its range), whereas in the case of DPS, it refers to characteristics of the population itself. However, insights from landscape genetics, which maps population characteristics to environmental features, could allow the Services to interpret the term *significant* in a

more consistent manner in relation to both the DPS policy and the SPR clause.

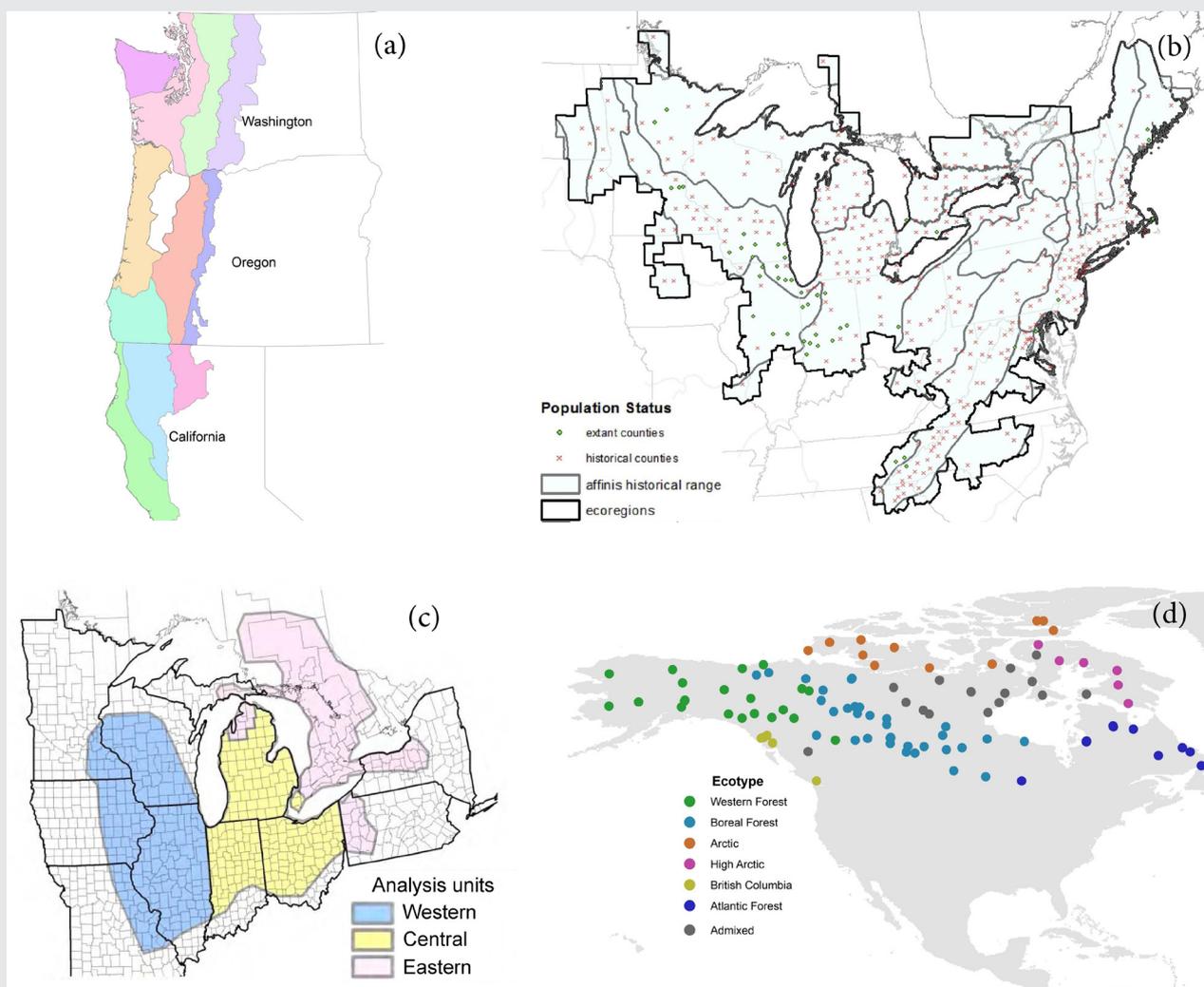
We propose a framework under which the relevant Service would consider both geography and genetics in assessing whether a population is in danger of extinction or likely to become endangered in the foreseeable future in a “significant” portion of its range. Figure 2 shows the decision tree that the framework envisions. If the Services were assessing a species that appeared to be under threat in only a portion of its range, but the species either was not a vertebrate or did not show marked isolation (i.e., discreteness), they would consider both of the following factors in assessing whether that portion of the species’ range is significant: a) the geographic extent of the area in which the population is imperiled, compared with both the species’s current and historical distributions and b) the current or potential future genetic distinctiveness and adaptive potential of the imperiled population.

