A Framework for Evaluating Mechanisms to Support Seasonal Migratory Species

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Introduction

Migration is a vital adaptation for many species, and experiencing the awe-inspiring sight of seasonal or life cycle migratory species (hereafter referred to as "migratory species"[1]) as they journey across their annual habitat can heighten the connection between humans and wildlife. Despite collective interest, protection of these species remains inadequate in settings worldwide (Runge et al. 2014).

The additional two articles in this symposium describe how the ecological characteristics of migratory species determine conservation needs and inform economic policy analysis. Migratory species make spatial–temporal movement decisions across their annual habitat to satisfy particular needs at different times and places, implying the need for coordination about both the timing and location of conservation actions across the annual habitat (Albers

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[1]For simplicity, we use "migratory species" to include species that migrate to access resource and habitat needs across seasons, such as Neotropical migratory birds; those that migrate across their life cycle rather than the year, such as sea turtles that return to beaches to lay eggs; and species that migrate over several generations across a year, such as monarch butterflies. This terminology distinguishes our focal species as cyclical migrators from species that disperse or migrate once to establish a new home range. Similarly, for simplicity, "annual habitat" is inclusive of all life cycle habitat for life cycle migrants.

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et al. 2023a). The annual habitat includes endpoints and the migration route itself, and its extent may include both private and public areas in jurisdictions and nations with different environmental rules and incentives for conservation (Albers 2023b). Thus, effectively supporting wildlife migration is a coordination challenge across both space and time.

The need for spatially coordinated conservation across multiple landowners has received substantial attention (e.g., Smith and Shogren 2002). Temporal coordination is less well studied. While permanent conservation is ready whenever a migratory species arrives, short-term conservation actions present potential cost savings—but a temporal coordination problem. Conservation that comes too early or too late relative to the species' use of a location has little value.

In this article, we present a framework to guide the selection and design of mechanisms to support migratory species by addressing their salient characteristics and different spatial and temporal needs. We focus on cost-effectiveness because the lack of ecological and economic information about these species challenges efforts to measure the social efficiency of different types and levels of migratory species support. We use the framework to explore how migration hampers the ability of existing mechanisms to meet species-support goals.

The remainder of the article is organized as follows: First, we briefly introduce existing species-support mechanisms and challenges associated with their implementation. We then present our definition of migratory species support, which includes traditional habitat conservation, actions that improve the connectivity of migratory habitat, and actions that reduce the risks faced during migration (either temporarily or permanently). To highlight the challenges of achieving cost-effective migratory species support, we explore four aspects that test spatial and temporal coordination: free riding, holdouts, transaction costs, and transboundary coordination. Next, we identify how characteristics of individual migratory species determine which of these challenges arise, informing the selection and design of effective mechanisms. Because of the unique nature of migration, no single mechanism is best suited to address the diverse habitat needs of a species during migration. Identifying the best context-specific approaches for species support is critical for better policy. Finally, we apply our framework to two particular species—mule deer and monarch butterflies—to highlight conditions under which existing mechanisms can be successfully implemented as well as conditions that might require combinations of, or modifications to, existing mechanisms.

Available Mechanisms to Support Migratory Species and Their Challenges

In this section, we first present brief overviews of the mechanisms available to motivate species-support actions on private and public lands and then discuss challenges to their implementation. Next, we discuss how to evaluate the viability of the available mechanisms in the context of migratory species support.

Available Mechanisms

The suite of mechanisms available for species support includes direct regulatory intervention, voluntary mechanisms, community-based conservation, and behavioral mechanisms. Direct regulatory intervention includes restricting use of public and private lands. Restrictions on public lands may be temporary (e.g., seasonal closures) or permanent (e.g., parks) and require sufficient legal and governance institutions for effective conservation. Restrictions on private land require adequate monitoring and enforcement to overcome the information asymmetry that arises when landowners know more than regulators about the presence of focal species in particular locations of suitable habitat.

Voluntary mechanisms provide incentives for conservation actions on private property. They can increase program cost-effectiveness relative to direct regulatory intervention by taking advantage of heterogeneity in marginal provision costs across program participants (Newell and Stavins 2003; Ferraro 2008). Such mechanisms include conservation easements, payment for ecosystem services (PES) programs, and market-based conservation credit programs. A conservation easement sells portions of the property title to an easement holder, transferring some development and management options from the owner to a conservation organization (Langpap, Kerkvliet, and Shogren 2018). PES programs compensate resource users for desired biodiversity or ecosystem service provision or conservation-friendly management practices. Market-based conservation credit programs (Fox and Nino-Murcia 2005; Hansen et al. 2017) rely on voluntary actions from stakeholders whose property includes habitat for wildlife that could be threatened by the pursuit of private profits. In other words, they are likely subject to thin markets unless there is regulation, monitoring, and enforcement to motivate participation on both sides of the market. Each mechanism can be used to motivate temporary or permanent species support; temporary actions are associated with lower opportunity costs but potentially higher transaction costs (because of repeated program enrollment, temporal coordination, or both) and lower benefits to species.

Voluntary mechanisms that motivate spatial coordination across program participants can be important for migratory species because they otherwise can exacerbate fragmentation (e.g., Panchalingam et al. 2019). An agglomeration bonus, offered in addition to other payments for coordinated conservation actions on adjacent patches, encourages coordinated conservation and has been shown to increase contiguous habitat in laboratory experiments (e.g., Parkhurst et al. 2002). Spatial conservation auctions can be used to increase the concentration or connectivity of conservation through coordination bonuses.

