BioScience, 2025, **0**, 1–10
https://doi.org/10.1093/biosci/biae134
Advance access publication date: 0 2025
Forum

Species recovery as a half empty process: the case against ignoring social ecology for gray wolf recovery

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Abstract

The criteria used to assess recovery under the US Endangered Species Act (ESA) often fall short when considering social, group-living species. To illustrate this, we use recent insights on sociality in gray wolves to highlight how such definitional failures in implementing the ESA limit the efficacy of recovery efforts for species with complex societal arrays. The loss of conspecifics in social species has an enhanced impact on demographic viability that is not captured by estimates of population abundance. The reproductive skew in social species reduces effective population size and exacerbates threats to genetic health of populations. For group-living species such as wolves, it is critical that regulations consider sociality in recovery guidelines. Biological processes that include social behavior and group structure need to be more fully considered for the ESA to effectively reflect biological reality. Until regulations and policy include language that incorporates these considerations, the species we try to protect will lose.

Keywords: social group, structured reproduction, conservation, gray wolves, species management

In 1992, Kent Redford defined the *half-empty forest* as a vast ecosystem where the vegetation is intact but large animals in the community are ecologically extinct because of their scarcity. Such defaunation (i.e., “the reduction of a species to such low abundance that, although it is still present in the community, it no longer interacts significantly with other species,” Estes et al. 1989, Dirzo et al. 2014) emphasizes the multiple dimensions of extinction (e.g., global extinction, local extirpation, and loss of ecological function). Addressing only one aspect of extinction clearly compromises the intent of the Endangered Species Act of 1973 (ESA 16 U.S.C. §§ 1531–44) to restore ecosystems (Pyare and Berger 2003, Berger 2007). Although the ESA includes language regarding conservation of both species and their ecosystems, the act’s implementation has been myopically focused primarily on supporting species recovery as it is universally evaluated via abundance and geographic distribution (Neel et al. 2012). These metrics are assumed to represent the full scope of species viability, based in part on the overly simplified assumption that abundance is negatively associated with inbreeding depression and deleterious genetic load (Kimura et al. 1963, Charlesworth et al. 1992). Legislation rarely deviates from the evaluative criteria of abundance when considering social species. In the present article, we discuss the need for conservation policy to consider and incorporate obligate sociality in developing conservation strategies and species recovery plans. Although this general idea applies to many species, we use gray wolves (*Canis lupus*) in the United States as a case study and develop an inclusive narrative for other species with obligate sociality with a significant role in the surrounding ecological community. We encourage the forthcoming national gray wolf recovery plan to elevate the social unit to an extent not evident in previous gray wolf conservation strategies and to set a precedent for other species where the most fundamental unit of recovery is their social group.

The structure and ecological importance of social groups

For social species, a population is not merely a set of independently acting entities. Individuals associate with each other by following rules learned early in life and through experience (Brakes et al. 2021). Intra- and intergroup interactions generate complex patterns that underpin life history and reproductive strategies, which structure genetic variation across space and time (Parreira and Chikhi 2015).

A common feature of obligately social species and many others is that not all individuals breed (Clutton-Brock 2021). For example, up to 15 well-studied mammal species (e.g., bush hyrax, *Heterohyrax brucei*; red deer, *Cervus elaphus*; African lions, *Pathera leo*; bison, *Bison bison*) show up to an 87% loss of unrelated social or family groups coupled with high variance in female or male reproductive success across an average study period of 12 years (Gompper et al. 1997). The mechanisms of reproductive suppression vary, but the genetic patterns emerging from mating structures are shaped by the severity of reproductive skew and measured by the ratio of the effective to census population sizes, which affects demography (Frankham 1995a). This ratio can substantially shift estimates derived from individual-based summary metrics, such as genetic diversity and inbreeding coefficients. Furthermore, the relationship between effective population size and natural selection is reciprocal (Wright 1931); once a population drops below a minimum viable size, survival probability declines precipitously

Received: May 30, 2024. **Revised:** December 8, 2024. **Accepted:** December 13, 2024

(Lynch and Lande 1998, Frankham 2005, Charlesworth and Willis 2009, Wittmann et al. 2018). This density-dependent phenomenon, referred to as *the Allee effect* (Allee 1931, Allee and Bowen 1932), leads to increased extinction risk in small populations that results from the combination of erosion of group cohesion and function, a loss of cooperative behaviors, suboptimal group size, and declining reproductive success (Angulo et al. 2007, Courchamp et al. 2008, Luque et al. 2016).

