A Framework for Evaluating Mechanisms to Support Seasonal Migratory Species

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Abstract: Effectively supporting migratory wildlife species requires spatial and temporal coordination of species-supporting actions (habitat conservation and risk mitigation) throughout their migratory journey and at their summering and wintering grounds. We develop a framework to evaluate the efficacy of various economic mechanisms to support migratory wildlife based on two salient characteristics of the species – their route plasticity and resilience. We then describe how these characteristics dictate species' needs and the ability of economic mechanisms to meet these needs, keeping in mind the impacts of the time commitments required for effective species support and temporal uncertainty. We conclude that species with low route plasticity, requiring support from fixed coalitions of stakeholders, can challenge incentive-based mechanisms due to holdout issues; however, if these species are highly resilient, community-based conservation and behavioral mechanisms may be well equipped to motivate effective species-support actions. When low route plasticity is coupled with low resilience, direct regulatory intervention may be the most appropriate protection mechanism. Species with high route plasticity may be best supported via performance-based payments if they have low resilience, while such species with high resilience may benefit from either conservation auctions or an agglomeration bonus, although these mechanisms may need to be modified from their conventional forms to offer the most beneficial species support. Descriptions of the particular needs of two quite different migratory species, mule deer and monarchs, provide insights into how the available mechanisms might best be combined to meet species' needs and also identify areas for future research.

Keywords: coordination, habitat protection, incentives, monarch butterfly, mule deer, migration, PES, plasticity, resilience

JEL Codes: Q57, Q28, Q24

Introduction

Migration is a vital adaptation for many species, and the appearance of seasonal migratory species (SMS) can heighten the connection between humans and wildlife. The migration of approximately two million ungulates in an 800-kilometer circuit between Tanzania and Kenya is the largest overland wildlife migration in the world and has drawn tourists to the region each year for decades. The Harney County Migratory Bird Festival in Oregon has been held annually since 1981, featuring guided bird tours, workshops, and other activities for all ages. Despite collective interest in wildlife during migration, protection of SMS remains inadequate in settings worldwide (Runge et al. 2014).

The previous two papers in this symposium describe how the ecological characteristics of SMS determine conservation needs and how those characteristics inform economic policy analysis for SMS. SMS make spatial-temporal movement decisions across their connected annual habitat to satisfy particular needs at different times and different places along their migratory journeys, implying the need for coordinated conservation actions across the annual habitat regarding both timing and location (Albers et al. 2021b). 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 et al. 2021a). Effectively supporting wildlife migration is a coordination challenge across both space and time due to migratory species' unique annual habitat requirements and the potential benefits of temporary conservation actions.

The unique characteristics of SMS pose challenges to the efficacy of conservation mechanisms that have successfully supported wildlife in other contexts (e.g., development density mandates, payments for habitat conservation and restoration), with unique challenges relating to spatial-temporal coordination of many actors. Successful mechanisms will benefit species by motivating adoption of species-support actions, defined here broadly to include traditional habitat conservation; actions that improve the connectivity of migratory habitat; and actions that reduce the risks faced during migration through temporary or permanent actions. The mechanisms must facilitate the required spatial-temporal coordination in the context of SMS, which means avoiding the pitfalls associated with achieving this coordination among stakeholders.

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 and is a critical concern for SMS because of the important links between spatial and temporal decisions as SMS migrate. While permanent conservation is ready whenever an SMS arrives, recent use of short-term conservation actions to reduce the risk of injury or death of wildlife during migration, such as turning out lights along flyways during nights with heavy movement of passerines (Van Doren et al. 2017), presents 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 paper, we present a framework to guide the selection and design of mechanisms to support SMS by addressing the salient characteristics and spatial and temporal needs of different SMS. Because measuring the social efficiency of different types and levels of SMS support is challenging due to a lack of both ecological and economic information about these species, we focus on the cost-effectiveness of species support. We explore how migration challenges the ability of existing mechanisms to meet species-support goals. After briefly introducing the available mechanisms and challenges associated with implementing these mechanisms, we present our definition of SMS support. To highlight the challenges of achieving cost-effective SMS support, we explore four aspects that challenge spatial and temporal coordination: free-riding, holdouts, transaction costs, and transboundary coordination. Next, we identify how characteristics of SMS determine which of these focal challenges arises, which informs the selection and design of effective mechanisms. Due to 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 any species support is critical for better policy. Finally, we apply our framework to two particular species 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 to provide adequate species support.