Community-based conservation refers to a community working collectively to achieve a conservation goal that typically links conservation with local benefits, engages local communities as active stakeholders, and devolves control over natural resources (Brooks, Waylen, and Mulder 2012). Motivation for community-based conservation derives from a recognition that biodiversity conservation and livelihood needs are complementary goals (Berkes 2007). Groups have been shown to work collectively to achieve socially optimal outcomes in situations involving public goods and common pool resources in many settings (Ostrom 1990, 2000). In contrast, externally imposed rules tend to crowd out endogenous cooperation by discouraging the formation of social norms (Reeson and Tisdell 2008). This mechanism may be quite well suited to motivate temporary conservation actions, with repeated adoption demonstrating commitment to the common good.

Behavioral mechanisms, like nudges, leverage the desire to conform to social norms, the influence of peers, emotional associations, and the power of ego to cost-effectively influence behavior to align with program goals, as in agri-environmental contexts (Palm-Forster et al. 2019). While appealing because of their minimal administrative costs, few studies consider the permanence of behavioral change achieved through the use of nudges (Croson and Treich

2014). Behavioral mechanisms may be appealing as motivation for adoption of one-time conservation actions that do not suffer from the challenges of repeated program enrollment, though repeated enrollment for temporary actions could be useful in changing the social norm.

Challenges to Mechanism Efficacy

The coordination required to support migratory species means that strategic behavior by stakeholders can impede migratory species support by inhibiting coordination. We focus on four key challenges to the coordination needed for successful, cost-effective migratory species support: free riding, holdouts, program transaction costs, and transboundary coordination.

Free riding is the classic challenge to the efficient provision of public goods. Given the nonrival and nonexcludable nature of public goods, a free rider can enjoy preferred private consumption while relying on the provision of the public good by others, leading to its underprovision. The benefits of habitat conservation can extend beyond the conserved area, and these positive spillovers (e.g., proximity to open space, larger fish available adjacent to marine reserves) make free riding more likely.

Strategic holdouts refer to landowners who wait to participate in a conservation program, such as a PES program purchasing forested parcels to prevent forest conversion, to capture rents. Strategic holdouts differ from honest holdouts for whom the offered price lies below their reservation price. Although previous work in an imperfect information setting finds that reservation prices can contribute to holdouts in the context of land assembly (Eckart 1985; Shavell 2010), imperfect information is only one driver of strategic holdouts. Miceli and Segerson (2012) explore Nash bargaining with complete information in land assembly efforts, finding that strategic holdouts arise in settings with (1) sequential bargaining between a buyer and multiple sellers, (2) commitment during bargaining (meaning that all sales are final), and (3) reservation prices that exceed the value of individual parcels to the buyer, making partial assembly inefficient.

Transaction costs are generally defined as the costs of participating in a market or administering a program or policy, including costs associated with gathering information, contracting, and monitoring and enforcing rules. High transaction costs on the part of both private individuals and agencies can reduce the cost-effectiveness of conservation mechanisms. Private individuals face transaction costs with conservation programs that compensate them for species-support efforts, including the costs of collecting information about actions and programs, submitting applications, and complying with program rules. From the conservation agency perspective, transaction costs associated with planning, implementing, and supporting conservation programs and policies comprise a substantial portion of the full administrative cost (McCann et al. 2005). Programs to support repeated temporary species-support actions may involve high transaction costs for individuals and agencies that could limit program participation and increase administrative costs.

Transboundary coordination is required for the adequate provision of public goods that cross jurisdictions but may be difficult to achieve given free riding and reliance on international agreements to spur cooperative action. The strategic decision to provide a transboundary public good depends on how contributions by individual nations affect its supply (Cornes and Sandler 1996). In the case of “weakest-link” public good supply, a minimum contribution amount is required by all suppliers; therefore, the total benefit of public good provision is limited to the level supplied by the nation contributing the least. Under the less restrictive "weaker-link" public good supply, the nation with the smallest contribution has the greatest influence on the production level of the public good, though the actions of other nations still increase provision.

Evaluation Context

Evaluating the social efficiency of different types and levels of migratory species support is difficult given the challenges associated with measuring nonmarket values of environmental amenities. In particular, we lack tools to conduct economic valuation of species fitness and ecological understanding of how habitat improvements across migration routes alter fitness. For these reasons, we use cost-effectiveness to evaluate mechanisms that support migratory species.

In evaluating the mechanisms to protect the quality of connected annual habitat, we consider a situation in which a species migrates between two endpoints (e.g., winter and summer habitats), traversing areas that may be highly degraded (e.g., metropolitan areas along flyways). To successfully protect the species, mechanisms must ensure access to sufficient habitat at endpoints and along the migration route. This is perhaps the most novel and challenging aspect of migratory species support because it potentially introduces a large-scale weakest-link problem. Coordination along two dimensions—spatial and temporal—may be necessary, depending on the requirements of the species.

An Evaluation Framework

Animal migrations vary greatly in terms of mode and medium of migration (e.g., aerial, aquatic, terrestrial), duration (minutes, days, or weeks), and distance (centimeters to thousands of kilometers). Evaluating where, how, and at what spatial and temporal scales mechanisms should be implemented to support migrations requires an understanding of the underlying salient characteristics of the species. In this section, we focus on two key ecological characteristics—route plasticity and resilience—to create a framework for evaluating which mechanisms best meet the unique needs of a migratory species at different points along its migratory route.

Route plasticity is the combination of stopover site fidelity, required connectivity, and temporal fidelity of migration (figure 1; for additional details, see the appendix, available online). High route plasticity means that the species' movements between endpoints can vary considerably across space and time in response to stochasticity and disturbances on their route. Variation in migration timing can be triggered by many factors, including local weather (Horton et al. 2020), seasonal resource availability (Geremia et al. 2020), and day length (Wingfield 2008). Conversely, low route plasticity means that species choose locations and timing consistently across years despite disruptions, which implies more certainty about the timing and location of migration.