There is limited empirical knowledge about the minimum viable population size that ensures adequate survival probabilities in the face of stochastic, ecological, or genetic events (which are likely to be additive; Shaffer 1981, Berec et al. 2018, Wittmann et al. 2018). When species are deemed isolated and in decline, conservation policy is focused on improving population connectivity and therefore gene flow. Such policy assumes that some amount of gene flow (e.g., the one migrant per generation rule; Mills and Allendorf 1996) is required to avoid an accumulation of deleterious genetic variation and therefore a downward spiral into an extinction vortex (Frankham 1995b). However, this focus fails to incorporate the vital role of complex social behaviors and groups as a foundational unit that would support species recovery and their long-term persistence.

Can species overcome the Allee effects?

When social groups are the fundamental structural unit of the population, their persistence is the cornerstone for the species' survival. Sociality results when the advantage of collective association exceeds the costs of isolating from conspecifics (Markham et al. 2015) and provides environments where offspring learn vital behaviors that directly link to individual fitness (hunting or foraging specializations) or culture (preferred locations or routes, and how to interact appropriately with group mates; Brakes et al. 2021). The attrition of such behaviors has been hypothesized to initiate the extinction vortex as observed by higher mortality rates than birth or recruitment and loss of genetic viability (Allee 1931, Allee and Bowen 1932). Social species therefore require added consideration, especially when their listing status results in new management regulations (Courchamp et al. 2008), but empirical evidence from wild population studies is quite limited (Stephens et al. 2002, Berec et al. 2007, Kramer et al. 2009, Brashares et al. 2010, Wittmann et al. 2018). Indeed, prior modeling studies have identified the predicted impacts of one or more Allee effects in reproduction, survival, genetics, or any combination of these and collectively suggest that any management design is rendered inadequate if the Allee effects are ignored (Berec et al. 2007). For example, a desert bighorn sheep (*Ovis canadensis*) study urged managers to reintroduce a greater number of individuals to negate the combined Allee effects of predation and trophy hunting when there were less than 50 individuals (Berger 1990, Mooring et al. 2004).

For highly social species, such as the critically endangered Vancouver Island marmot (*Marmota vancouverensis*; Jackson et al. 2015), group members experience increased fitness when living in intact social groups for survival, reproduction, and resource acquisition (Brashares et al. 2010). By contrast, small disparate isolated populations experienced 90% population declines (Bryant and Page 2005, Brashares et al. 2010). Temporal data analysis on these marmots provided strong evidence of Allee effects: lower rates of social group stability, increased mate searching and ranging behaviors, less time feeding, more frequent vigilance behaviors, higher conspecific aggression, and delayed entry into hibernation (Brashares et al. 2010). The Vancouver Island marmot reintroduction program has therefore focused efforts to increase the number of marmots released to help densities rebound and optimistically reestablish their fitness enhancing social behaviors at the core of their fitness needs.

These sorts of empirical and modeling insights enforce the critical recognition of nested levels of organization in social species and why the social group needs to be incorporated into plans as a unit of measurement for actionable conservation. Recovery programs that promote larger cohorts of reintroduced individuals are poised to alleviate Allee effects, to strengthen population-level demography and intergroup interactions, and to increase reproductive success (Lurch et al. 2017, Angulo et al. 2018).

Is recovery ecological or demographic?

The broader objectives for both ecosystem and species recovery expressed in the ESA (16 U.S.C. §1531(b)) as a mandate for ecological restoration has historically received insufficient emphasis when the law is implemented (Rylander et al. 2020). The ESA is often seen as a law of last resort, an emergency room measure when state-level management has failed to prevent species from spiraling toward extinction before species are federally listed (Patlis 1996, Fischman 2004, Schwartz 2008). Although the ESA provides a process for returning species management to state and tribal governments once threats are ameliorated and adequate regulatory mechanisms are in place, lawmakers did not anticipate or realize the biological consequences of local entities managing delisted species at their minimum population size threshold in perpetuity (Zellmer et al. 2020). Federal agencies have, however, recognized that the heightened risk of extinction if listed species are sustained at low abundance may constitute jeopardy (i.e., appreciably reduces the likelihood of survival and recovery; NOAA 2004).