This means of incorporating genetics into the assessment of SPR is also consistent with the DPS policy’s consideration of a population segment’s genetic characteristics compared with the species as a whole in assessing whether the population is “significant.” Such an approach in the context of assessing SPR would resemble current guidance on identifying recovery units (NMFS 2018) but would establish a consistent science-based policy linked to delisting rather than an ad hoc application of recovery guidance. By encompassing geography as well as genetics, this analytical approach allows the Services to also consider the range of “esthetic, ecological, educational, historical, recreational, and scientific” benefits cited in the ESA as provided by a species’s presence across its range (Carroll et al. 2010). We consider in supplement S1 the related question of what regulatory actions follow if the Services find a species endangered or threatened within only a significant portion of its range.

Even if recolonizing populations of formerly widely distributed species have not yet diverged genetically, their significance can be evaluated in a forward-looking manner as contingent on a degree of differentiation great enough for evolutionarily important contrasts to accumulate in the future (Waples 2006). Bowen (1998) coined the term *geminant evolutionary unit* to describe a regional population that shows morphological, behavioral, or biogeographical differentiation but does not yet show genetic divergence at neutral loci. Such a population can be considered significant on the basis of its ability to contribute to future evolutionary potential—for example, because of colonization of a new habitat (e.g., as defined by ecoregions or climatic zones) with novel selective pressures. For example, the North Cascades region of Washington State, which may currently contain only transient grizzly bears, has nonetheless been the object of substantial recovery planning efforts in part because it represents a unique ecological and evolutionary context for the species within the contiguous United States (USFWS and NPS 2017).

### Box 1. Distinguishing significant units within a species' distribution.

Federal agencies have employed a variety of approaches to identify intraspecific conservation units on the basis of how they contribute to a species's intraspecific variation and adaptive potential (Funk et al. 2019). Recovery units are often delineated on the basis of general ecosystem or habitat boundaries that are hypothesized to be relevant to adaptive variation in the species. The recovery plan for the northern spotted owl (*Strix occidentalis caurina*) designated 11 recovery units on the basis of the physiographic provinces found within the species's distribution (figure 3a; USFWS 2011). For species whose distribution has contracted, planners may consider the breadth of ecoregions encompassed by their historic distribution. The status assessment for the rusty-patched bumblebee (*Bombus affinis*) evaluated current and historical representation of the species in all ecoregions within its historical range, and projected the number of "representation units" (a surrogate for adaptive potential) that the species would inhabit under contrasting management scenarios (figure 3b; Szymanski et al. 2016a). Units can alternately be delineated on the basis of genetic data when such information is sufficient. In its status assessment of the eastern massasauga rattlesnake (*Sistrurus catenatus*), the FWS identified three genetically distinct regional units needed to maintain the adaptive potential of the species (figure 3c; Szymanski et al. 2016b).