Resilience is the combination of behavioral plasticity—the species' ability to change behavior to cope with habitat disturbance—and niche breadth, which characterizes the diversity of species' resource use (figure 1). Low behavioral plasticity precludes the ability to respond to shifts or disturbances by changing temporal migration decisions, and narrow niche breadth

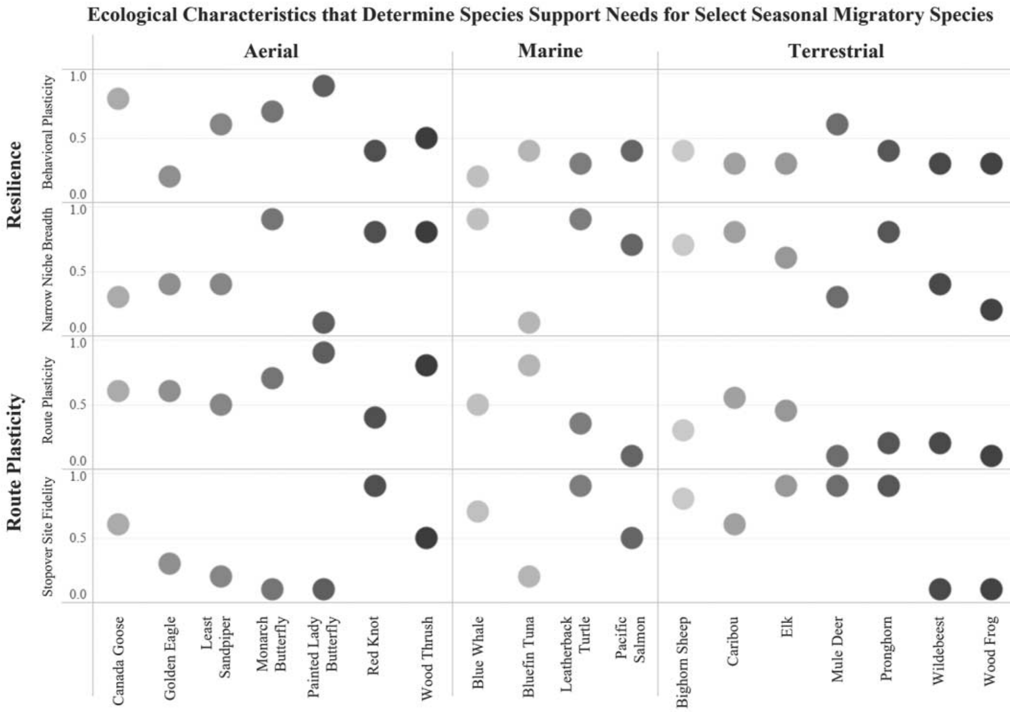

Figure 1 Relative importance of resilience and route plasticity, and their underlying ecological attributes, for various migratory species. Circles indicate the relative importance of each attribute, with one indicating that the attribute is a critical feature during migration. See the appendix (available online) for methods and sources used to develop these rankings of resilience and route plasticity. A color version of this figure is available online.

is associated with high vulnerability to shifting biotic or abiotic factors. Taken together, high resilience is associated with an ability to adjust temporal behavior and address resource needs in a range of habitats, leading to low vulnerability to disruptions along the migration route. The levels of these two characteristics determine the conservation needs for migratory species throughout migration.

Using the four quadrants of high–low resilience–route plasticity space as our evaluation framework (figure 2), we consider how migratory characteristics (figure 2*a*) inform mechanism choice (figure 2*b*) and related challenges. Then, we discuss the additional challenges of transboundary coordination.

Quadrant I: High Resilience and High Route Plasticity

When migratory species display high route plasticity and high resilience, programs can be effective without many restrictions about where, when, and how actions need to be taken. In this case, agencies can use cost-effective voluntary PES programs with streamlined application and enrollment procedures to generate species support. The availability of substitute migratory routes removes the weakest-link supply issues but creates opportunities for free riding; thus, program participation is critical to success, and mechanisms that provide incentives for migratory species support are likely important.