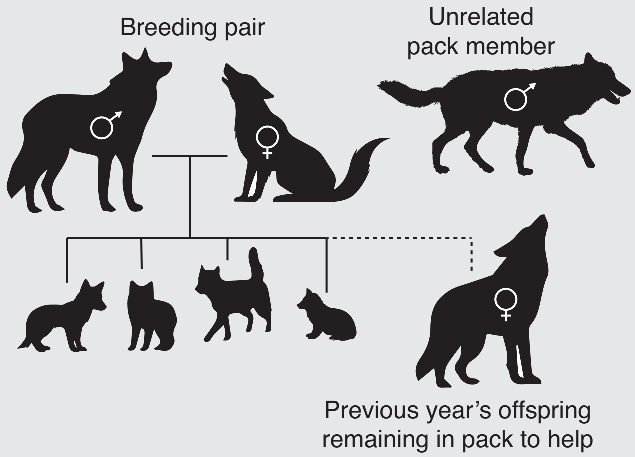
Recovery plans are often structured to encompass the 3Rs of conservation biology: *resiliency* (the ability to respond to stochastic or transient events), *redundancy* (the ability to respond to catastrophic mortality via existence through multiple populations), and *representation* (the inclusion of the breadth of geographic variation and adaptive potential with respect to long-term changes in the environment and ecological process; Shaffer and Stein 2000, Wolf et al. 2015). Under the 3Rs framework, recovery means a species should be present in many large populations arrayed across a range of ecological contexts (Shaffer and Stein 2000). We argue that the social group is the foundational unit for social species and is an essential element to consider for their recovery to historic levels or for reinstalling a functional ecological role.

The USFWS fails to consider gray wolf sociality in their recovery plan

The gray wolf is a good illustration of our broader theme for several reasons. Wolves have a fast-paced life history, are territorial, and possess rich social lives with distinct cultures that are vertically transmitted through social learning (box 1; Packard 2012, MacNulty et al. 2020, Smith et al. 2020). Gray wolves were originally provided protection as one of the first species listed under the ESA in the United States. Their protection has cycled between ESA listing and delisting for decades as the courts have repeatedly found agency recovery guidelines inadequate from a scientific and legal perspective and their relative protection has varied across political boundaries (Greenwald et al. 2006,

Box 1. The importance of wolf social groups and roles in packs.

Females often remain in their natal pack, assist in pup rearing, and wait to acquire a breeding position when available (on average, natural breeding pair turnover occurs every 2–3 years; Smith et al. 2020). Breeding wolves are more likely to lead the pack during travel, exhibit new behaviors, and initiate new pack activities (Murie 1944, Mech 1966, Peterson 1977, Peterson et al. 2002). As pups mature, they typically disperse from their natal pack between 1–2 years of age, providing a mechanism both for inbreeding avoidance and to search for an unrelated mate (Mech and Boitani 2003, Smith et al. 2020). Alternatively, nondispersers may compete to elevate their social rank within a pack and potentially rise to become a breeder. The wolf pack also is central for learning dominance, conflict management, and developing relationships with others (Palagi et al. 2016).



Packs can be composed of a mixture of maturing offspring and unrelated wolves (Mech and Boitani 2003, Smith et al. 2020), each with specific roles in their social group to support pack activities as well as provide learning experience for pups as they develop (Mech 1999, Cassidy and McIntyre 2016).

Packs engage in a plethora of rich social and nonsocial interactions that include group defense and resource acquisition, and are often mixed in composition across sex, age, and social roles or ranks (Packard 2012, MacNulty et al. 2014, Cassidy and McIntyre 2016).