**Figure 3.** Examples of consideration of the significance of portions of a species's range in terms of their contributions to the species's adaptive potential: (a) the recovery plan for the Northern Spotted Owl (USFWS 2011) designated 11 recovery units on the basis of the physiographic provinces found within the species's distribution; (b) the status assessment for the rusty-patched bumblebee (Szymanski et al. 2016a) projected the number of representation units the species would inhabit under contrasting management scenarios; (c) the status assessment for the eastern massasauga rattlesnake (Szymanski et al. 2016b) identified three genetically distinct regional units needed to maintain the adaptive potential of the species; and (d) Schweizer and colleagues (2016) delineated six significant ecotypes for wolves inhabiting Canada and Alaska on the basis of associations between genetic clusters and 12 environmental variables. Source: (a–c) USFWS, (d) Rena Schweizer.

**Box 1. Continued.**

Although many examples of delineating subspecific units are based solely on either genetic analysis or habitat discontinuities, stronger inferences can be drawn by using environmental data in combination with genetic information (Funk et al. 2012, Hendricks et al. 2019a). Landscape genomics techniques, such as selection tests and genotype-by-environment associations, provide powerful methods for distinguishing significant adaptive variants and ecotypes on the basis of the degree of adaptive differentiation between them (Carmichael et al. 2007, vonHoldt et al. 2011, Funk et al. 2012, Schweizer et al. 2016, Hendricks et al. 2019a).

Schweizer and colleagues (2016) were able to accurately infer the genetic cluster to which a gray wolf belonged on the basis of the habitat type (as defined by 12 environmental variables) where it was collected, allowing the delineation of six significant ecotypes for wolves inhabiting Canada and Alaska (figure 3d). Hendricks and colleagues (2019b) similarly used a maximum entropy approach to model distinct coastal and interior environmental niches for wolves in the US Pacific Northwest. The most relevant type of genetic information may differ when delineating DPS versus SPR. Intraspecific conservation units such as DPS, whose genetics have been shaped by both historical isolation (i.e., discreteness) and adaptive processes, can be delineated using both neutral loci and loci under selection (Funk et al. 2012). Other less-isolated but significant subunits of species (SPR) can be delineated primarily using loci that exhibit signatures of divergent selection (Funk et al. 2012).

The question remains as to how finely to divide a species's range—that is, how to discern “significant” intraspecific adaptive variants. DPS designation has been criticized as being partially subjective because there is no universally accepted threshold for the level of differentiation that confers evolutionary significance (Waples 1995). Although this criticism necessarily extends to identification of potential SPR, model selection metrics such as the Deviance Information Criterion (Gao et al. 2011) are frequently used to determine the best-supported number of clusters or subunits within a sample on the basis of genetic and environmental data. As Winker (2010) states, “the process of diagnosing states that exist along a continuum of differentiation can be difficult and contentious and necessarily has some arbitrariness; professional standards can be developed so that such diagnoses are objective.”

The elements we propose the Services consider in identifying a “significant” portion of a species's range are also identified in the DPS policy as relevant to assessing a discrete population's significance. Therefore, it is feasible to coordinate the definitions of significance in the DPS and SPR policies. For example, recognition of evolutionary potential and the importance of geography are inherent in the DPS policy's consideration of the significance of unique ecological settings and potential gaps in a species's range created by the loss of a population, respectively. However, our framework (figure 2) allows for differences in emphasis and implementation to remain between the DPS and SPR policies' definitions of significance. In addition, although existing guidance regarding recovery units informs our proposed SPR definition, the Services could retain the flexibility to identify recovery units for the purposes of recovery planning and implementation, even if such units were not identified as SPR.

### **Gray wolf listing and delisting demonstrates the need for a consistent approach to conserving intraspecific variation**

The several subspecies of North American gray wolf were among the earliest taxa listed as endangered under the ESA. The FWS shifted in 1978 to listing the wolf at the species level, except the Mexican wolf subspecies (*Canis lupus baileyi*), which remains listed separately (43 FR 9610). As wolf population numbers increased under ESA protection, the FWS repeatedly sought to remove some or all of the US population from the list of endangered and threatened species, only to be blocked by the courts in at least nine separate decisions since 2005 (table 1). The successive wolf

delisting proposals have been characterized by scientific as well as legal controversy. The FWS withdrew a 2013 delisting proposal after a panel of scientific peer reviewers found flaws in the agency's taxonomic analysis (NCEAS 2014). A panel of invited scientific peer reviewers (including two of the present authors, CC and AT) also found significant shortcomings in the 2019 delisting proposal (Atkins 2019).