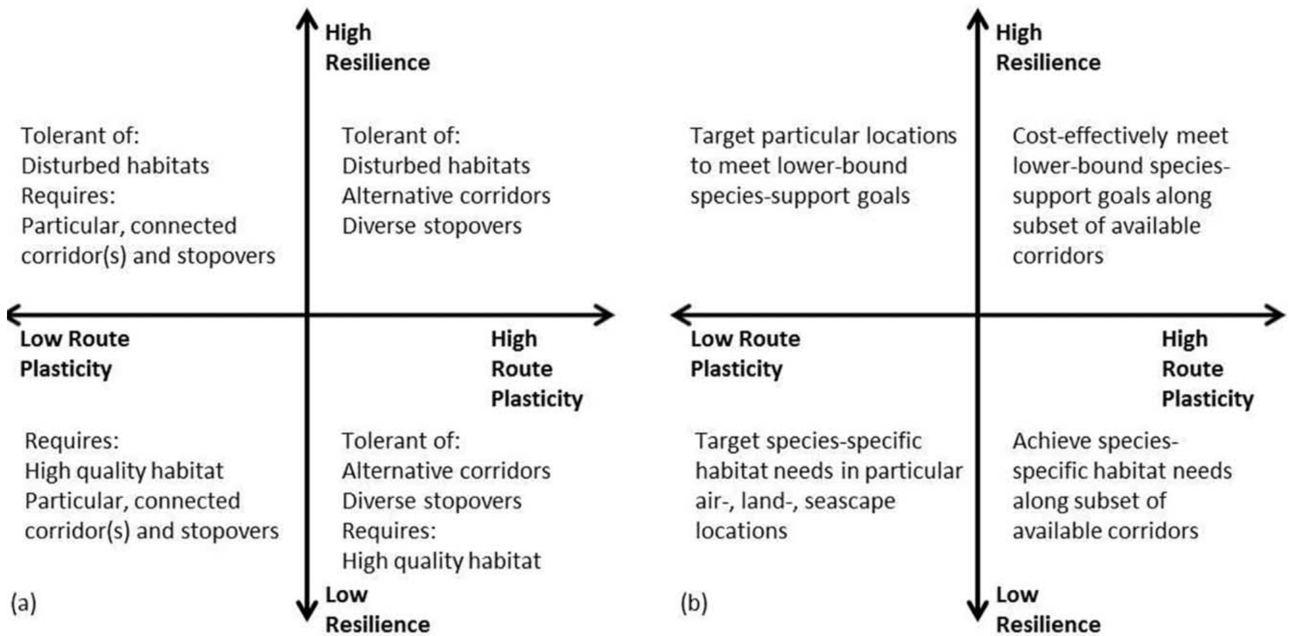

Figure 2 Framework for evaluating migratory species-support mechanisms, identifying characteristics that determine migratory species' needs (*a*) and the resulting prioritized objectives of mechanisms based on these characteristics (*b*). Free riding is a problem with high plasticity, while holdouts are a major concern with low plasticity. Transaction costs are a challenge with low resilience.

Conservation auctions are appropriate in these settings, but the bidding process must be simple and streamlined to moderate the challenges of bid formation (e.g., identifying which available species-support action to provide at what offered bid, which affects the probability of winning the auction and the payment conditional on having the bid accepted) and to achieve widespread participation (Banerjee and Conte 2018). In practice, high transaction costs, such as those associated with program enrollment and bid formation, can limit participation in auctions (Palm-Forster et al. 2016; Rolfe et al. 2018).

Traditional mechanisms that offer financial incentives for migratory species support—such as conservation easements and PES programs—also are appropriate for species demonstrating high resilience and route plasticity, but extrinsic motivation can reduce voluntary provision by crowding out the intrinsic motivation to contribute to the public good (e.g., Reeson and Tisdell 2008). Programs that recognize individuals' actions send an important signal and can be helpful in achieving the high levels of participation needed in this setting by establishing social norms (Dessart, Barreiro-Hurlé, and van Bavel 2019). For example, stewardship recognition programs (e.g., Certified Wildlife Friendly) and ecolabeling initiatives recognize actions that protect vulnerable species and can reward such actions via price premiums. Publicly committing to taking an action is a powerful behavioral driver because people generally aim to be consistent with public promises.

Community-based conservation is another useful tool for drawing out intrinsic motivation for migratory species support because it reflects community goals and values. Community-based conservation is particularly well suited for species with migratory routes that cover relatively limited distances in a small number of jurisdictions. Community-based conservation may also be appealing when species-support actions are temporary, because stakeholder knowledge of local habitat conditions can reduce uncertainty and transaction costs. Success will correspond to the value of the species in that community. We expect that these values could be high when species display high resilience because they may have larger, more visible populations. However, species abundance could make their conservation less salient. For more disparate migrations, which are associated with species when they display high route plasticity, complementary conservation mechanisms will likely be needed in tandem with community-based conservation to increase the scale of habitat and biodiversity protection.

The broad array of conservation actions suitable in these settings means that species support might be achievable at low private costs to program participants. For example, choosing an action with low opportunity costs may generate greater participation, and greater participation, in turn, can improve cost-effectiveness of migratory species support. However, if participants seek out the lowest-cost actions that generate few social benefits, cost-effectiveness is eroded. Preferences for low-cost actions also may lead to excessive rent seeking in conservation procurement auctions (Conte and Griffin 2019), particularly when the distribution of private benefits has high variance, reducing competition in the auction.

These possibilities suggest that species-support actions with low opportunity costs may still have high total costs if expensive monitoring and enforcement are needed to ensure increased provision of migratory species support. Programs targeting temporary species support also may have higher transaction costs if they require repeated program enrollment and impose a fee each time. Thoughtful program design—such as a uniform payment program with an easy enrollment process—is quite beneficial for short-term interventions that suffer from limited participation when transaction costs are high.

Quadrant II: High Resilience and Low Route Plasticity

When species display high resilience and low route plasticity, connectivity is key, requiring mechanisms that can promote spatial coordination—in particular, tools that motivate support actions at particular locations on the landscape. In this setting, an agglomeration bonus, whether offered in addition to a uniform payment or incorporated into a spatial conservation auction targeting action at particular locations along the route, rewards the coordinated adoption of conservation actions across properties. Such bonuses may have benefits in the temporal dimension as well, with additional payments available for long-term commitments to provide temporary migratory species support.

For an agglomeration bonus or spatial conservation auction to be useful in this context, payments must be restricted to properties crossed by the migration route. This additional targeting of potential participants could signal to property owners the importance of their participation, increasing the potential for strategic holdouts to erase the cost-effectiveness potential of such mechanisms. One path forward for conservation auctions would be to limit the amount of information shared with participants about the environmental quality of their potential species support (Conte and Griffin 2017).

Strategic holdout threats may lead some jurisdictions to opt for direct regulatory intervention over voluntary mechanisms reliant on extrinsic motivation for species support. Under the US Endangered Species Act, direct regulatory intervention has conserved habitat on private lands through temporary and permanent land use restrictions (Innes and Frisvold 2009). Examples include seasonal closures and/or use restrictions in key migratory nesting grounds, such as for migratory shorebirds along the Atlantic and Pacific coasts.

Alternatively, collective action of multiple stakeholders at the community level may generate spatial coordination locally. This specificity in the areas where species support is needed may lead to conditions that favor the self-governance that occurs under community-based conservation, including trust among stakeholders.