The benefits of forming social groups are enhanced when combined with active defense of territories, which increases survival of offspring, collective protection, and provisioning for the group (Kittle et al. 2015). Natural variation in prey availability, territory quality, disease, and degree of direct competition with other packs influence the lifespan and resiliency of a pack. Variation in social learning between gray wolf packs in Yellowstone National Park drives cultural variation (Tallian et al. 2023). Smith and colleagues (2000) studied how 41 Yellowstone National Park gray wolves interacted with bison, a formidable prey species three times more difficult to hunt than elk and requires a larger pack size to mitigate this risk (MacNulty et al. 2014). From their observations, only two wolves had encountered bison prior to their reintroduction. Despite coexisting with each other over their evolutionary history, wolves that are entirely naive to bison learned hunting strategies from conspecifics who were experienced bison hunters. They further show that wolves can learn to prey on livestock following expansion into agricultural lands (Fritts and Mech 1981).

Carroll et al. 2010, 2021, USFWS 2024a). On 2 February 2024, the USFWS announced a ruling that included a call for a first-ever national gray wolf recovery plan to be completed by December 2025. At the same time, Montana and Idaho adopted laws and regulations “designed to substantially reduce gray wolf populations in their states using means and measures that are at odds with modern professional wildlife management” (USFWS 2024b, 2024c). Secretary of the Interior Haaland said, “I am committed to ensuring that wolves have the conservation they need to survive and thrive in the wild based on science and law.… It is critical that we all recognize that our nation’s wolf populations are integral to the health of fragile ecosystems and hold significant cultural importance in our shared heritage” (USFWS 2024b). However, the USFWS has been inconsistent in the application of the 3Rs in recovery planning for gray wolves. The recent Species Status Assessment Report for the gray wolf in the western United States (USFWS 2023) claims that peripheral gray wolf populations could be lost without imperiling the core population’s viability and resilience (USFWS 2023). From this, we conclude that the USFWS is considering each of the 3R elements in isolation, rather than as the coherent framework to ensure long-term genetic viability, adaptive potential, and ecosystem health as originally proposed (Shaffer and Stein 2000). Effective recovery strategies should coherently assess the genetic and demographic effects of population structure at scales ranging from the fundamental social unit (i.e., a pack) to metapopulation. Recovery is more than population viability and should include sociality, which is a foundation for eco-evolutionary potential and ecological function (Pyare and Berger 2003).

The USFWS historically included language that considered the social unit and, minimally, the effective population size for two *in situ* wolf recovery plans. The original recovery plans for the northern Rocky Mountain and the eastern timber wolf included specific criteria for the number and tenure of breeding pairs for delisting to occur (USFWS 1987, 1992). For long-term viability and persistence, the former plan stipulated delisting after "securing and maintaining a minimum of 10 breeding pairs of wolves in each of the three recovery areas for a minimum of three successive years" (USFWS 1987). The latter revised plan stated that "a healthy, self-sustaining wolf population should include at least 100 interbreeding wolves," but the definition of *interbreeding* was not provided and is expected to elicit divergent interpretations (USFWS 1992). Furthermore, the only context in which the USFWS has considered Allee effects is with their continued reference only to genetic diversity (USFWS 2020), where they dismiss the potentially negative effects of human-caused mortality at the population level "due to the life-history characteristics of gray wolves," where there is an assumed plethora of available replacement breeders (USFWS 2020). This assumption fails to consider the dynamics and natural selection on pack structure, roles, dispersal, available territory, and reproduction (Packard 2012).

Although sexual maturity can occur at younger ages when wolf densities are low (Wikenros et al. 2021), the reliance of approved management plans on increased reproduction following human-caused mortality therefore permits suboptimal individuals (and reduced genomic diversity) to enter the breeding population. A recent study reported that wolves in Yellowstone National Park who were successful in naturally entering into a breeding position in the pack had significantly lower inbreeding coefficients, shorter tracts of homozygosity, and longer lifespans than nonbreeding individuals (vonHoldt et al. 2024). Furthermore, the USFWS also declared an understanding that pack dissolution often follows the mortality of breeding individuals (USFWS 2020). To that end, the USFWS has built a management design that "wolf populations can rapidly overcome severe disruptions, such as intensive human-caused mortality or disease, provided immigration from either (or both) within the affected population or from adjacent populations occurs" (USFWS 2020). These assumptions illustrate how there is clear dismissal of social behavior and interindividual relationships. Much of the wolves' recovery has been focused on an overly simplified goal that "recovery success" is when "the [wolf] population size [is] to remain large enough, with sufficient connectivity and genetic diversity, to avoid consequential levels of inbreeding or inbreeding depression in the future" (USFWS 2024b). This interpretation conflates *adaptive capacity* with representation without considering its nexus with resilience. The agency's aim is merely to avoid complete human-caused extirpation of wolves from the entire western United States without considering the value of complex life histories and critical social attributes.