A notable feature of the successive delisting proposals is that they have varied widely in how they defined appropriate gray wolf conservation units, ranging from a focus on *C. lupus* as a whole to a focus on one or more DPS or populations inhabiting individual states (table 1). The most recent (2019) delisting proposal asserted that gray wolves in the contiguous United States (except for the separately listed *C. l. baileyi*) no longer merit ESA protection, on the basis of the premise that the agency can delist a species when a single regional population (in this case wolves inhabiting the Great Lakes states; figure 1) has recovered to a status the agency deems presently secure (84 FR 9683).

The roughly 4000 wolves estimated to inhabit the Great Lakes region constitute approximately two-thirds of the total population currently inhabiting the contiguous United States (figure 1). But is total population the only relevant metric for assessing the conservation status of a species? The Great Lakes population occupies only 3 of the at least 17 states within the species's historical range that hold substantial areas of habitat (figure 1). The approximately 2000 wolves inhabiting the Northern Rocky Mountain (NRM) region form the only other large regional population within the contiguous United States (figure 1). Because the US Congress passed legislation (Pub. L. No. 112-10, § 1713, 125 Stat. 38) removing ESA protections from the NRM

population (the only instance of such legislative delisting since the ESA's passage), that population is counterintuitively not part of the listed entity considered in the 2019 proposal.

By arguing in the 2019 proposal that “wolves that occur outside the Great Lakes area... are not necessary for the recovered status of the gray wolf entity” (84 FR 9683), the FWS took a dramatic step away from its policy at the time it consolidated wolf subspecies into a single listing in 1978, when the agency offered “the firmest assurance that it will continue to recognize valid biological subspecies for purposes of its research and conservation programs” (43 FR 9610). The FWS's evolving position on wolf delisting exemplifies how the agency has moved away from Congress's vision of an ESA that protects intraspecific variation toward a more politically expedient approach predicated on a misrepresentation of the extent of intraspecific variation found in most geographically widespread species. For example, the FWS justified the central premise of the 2019 wolf delisting proposal—that wolf populations outside the Great Lakes region do not contribute to recovery—to a large degree on an assertion that the North American wolf population is genetically unstructured because the wolf's ability to disperse long distances would prevent genetic variation among subpopulations (84 FR 9685).

The development of high-throughput genotyping methods over the last decade has enabled an increasingly detailed analysis of historical and current population structure of North American wolves (Hendricks et al. 2019a). Wolf populations are now known to be characterized by complex genetic clines at several spatial scales, driven by historical biogeographic factors, isolation by distance, and association with particular ecosystems (Geffen et al. 2004, Carmichael et al. 2007, vonHoldt et al. 2011, Schweizer et al. 2016). Environmental factors related to climate zones significantly contribute toward genetic isolation by distance in North American gray wolves, likely through habitat matching decisions made by dispersers (Geffen et al. 2004). Environment factors, along with intraspecific competition for prime territories, resources, and access to reproduction, result in a nested structuring of genetic variation at both the continental and regional scales (Carmichael et al. 2007, vonHoldt et al. 2011, Schweizer et al. 2016).

### Distinct population segment policy as applied to the wolf

The highly structured North American wolf population revealed by genetic analyses has implications for determining whether conservation units below the species level are appropriate under the ESA (vonHoldt et al. 2011, Hendricks et al. 2019a). Wolf habitat in the contiguous United States is discontinuous enough to allow identification of DPS for some regional populations, despite occasional dispersal between regions (Carroll et al. 2006, CBD and HSUS 2018). For example, the FWS itself concluded in 2007 that despite “occasional individual wolves or packs [that] disperse among populations,” Northern Rocky Mountain

wolves were markedly separated from other regional wolf populations (73 FR 10519).