Because low-route-plasticity settings call for connectivity, support mechanisms are susceptible to the weakest-link problem. If the level of the public good provided is a function of the lowest support-providing stakeholder's actions, the incentive to free ride is mitigated.

Quadrant III: Low Resilience and Low Route Plasticity

Migratory species displaying low resilience and low route plasticity require particular types of habitat quality and configuration. Long-term conservation is likely needed to reduce the risk of habitat conversion to which species in low-resilience settings and low-route-plasticity settings cannot adjust.

Programs motivating repeated temporary conservation actions over a long time horizon or more permanent conservation may involve relatively low transaction costs. Additionally, long-term conservation of particular habitats favored by low-resilience species may mitigate the emergence of strategic holdouts by limiting the number of program enrollments and, therefore, the opportunities for stakeholders to learn about their importance to successful migratory species support.

Mechanisms like conservation easements or the establishment of protected areas through direct regulatory intervention are helpful, although potentially costly. Agency transaction costs of direct regulatory intervention can be high because of expensive monitoring and enforcing protections. These costs are lower when agencies or private organizations use conservation easements or buy critical land parcels, but transaction costs of one-time purchases can still be significant, implying that the cost-effectiveness of mechanisms that change property rights increases with contract length (Schöttker and Wätzold 2018). Conservation easements afford appealing flexibility to accommodate shifts in the use restrictions needed to achieve species-support goals.

PES programs are also helpful to support species with particular habitat needs, because they can target funds to locations and actions that achieve the desired habitat and configuration. Species displaying low resilience in particular may benefit from programs that pay for outcomes rather than inputs. However, the transaction costs involved with targeted and results-based PES programs are typically higher relative to uniform-payment PES programs for both the agency and participants (Palm-Forster et al. 2016; Wätzold et al. 2016). From the agency's perspective, transaction costs of targeted programs stem from the need for site-specific information about the effectiveness of different types of species-support actions: estimating these benefits requires time and expertise. From the individual's perspective, these programs can also be time-consuming, especially if novel mechanisms that take time to understand are used to allocate program funds (e.g., reverse auctions). This effort may be worthwhile for agencies and individuals in programs that provide payments over a long time horizon, but high transaction costs can significantly reduce the cost-effectiveness of programs focused on repeated short-term actions.

Strategic holdouts present a primary challenge when a species displays low resilience and low route plasticity. Given the weakest-link characteristic and location-specific support needs that arise in this setting, stakeholders have considerable power to wield. In the extreme case of species with a fixed migratory route that need connectivity across specific parcels, any mechanism seems susceptible to strategic holdouts (Munch 1975; Blume, Rubinfeld, and Shapiro 1984). The basic challenge involves distinguishing a strategic holdout from a genuine disagreement over the negotiated price, as the offer may indeed be less than a seller's true willingness to accept for their land.

Miceli and Segerson (2007) show that adding an outside threat into a bargaining model can overcome the holdout problem at the risk of putting too much land into conservation. Here, that threat could include eminent domain, with the government claiming land for conservation to prevent holdouts. Applying eminent domain in the context of nonresident migratory species could prove challenging, however, and eminent domain for temporary periods appears rare, suggesting the use of this threat only when the risk of holdout is large.

Quadrant IV: Low Resilience and High Route Plasticity

The need for particular habitat quality along multiple substitutable migratory routes means that opportunities to achieve cost-effective species support must overcome challenges associated with free riding and transaction costs. The opportunities for substitution across routes can mitigate the issue of strategic holdouts, so long as neither the social value of migratory species support by a particular stakeholder nor the costs of coalition formation are sufficiently high.

The migratory species' use of alternative routes could be tapped into via conservation procurement auctions with joint bidding (such that stakeholders along one potential route form a bidding coalition) to achieve cost-effective species support. Joint bidding codifies the coalition formation along the target migratory routes to establish corridors. However, for species that migrate across regions with diverse stakeholders, the transaction costs of coordination via conservation auction may be prohibitive. The availability of substitutable routes that contain adequate levels of required habitat also provide robustness to the threats that habitat conversion and climate change pose to migratory species, suggesting conservation strategies that might mitigate the risks of these threats through a portfolio of conservation actions across substitute locations.

Transaction costs may be substantial in the case of low resilience, due to the need for habitat that meets certain quality requirements. Mechanisms whose efficacy is less sensitive to transaction costs may be preferred in this case. Unlike voluntary mechanisms that might suffer from low participation rates due to high transaction costs, direct regulatory intervention and community-based conservation may be effective with low resilience.

Transboundary Coordination

Transboundary coordination can heighten the challenges of temporal and spatial coordination for migratory species with migration routes that cross international boundaries, especially when they display low route plasticity. Because a species with low route plasticity does not change its route in response to a nation's lack of action, it creates a weakest-link problem, in which unilateral actions do not benefit species. In this situation, nations prefer not to contribute unless they expect contributions from a substantial coalition of other nations. On the other hand, nations prefer to cooperate and may take the lead in supporting species if they have sufficiently strong expectations that other nations will follow (Touza and Perrings 2011; Vogdrup-Schmidt et al. 2018).

In contrast, high resilience across international boundaries creates weaker-link supply, given that the species can successfully traverse degraded habitats. With weaker-link supply, the nation with the smallest level of effort has the greatest influence on the level of public good produced, as with curbing the spread of invasive species or controlling the trade of endangered species (Touza and Perrings 2011). Here, nations prefer to take unilateral action rather than potentially forgo the benefits of the transboundary public good, and their actions can generate positive global benefits, even if other nations do not offer any provision. Still, nations find it more beneficial to defect from an international agreement once provision is guaranteed by others. Such support also serves as a commitment signal in a repeated coordination assurance game, in which the repeated nature is emphasized for resilient migratory species that can benefit from temporary support actions.