The consequences of anthropogenic disruption of social groups

Humans have a demonstrable negative demographic effect on many carnivores, directly through hunting but also via indirect or multiplier effects mediated by social structure. For example, human-caused mortality of male brown bears (*Ursus arctos*) led to increased infanticide rates, which, in turn, reduced the population growth rate (Swenson et al. 1997). Similarly, wolves living near humans experience a variety of deleterious demographic consequences, directly through wolf killing and more indirectly through the modification of landscapes (urbanization, managed forests, agriculture), which changes the ecosystems in which wolves live (Tallian et al. 2023). Although wolves will modify their daily activity to minimize their interactions with humans and will find ways to continue their natural ecological role as a predator (Ciucci et al. 1997, Fritts et al. 2003, Ordiz et al. 2013, 2021, Milleret et al. 2018, Mancinelli et al. 2019, Johnson-Bice et al. 2023), that role is inversely related to the degree that their landscape is modified (Tallian et al. 2023). Such modifications increase the probability that wolves will consume livestock or anthropogenic food items, dampening their role as a top-down predator in less modified ecosystems. Wolves will use artificial structures such as roads or will follow fence lines for movement corridors, thereby increasing the opportunities for conflict with humans and concomitant wolf mortality. Because social structure directly defines wolf fitness, lethal removal of individuals can have deleterious consequences beyond lineage loss (Gompper et al. 1997), such as group fracturing, which will deteriorate behaviors that reinforce social structure and learning (Shannon et al. 2013, Borg et al. 2015, Snijders et al. 2017, He et al. 2019, Maldonado-Chaparro and Chaverri 2020).

Although conspecific mortality is common in the wild (Cassidy and McIntyre 2016), anthropogenic disturbance is known to be one of the most important determinants of wolf pack size (Tallian et al. 2023) and dispersal (Sanz-Pérez et al. 2018, Morales-González et al. 2021). Once packs lose breeding individuals, the pack's persistence, reproduction, and pup survival are all compromised (Brainerd et al. 2010). The negative impacts of wolf mortality, even the loss of a single wolf, especially a leader, is detrimental to the wolf pack's persistence and reproduction, with smaller packs less able to rebound (figure 1; Cassidy et al. 2023). Consequently, if a wolf pack drops below a minimal viable size because of reduced reproduction combined with lowered recruitment, it may fully dissolve (Courchamp and Macdonald 2001, Smith et al. 2008, Ausband et al. 2015). It is noteworthy that when human-caused wolf mortality is reduced, pack structure may be restored (Rutledge et al. 2010). The timing at which wolf loss through mortality occurs is also vital, with negative effects on pack viability amplified during critical life history stages such as breeding, denning, and parental provisioning. Pack-level disruption and dissolution are often masked by the appearance of population-level stability in abundance estimates and are therefore commonly overlooked when population assessments fail to consider subpopulation dynamics. Therefore, it is essential that management policies and conservation planning include an objective to maintain functionally healthy and stable social groups.

The problem with political boundaries for conservation

Populations of social species may be particularly vulnerable to the effect of contrasting management across political boundaries. Of course, we do not expect wide-ranging animals to restrict their activity to protected areas, and many of the negative consequences of human-caused wolf mortality occur outside the protective and management authority boundaries of national parks (Hebblewhite and Whittington 2020, Sells et al. 2022). Nevertheless, transboundary movements place wolves in potential death zones; gray wolves, for instance, spent significantly less time in adjacent unprotected landscapes (4%–43%) with a human-caused mortality rate of 22%–58% above that in protected zones (Cassidy et al. 2023). The striking question is this: If collared wolves have upward of a 58% chance of human-caused mortality, and the percent of collared wolves per population is small (approximately 25%–40%), what is the estimated human-caused mortality rate for noncollared wolves in unprotected or transboundary landscapes? A 30-year study of transboundary gray wolves in Banff National Park similarly reported significantly lower survival rates when wolves left the protective boundaries