In 2008, the FWS embarked on an effort to develop a comprehensive national strategy for gray wolf conservation by identifying appropriate wolf listing units within the broader continental distribution of the species (76 FR 26086). This national strategy was necessary because earlier proposals to remove protections for individual regional wolf populations by piecemeal designation and delisting of a single DPS within the larger range had been rejected by the courts (table 1; Alexander 2010). Five assessment units, including several potential DPS, were identified throughout the contiguous United States (figure 1). Although this closed-door process involving federal and state agencies lacked the inclusivity and scientific guidelines typical of recovery teams (PEER 2013), it nonetheless attempted (but never finalized) a comprehensive analysis of what recovery efforts might be appropriate in the different regions that include habitat for the species (Runge 2011).

In contrast, the 2019 proposed delisting rule did not attempt a comprehensive analysis of potential DPS status for regional populations but instead asserted that no regional wolf populations meet the DPS policy's standard for discreteness because the entire range of the gray wolf in the contiguous United States constitutes a single metapopulation (a term used in the rule in the broad sense of subpopulations linked by immigration and emigration). However, the Great Lakes and Pacific wolf populations, situated at the periphery of currently occupied wolf range, are separated by 1800 kilometers (km), much of which is transformed by agriculture. Although wolves inhabiting the Northern Rocky Mountains could provide an intermediate stepping stone population, any genetic interchange between these distant groups would necessarily be indirect and attenuated, allowing substantial genetic divergence (Schweizer et al. 2016).

The FWS has identified DPS for other large mammalian carnivores such as the grizzly bear (*Ursus arctos horribilis*) and does not claim that grizzly bear recovery in one region renders recovery efforts elsewhere unnecessary. Connectivity between regional grizzly bear populations, far from precluding DPS designation, has been judged by the FWS to be essential to long-term genetic health and recovery of those populations (82 FR 30502). The degree of genetic differentiation between regional wolf populations (e.g., between the NRM and Great Lakes populations) resembles that between grizzly bears inhabiting separate DPS in the Northern Rocky Mountains (vonHoldt et al. 2011, Cronin and MacNeil 2012).

Because average natal dispersal of male and female wolves (114 and 78 km; Boyd and Pletscher 1999) is several times that of male and female grizzly bears (42 and 14 km; Proctor et al. 2004), several grizzly bear DPS might occur within a single wolf DPS, as has been the case in the Northern Rocky Mountains. However, the entire gray wolf distribution in the contiguous United States cannot be considered a single

genetically undifferentiated population, as was proposed in the 2019 delisting rule. The divergence in application of the DPS policy to grizzly bears and gray wolves demonstrates the need for a more consistent application of the DPS policy. Our proposed framework coordinating the DPS and SPR policies would not require modification of the existing DPS policy's criteria but, rather, their consistent application even to controversial species such as the wolf, enabled by strengthened support for scientific integrity from agency leadership (Carroll et al. 2017).

### Significant portion of range as applied to the wolf

While acknowledging the absence to date of a legally sufficient definition of SPR, the FWS in the 2019 proposed wolf rule attempted to satisfy future judicial review by evaluating whether regional populations outside the Great Lakes are "significant." To support its claim that recovery of the Great Lakes population allows the agency to delist wolves throughout the contiguous United States, the FWS concluded that any currently listed wolf population found outside the Great Lakes region is not significant "because it is not biologically important" because of the small size of peripheral populations and the purported lack of genetic differentiation within the North American wolf population (84 FR 9648). This conclusion requires both a particularly narrow reading of the 3R criteria and a misrepresentation of research regarding wolf genetic population structure.