Uncertainty about how various actions to support species in a range of locations contribute to overall migratory species success further complicates coordination efforts, especially in a transboundary situation. If nations are unsure about the value of the contribution of other nations and the value of their own contribution, they will have a harder time identifying the likely behavior of others to determine their best responses. That challenge may influence the transaction costs of such international environmental agreements at all levels of resilience and route plasticity, with the availability of substitute locations and actions for species support, as in the case of high resilience and high route plasticity, magnifying this concern.

The challenges of international coordination seem to hold whether the respective nations rely on regulatory or voluntary mechanisms with extrinsic motivations to provide species support within their borders. Depending on the relationship between the involved nations, community-based conservation could be effective in changing norms for relevant stakeholders across borders to emphasize the private benefits of species support to each nation. Changing expectations about social norms could help with the formation of international environmental agreements to aid the focal migratory species, as nations typically join and comply with such agreements only when the agreement makes them better off (Barrett 2003).

Applying the Framework: Mechanisms to Support Mule Deer and Monarchs

We apply our framework to determine the mechanisms best suited to support the migration of two species, mule deer and monarch butterflies. These species have different resilience and route plasticity characteristics within and across their migratory routes (figure 3) that lead to varied exposure to the challenges facing conservation mechanisms. We use the framework to identify opportunities for improved species support in the future.

Mule Deer

Mule deer (*Odocoileus hemionus*) are migratory ungulates indigenous to western North America, ranging from northern Mexico to the Yukon Territory and California to the Great Plains states (Anderson and Wallmo 1984). Mule deer populations have been declining range wide, driven by diminished habitat condition from long-term drought and anthropogenic disturbances that fragment the landscape (Mule Deer Working Group 2020). Most mule deer populations overwinter in lower-elevation basins dominated by sagebrush steppe shrublands, migrating each spring to higher elevations as the seasonal green-up progresses and returning in the autumn along the same migration corridor. In western Wyoming, migration length varies between and within populations, ranging from 18 to 241 kilometers. These mule deer complete their migration in an average of three weeks, spending 95 percent of their spring migration foraging in stopover sites on emerging plants that are low in fiber and high in nutritional content to restore fat stores (Sawyer and Kauffman 2011). Migration in mule deer is a learned behavior that is passed from mother to young (Jesmer et al. 2018); as a result, they use the same stopovers between seasons and years, with little variation in migration corridors (Merkle et al. 2019). Mule deer migrations are negatively affected by semipermeable barriers to migration, such as fences and noise/lights from energy development. The property-right pattern along migration corridors and in stopover areas is a mosaic of public (federal and state) and private land, with many stopover areas overlapping parcels with different owners.

As inputs into our mechanism choice framework, we define mule deer as having low route plasticity and high resilience, because they exhibit high stopover site fidelity and require connectivity along corridors, and they forage among a variety of species, indicating their wide niche breadth. In addition, mule deer increase their rate of movement and reduce time in stopovers in response to semipermeable development, which can reduce population fitness (e.g., Wyckoff et al. 2018).

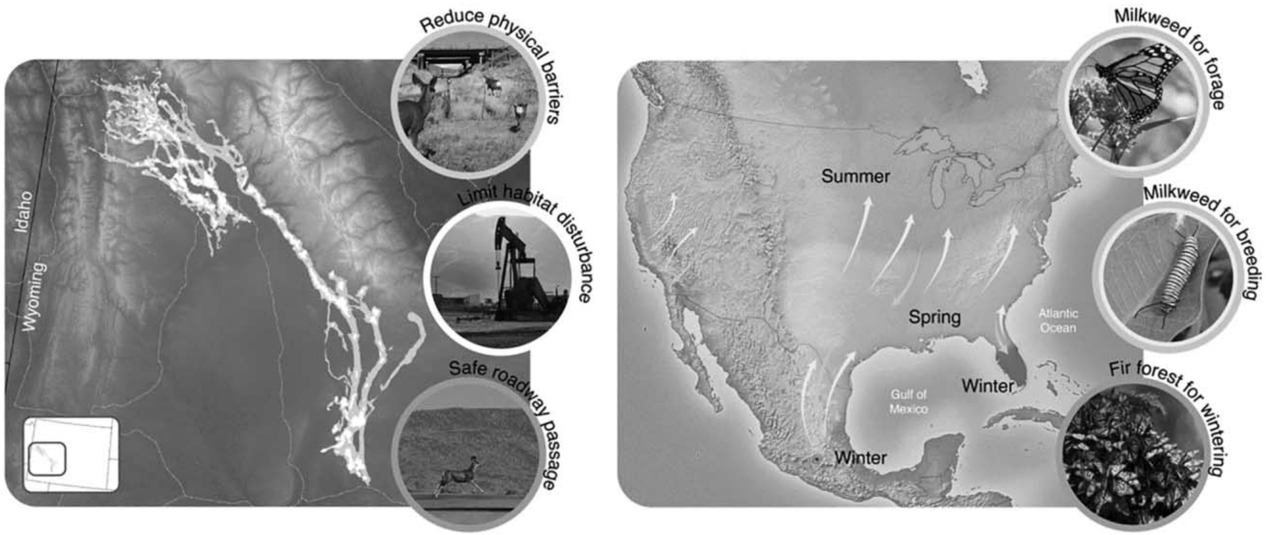

Figure 3 Illustrations of the migratory journeys of mule deer (*left*) and monarch butterflies (*right*). A color version of this figure is available online.