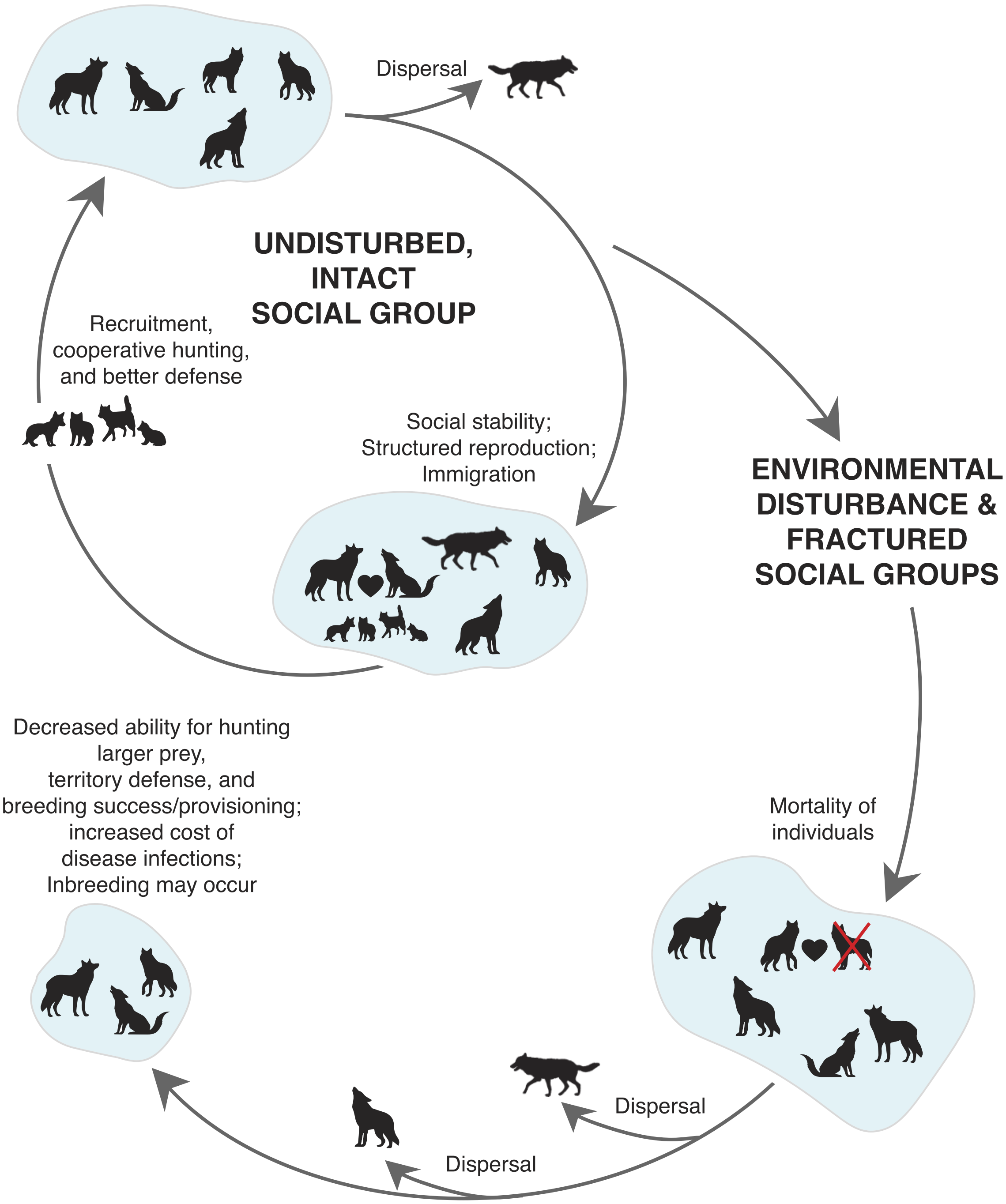


Figure 1. Consequences on pack structure after loss of critical members. Source: Adapted from Stahler and colleagues (2013).

relative to rates within the protected area (0.44 versus 0.84, respectively; Hebblewhite and Whittington 2020). It is obvious that when wolves leave the boundaries of protective landscapes, they have a significant increase in risk of human-caused mortality. Improved knowledge about such mortality is requisite to modeling population recovery across the population's range, especially outside of protected areas.