Under our proposed framework (figure 2), DPS could be identified for regional wolf populations that showed marked separation from other populations, whereas wolf populations inhabiting intergradation zones might instead qualify for delineation as SPR. The coastal Pacific Northwest (western Washington and Oregon and northern California; figure 1), one of the five regions assessed in the 2008 process, provides an example of a regional wolf population that meets the DPS discreteness criterion (figure 2). Marked separation can be established for this regional population as a consequence of several factors: physical (separation from larger inland populations by areas of nonhabitat), ecological (occupation of coastal rainforest ecosystems), genetic (unique genetic contributions from wolves from coastal British Columbia; Hendricks et al. 2019b), and an international governmental boundary separating US populations from coastal wolves in Canada that have different management status. Once discreteness has been established, wolves in the Pacific Northwest could merit significance because of their persistence in a unique ecological setting, which is used as a proxy for adaptive genetic differences, as well as the fact that loss of the population would result in a significant gap in the range of the taxon (Carroll et al. 2001, Waples et al. 2018).

The Colorado and Utah assessment unit considered in the 2008 process (figure 1), which historically formed a zone of intergradation between northern and southwestern wolf subspecies (Leonard et al. 2005), provides an example of an area that should be evaluated as a SPR, even if it is found to not show marked separation from adjacent populations

(figure 2). This region, although currently supporting only a handful of wolves, represents a valid SPR because it holds abundant suitable habitat in a unique ecological setting (based on ecoregions or climate zones) subject to novel selective pressures (Carroll et al. 2006). Although we recognize that policy alone cannot ensure against inappropriate political influence in agency rulemaking, a coherent approach to DPS and SPR evaluation would be more likely to withstand litigation than the current ad hoc approach to wolf delisting, and more likely to result in the robust conservation outcomes envisioned by the lawmakers who drafted the ESA.

### Conclusions

In 2019, the US federal administration enacted sweeping changes to regulations interpreting the ESA that limit the statute's reach (83 FR 35174, Lambert 2019). The 2019 wolf delisting proposal forms part of this effort to advance a minimalist interpretation of the ESA's mandate, in that its central premise goes beyond what is necessary to support wolf delisting and seeks to establish a precedent that the ESA allows for a narrow view of what constitutes recovery of widely distributed species. By extending the assumptions of previous agency policy regarding the significant portion of range clause to their extreme, the proposed wolf delisting rule highlights the degree to which the conservation of intraspecific variation is central to ESA implementation and underlines the need to develop more effective policy concerning this issue. If applied generally to other species, the 2019 rule's approach to ESA implementation would represent a significant scaling back of recovery efforts for widely distributed species that would increase both short-term vulnerability and long-term loss of adaptive potential.

The recovery of formerly widely distributed species such as the wolf poses practical challenges for delisting and recovery planning (Treves and Bruskotter 2011). In some instances, an approach that requires continued federal management of the species throughout its range until the weakest regional population is secure may consume scarce conservation resources. An efficient strategy for recovery of such species could allow reduction of regulatory protections in regions that already hold abundant populations while maintaining protections in other regions that hold small recolonizing populations. The strategies we propose, based respectively on DPS and SPR designation, represent complementary approaches to achieving this flexibility that build on the Services' existing standards for evaluating the significance of regional populations under the DPS policy and recovery unit guidance. Our proposed approach has relevance beyond the United States in the context of international regulations such as the European Union's Habitats Directive, which requires member states to achieve "favorable conservation status" for protected species without clarifying at what scale this status is to be achieved (Laikre et al. 2016).

When initially defining their resiliency, redundancy and representation criteria, Shaffer and Stein (2000) noted that

successful conservation “will require identifying conservation targets not simply as species and communities but as the complexes of populations, communities, and environmental settings that are the true weave of biodiversity.” As advances in genomics increase our understanding of patterns of intraspecific variation, the conservation of adaptive potential merits increased emphasis as a key element in achieving the ESA’s goal of “saving all the pieces” (Leopold 1968).

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### Supplemental material

Supplemental data are available at *BIOSCI* online.

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