Given these characteristics, our framework indicates that mechanism choice should prioritize support of lower-bound species needs along key corridors—and that these efforts are likely to be confronted by the challenges of holdouts, with some transaction costs issues. If landowners are unaware of their land's value in the migratory path, spatial mechanisms, such as targeted conservation easements for high-value stopover sites or an agglomeration bonus for connected habitat, may be possible.

Due to low route plasticity, holdouts might recognize the value of their actions and their land, given the weakest-link characteristic of migration paths, creating a risk of coordination failure. As a result, direct regulatory intervention may be necessary to ensure preservation of a specific mule deer population's migratory route. The short duration of mule deer migration and their resilience across potentially degraded habitats mean that temporary interventions can be beneficial. Examples include seasonal reductions in activities on energy sites and seasonal dropping of fences on the migratory route.

Community-based conservation and behavioral nudges may have a role to play in preserving portions of mule deer migratory paths in ranching communities, where landowners may value wildlife viewing (e.g., agritourism revenues) or place personal value on migrating species. Either mechanism could induce cooperation in taking conservation actions to improve migratory success on the specific route and in stopovers of the local mule deer.

Ungulates in general, and mule deer in particular, are not currently managed and conserved through a coordinated policy across jurisdictions (local, state, federal) or across annual habitats, including the migration routes (Middleton et al. 2022). State policies designate migration corridors, bottlenecks, and stopovers to establish conservation measures and coordinate with other departments such as the US Department of Transportation—for example, to construct wildlife bridges over/under highways. Federal lands in the migratory routes are managed for many outputs including habitat quality for migratory ungulates. Although the emphasis in current management is on direct provision of the public good by public agencies, our framework calls for direct regulatory intervention on some critical pieces of private land as well.

A private organization, the Conservation Fund, purchased an important parcel within the Fremont Lake Bottleneck and donated that land to create the permanently protected, public Luke Lynch Wildlife Habitat Management Area (Elsbree 2015). Stakeholder participation in the planning process is a first step toward integrating private land conservation into broader conservation plans for migratory mule deer. For example, Wyoming establishes working groups of people from many perspectives to recommend conservation actions within migratory corridors that balance many objectives. In addition, the Wyoming Natural Resource Trust pays ranchers to make permanent wildlife-friendly modifications to fences.

Although no large-scale programs offer incentives to private landowners for temporary conservation, some rancher groups take down fences on a voluntary basis during migrations. Seasonal closures and timing restrictions on oil and gas leases on federal land also provide temporary improvements in connectivity.

Monarch Butterflies

Each year, millions of monarch butterflies (*Danaus plexippus*) traverse North America as they move between wintering and breeding (summering) grounds, a migration that spans thousands of kilometers and involves multiple generations of monarchs. Despite their status as an iconic

North American species, in the past 30–40 years, monarch populations have declined precipitously, by as much as to 99 percent (e.g., Pelton et al. 2019). A host of threats to wintering grounds and stopover locations in their breeding grounds are central to these declines, including habitat loss, climate change, and insecticide use.

Monarch migrations are the result of approximately four successive generations making latitudinal advances, rather than single individuals making round trips. Spring movements include a sequence of breeding, egg laying, development, and metamorphosis followed by northward flights, while one generation makes the fall migration and overwinters. Connectivity for migratory monarchs requires a distribution of milkweed at stopover locations across their flyway, and monarchs can shift their migratory route to align with the presence of their required habitat. However, grassland conversion and pesticide use have reduced the prevalence of milkweed throughout North America. In their overwintering habitat, monarchs are highly reliant on oyamel firs (*Abies religiosa*), which are concentrated in areas of Central Mexico and California. This creates a limiting overwintering habitat requirement. More than three-quarters of the overwintering habitat exists within the Monarch Butterfly Biosphere Reserve (MBBR), a world heritage site near Mexico City (Vidal, López-García, and Rendón-Salinas 2014). Deforestation and forest degradation in and near these forests, including in the MBBR, jeopardizes the monarch overwintering habitat.

Using our mechanism choice framework, we account for the needs of monarchs at different points in their migration. Monarchs move through breeding grounds for most of their migration; during this period, we define monarchs as having high route plasticity based on their ability to adapt to alternative corridors and low resilience due to their reliance on milkweed. Bottlenecks exist as they leave and approach their narrow overwintering habitat: during these periods, we define monarchs as having low route plasticity and low resilience. The distinct needs of monarchs during these portions of their migration suggest that a mix of mechanisms is required to support this species. Additionally, transboundary coordination is required due to the scale of the monarch migration, which spans multiple national-, state-, and local-level boundaries.

With breeding-ground migration characterized by high route plasticity and low resilience, our framework emphasizes achieving species-specific habitat needs (e.g., milkweed) along subsets of available migration corridors, while addressing free riding and transaction cost concerns. The US Department of Agriculture provides technical and financial support for agricultural practices that support monarch habitat. Voluntary mechanisms that create financial incentives can motivate provision of critical habitat through PES contracts that may be either practice based (e.g., payments for prescribed burning to manage native habitat) or results based (e.g., payments for the presence of milkweed). The Monarch Butterfly Habitat Exchange coordinates investors to pay for monarch support with landowners who will provide milkweed habitat, although participation in this market-based habitat exchange has been limited. Given species characteristics, these voluntary programs should be developed in ways to address free riding. Education about the impact of land use and agricultural inputs (Pleasants and Oberhauser 2013) and behavioral nudges also can improve program outcomes.

The low resilience in this portion of the migration raises the issue of high transaction costs for programs targeting temporary species-support efforts along monarchs' migratory routes. Participants in such programs manage habitat by planting nectar-rich native plants in critical areas and using butterfly-friendly practices in established habitats during summer months. Working-lands programs support in-field management changes, including using integrated pest management and reduced tillage practices. These short-term, repeated management actions are difficult to observe, which can generate high agency transaction costs related to monitoring and verification.