In Yellowstone National Park, gray wolf harvest mortality is additive rather than compensatory, as would be expected in a highly social species where individual fitness depends on a functional pack, with the lowest survival rates occurring in years with unlimited wolf killing (0.72, relative to no harvest years of 0.86 and years with quotas of 0.78; Cassidy et al. 2023). The ultimate consequences of additive mortality will be greatest on transboundary wolves and manifest as negative social, genetic, and ecological effects. Limiting the harvest quota size through an informed lens focused on supporting social ecology will ultimately minimize negative impacts on wolf populations and avoid the social meltdown of Allee effects. But as wolf management is currently structured, policymakers must balance the needs of communities and the universal value of a healthy gray wolf population. The immediate challenge is to cooperatively create shared values for transboundary wolf management. Tourism may be one such shared value because wolf-related tourism was estimated to add at least $82 million per year into the local economy with the greater Yellowstone area (Idaho, Montana, and Wyoming) from national park–bound visitors (RRC 2022). Cooperation of the greater Yellowstone states could increase economic efficiency through sharing costs and activities, giving higher economic benefits (almost $1 million) to these states, and such cooperation would result in higher wolf numbers being maintained (the model expectation is projected to be approximately 2300 wolves; Goodwin et al. 2022).

Federal funding for endangered species recovery is perennially inadequate to the task, and some have argued that more ambitious recovery goals for species such as wolves would expend resources needed for other lesser-known species of concern. However, agency funding levels fluctuate on the basis of political trends, and there is no guarantee that a reduced effort for one species will result in increased resources for the recovery of other species. Ambitious recovery efforts for a keystone species can have cascading effects both ecologically and sociopolitically, by increasing societal appreciation for the natural world and biodiversity or conversely increasing political opposition to recovery efforts. There is no simple trade-off between resource allocation and species recovery, nor is there a simple path to building value of nonhuman nature (Vucetich et al. 2017).

We must all do better and construct conservation policies in light of social species

For the approximately 6000 gray wolves estimated to live across 11 lower continental US states and upward of 11,000 in Alaska and in landscapes shared with more than 330 million people, large carnivores continue to face uphill battles for being valued among the Earth's biodiversity (Boitani et al. 2022, Ripple et al. 2022, Ausband and Mech 2023, Cardini and Crist 2024). Wolves will not be saved simply by preventing their numbers from declining; we must value the entire ecosystems in which they live and function and must preserve their entire communities as parks and protected areas, which inherently include social group structures. The space required for natural behavioral ecology to persist, especially for large, social species, is often larger than protected spaces (Berger 2017). Beyond the desire to have more protected space, we can more immediately design new plans and adjust existing plans to incorporate the fundamental unit is the social group. For humans and other wild animal species, social environment and interindividual relationships shape health and survival and are the foundation for longevity in obligately social species (Snyder-Mackler et al. 2020).

Of the delisting benchmarks used, the placement and importance of carnivores within their ecosystems has been notably absent and can be interpreted as this being less appropriate than a demographic benchmark (Pyare and Berger 2003). The current strategy has explicitly valued humans where decisions are prioritized on the basis of the resulting impact on what people value and placing our world undeniably on the path for a nature-based dystopic planet (Vucetich et al. 2017, Bradshaw et al. 2021, Berger et al. 2024). There is an immediate need to improve management plans, especially for endangered or threatened species, and such must necessitate statutory recognition and protection of the social structures in group-living species; it is only through the group that we humans as arbiters of Earth's biodiversity can we prevent or mitigate the negative impacts of anthropogenic activities and climate change (box 2). The argument is not about the correct model or the correct control used to understand the ecological value of gray wolves but about how to value the future of ecosystem health and viability (Vucetich et al. 2017).

Box 2. Constructing a policy framework that incorporates social behavior.