In and around their overwintering sites, monarchs demonstrate low route plasticity and low resilience, which creates holdout problems that may be overcome by a mix of policy mechanisms, including direct regulatory intervention, community-based conservation, and incentives for habitat protection. Direct regulatory intervention may be most effective to protect the particular habitat requirements in the monarchs' migratory path that ensure connectivity to overwintering sites. However, regulation may be insufficient if monitoring and enforcement are inadequate or if the government lacks the capacity or authority to protect habitat. Given the existing community-based conservation in this region, incentives for habitat protection (e.g., PES contracts to participating institutions) and behavioral approaches (e.g., promoting social norms and recognizing stewardship) can be used to support community-based conservation by rewarding and publicly recognizing individuals who contribute to the greater public good. In Mexico, direct payments and tourism-related benefits provide incentives to forfeit logging permits and to undertake conservation efforts. Careful orchestration of these alternative mechanisms is required to ensure that the extrinsic motivations of incentive-based mechanisms do not erode the intrinsic motivations that can be essential for the voluntary provision of public goods, including species-support actions.

Canada, Mexico, and the United States participate in international agreements and conservation plans, but monarch populations continue to decline as a result of deterioration of both overwintering habitat in Mexico and breeding habitat in the United States and Canada. Mexico's conservation efforts provide $12 million in cultural benefits to the United States and Canada (López-Hoffman et al. 2017). Within the United States and Canada, benefits of monarchs in more populated areas are subsidized by the efforts of individuals in rural areas. The uneven distribution of benefits and costs suggests the need for mechanisms that transfer financial support from areas deriving benefits to communities that face substantial costs associated with monarch conservation.

Discussion and Conclusion

Coordination among stakeholders along migratory corridors and at overwintering and summering locations is required to achieve cost-effective migratory species support. The requirement for spatial and temporal coordination among stakeholders engaged in migratory species support suggests unique opportunities and challenges relative to traditional habitat conservation that could benefit from additional research by ecologists and economists.

First, temporary actions to support species can benefit migratory species. The allure of these low opportunity–cost actions must be weighed against their efficacy relative to permanent habitat conservation. This comparison is currently impossible given a lack of ecological understanding of the fitness implications of various actions to support migratory species and the lack of economic understanding of the value of different population levels of migratory species, which creates a policy-relevant research agenda. Because temporary actions rely on forecasts of species' arrival, forecast uncertainty and errors may result in reduced program participation. Work exploring the trade-offs between forecast lead time and forecast error rate seems essential to boost migratory species support. Finally, the rate of habitat loss and degradation worldwide calls for long-term conservation actions. To the extent that temporary support increases the risk of habitat conversion relative to long-term support, low opportunity costs will be offset by program inefficiency. This result is magnified if temporary actions require multiple rounds of program enrollment that can increase the transaction costs associated with such actions. Research into mechanisms that integrate both temporary and permanent actions to support migratory species in contracts of different lengths will provide more evidence.

Second, although research exploring mechanisms to aggregate conservation actions across properties has existed for decades, migratory species conservation poses additional questions. Migratory species support can require conservation in particular configurations at particular times. An exciting area for future research involves designing mechanism extensions that can address these spatial–temporal aspects through combinations of voluntary and regulatory actions.

Third, although this discussion of conservation mechanisms on a theoretical migratory route assumes that property rights are secure, many migratory species travel through landscapes where property rights are contested or not assigned, such as open oceanic waters and developing-nation commons. Property rights are necessary for voluntary mechanisms with extrinsic motivations to be viable. The lack of adequate governance and institutions may also challenge direct regulatory intervention in these locations, especially when migratory species face threats from stakeholders operating at different scales with different degrees of tenure security, such as capital-constrained small holders and internationally financed plantations that might respond differently to the restrictions associated with protected areas or seasonal closures (e.g., Conte and Shaw 2018). The set of viable mechanisms shrinks substantially when responsibility for actions that support or harm migratory species cannot be credibly assigned, either via property rights or community-level norms. Additional work on mechanism design and impact in the absence of property rights, likely focusing on community-based conservation and behavioral interventions, would fill this gap.

Fourth, transboundary coordination to support migratory species requires research to determine mechanisms that operate at the international level rather than the individual property rights level. Still, the weakest-link supply of species support associated with low route plasticity in the extreme does provide an incentive for nations with greater support ability to invest in nations with less capacity for support. This motivation for cross-boundary investment might offer nations opportunities to demonstrate commitment to the common good in ways that spill over to other problems, notably climate change, requiring international environmental agreements.

Fifth, coordination among mechanisms appears understudied in the literature but is important for migratory species support. The movement of wildlife demands stakeholder coordination, both spatially and temporally, and the preferred mechanisms may vary over space and time. More research is needed that combines mechanisms to achieve support. A more detailed investigation of the tensions and/or synergies between mechanisms relying on a combination of intrinsic and extrinsic motivations for species support in this context would be a welcome contribution to our understanding of this issue.

It is our hope that researchers and practitioners will use the framework we present in this article to identify and modify mechanisms to provide effective migratory species support.

The potential challenge of strategic holdouts in the face of low route plasticity and weakest-link supply suggests that conservation practitioners may find mechanisms reliant on financial incentives for conservation actions (e.g., easements, PES programs, etc.) less cost-effective than direct regulatory intervention, which is less susceptible to holdouts. Free-riding concerns will be at the fore when conservation practitioners face settings with high route plasticity due to available substitute routes. Finally, conservation practitioners working with migratory species that display low resilience must be wary of transaction cost challenges stemming from the need for particular habitats and configurations that involve coordination and information.

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