Policy infrastructure

Collect evidence for social behavior and animal culture, either directly through field studies or indirectly through documenting variation in behavioral strategies. Additional critical evidence would be the transgenerational transmission of such behaviors, equating to cultural inheritance.

Assess the degree to which behavior and culture are associated with vital rates (e.g., survival, reproduction, dispersal).

If there is variation in social behavior and culture in a population and between social groups, this suggests that social groups are repositories of social knowledge and culture, which require conservation.

Implications are for policymakers to construct management units on the basis of the phenotype of the social group and culture and habitat preserves, which support the persistence of social groups and culture.

Suggested regulations and structural designs

The objective is to maintain as many functional social groups that the habitat supports and to support the fitness of the individual members. An assumption is that larger social groups buffer the loss of a single individual and retain the ability to reform social connections through redundancy (Naug 2009).

Limit anthropogenically driven mortalities in adjacent jurisdictions to match natural mortality rates within protected national park landscapes. This extends beyond intentional wolf mortality (i.e., hunting or harvest or poaching) to include vehicular collisions, which cause 9% of wolf mortality rates (Cassidy et al. 2023), through signage, speed limit restrictions, or green bridges.

Implement a buffer zone design on the basis of the landscape used by wolves when they traverse political boundaries into neighboring jurisdictions.

No hunting permitted during the breeding season and no killing of dispersers.

Maintain full protection of wolves regardless of where wolves occur with increased legal consequences for wolf poaching.

Study the consequences of wolf removal as a function of pack size to identify whether it is possible to reduce the population without impeding social function.

Genetic recommendations

Protect and support bidirectional dispersal with subsequent reproduction (effective dispersal) to ensure at least one genetically effective migrant per generation.

Increase local effective population size to achieve an increased regional effective population size that approaches 1000 for long-term sustainability.

The language used within section 2b of the ESA (1973) supports the consideration of ecosystem value when conserving species: “The purposes of this Act are to provide a means whereby the ecosystems upon which endangered species and threatened species depend may be conserved, to provide a program for the conservation of such endangered species and threatened species, and to take such steps as may be appropriate to achieve the purposes of the treaties and conventions.”

Conservation programs and delisting assessments are well supported by the ESA to include relevant studies and objectives pertinent to restoring, monitoring, and preserving the function of the endangered species’ ecosystem. Although alternative stable states exist for ecosystems (Folke et al. 2004, Hobbs et al. 2023), restoring an apex species such as wolves to an ecosystem is valuable (Phillips 2020) but is not an immediate solution for maintaining ecosystem health (Allen et al. 2017, Brice et al. 2022). We must prevent their extirpation to ensure ongoing ecosystem services rather than attempting to restore those services after their loss. Because wolves cross political and regulatory boundaries, it is critical that all possible governing bodies work under common values and goals for conserving species in healthy ecosystems. Across the species and political boundaries, it is essential that regulatory plans include social structures as a core features recovery guidelines on which genetic, species, and ecosystem health relies.

Acknowledgments

We are grateful for early conversations with and feedback from Robert Crabtree, L. David Mech, Daniel Stahler, Rick McIntyre, Jeremy Sunder Raj, Kira Cassidy, and Brenna Cassidy. BMV is an active member of the Red Wolf Recovery Team and has received funding from the US Fish and Wildlife Service for genomic studies of red wolves and coyotes along the Gulf Coast of the United States, as well as funding from the Turner Foundation for genomic studies of gray wolves but declares no conflict of interest with respect to this paper. DTB has served on recovery teams in the US and Canada but declares no conflicts of interest with respect to this paper. JB has no conflicts of interest with respect to this paper. CC has served on recovery teams in the US and Canada and declares no conflicts of interest with respect to this paper.

Author contributions

Bridgett M. vonHoldt (Conceptualization, Visualization, Writing - original draft, Writing - review & editing), Daniel T. Blumstein (Conceptualization, Writing - original draft, Writing - review & editing), Joel Berger (Conceptualization, Writing - original draft, Writing - review & editing), and Carlos Carroll (Writing - original draft, Writing - review & editing)

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Received: May 30, 2024. **Revised:** December 8, 2024. **Accepted:** December 13, 2024