II Available Mechanisms, Challenges Faced, and the Evaluation Context for SMS support

We first present brief overviews of the mechanisms available to motivate species-support actions on private and public lands and then discuss challenges to implementation of those mechanisms. Each of these mechanisms can motivate both permanent and temporary species support. Last, we discuss how we evaluate the viability of the available mechanisms in the context of SMS support.

Available Mechanisms

Direct Regulatory Intervention (DRI) includes restricted use of public lands -- both temporary (e.g., seasonal closures) and permanent (e.g., parks) -- that requires sufficient legal and governance institutions for effective conservation. DRI also includes restrictions on human behavior and habitat use on private lands. To achieve their intended species-support goals, such restrictions on private land require adequate monitoring and enforcement to overcome the information asymmetry about the presence of focal species in particular locations of suitable habitat.

Voluntary Mechanisms provide incentives for conservation actions on private property and can take advantage of heterogeneity in marginal provision costs across program participants to increase program cost-effectiveness relative to DRI (Ferraro 2008; Newell and Stavins 2003). 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 et al. 2018). PES programs compensate resource users for desired biodiversity or ecosystem-service provision or for implementing conservation-friendly management practices. Market-based conservation credit programs (Hansen et al. 2017; Fox and Nino-Murcia 2005) rely on voluntary actions from stakeholders whose behavior threatens wildlife and can rely on demand from within this same set of stakeholders, meaning that they are likely subject to thin markets unless there is regulation, along with monitoring and enforcement, to motivate participation on both sides of the market. Each of these mechanisms can be used to motivate temporary or permanent species support, with temporary actions associated with lower opportunity costs but potentially higher transaction costs associated with repeated program enrollment, temporal coordination, or both.

Voluntary mechanisms that motivate spatial coordination across program participants can be important for SMS, because mechanisms without a focus on spatial coordination can exacerbate fragmentation (e.g., Jones-Ritten et al. 2017). 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 (CBC) 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 et al. 2012). Motivation for CBC 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 2000, Ostrom 1990). 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 due to 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

Because SMS support involves the coordinated participation of many actors, those actors' decisions affect the design and mechanism choices best suited to achieve SMS support. We focus on four key strategic behaviors by stakeholders that challenge the coordination needed for successful, cost-effective, SMS 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 non-rival and non-excludable nature of public goods, a free rider can enjoy their preferred private consumption while relying on the provision of the public good by others, leading to its under-provision. 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, etc.) make free-riding more likely.

Strategic holdouts refer to landowners who wait to participate in a conservation program – to hold out – in order to capture rents from the program, such as one to conserve a particular pattern or set of parcels. 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 (Shavell 2010; Eckart 1985), 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 transboundary public goods, 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 SMS support is difficult given the challenges associated with measuring non-market values of environmental amenities. For SMS, the lack of ecological understanding of how habitat improvements across migration routes alter species fitness and the lack of economic valuation of species fitness constrain attempts to define socially-optimal SMS conservation. For these reasons, we use cost-effectiveness to evaluate mechanisms that support SMS.

In evaluating the mechanisms to protect the quality of connected annual habitat for SMS, we consider a situation in which a species migrates between two endpoints (e.g., movement between 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, and we evaluate the ability of available mechanisms to motivate provision of SMS support.

The most novel and challenging aspect of supporting SMS is the requirement of addressing the specific needs of species *along* the migratory route, with that route requiring connectivity and interdependence of habitats, which potentially introduces a large-scale weakest-link problem. The two dimensions of coordination —spatial and temporal — may be necessary, depending on the requirements of the species, to ensure adequate species support is provided in the right locations and at the right times. This paper considers how the specific characteristics of different SMS determine which mechanisms are most likely to motivate cost-effective species support.

III SMS Characteristics and their Implications for Preferred Mechanisms

Migration is a common strategy shown in nearly all taxonomic groups to maximize fitness. Animal migrations vary greatly in terms of mode and medium of migration (e.g., aerial, aquatic, terrestrial), time (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 first describe the characteristics of SMS that are germane to mechanism selection, before discussing how these different characteristics mitigate or exacerbate the four challenges presented above to help highlight preferred mechanisms for different combinations of SMS characteristics.

Salient SMS Characteristics and Conservation Needs

We focus on four key attributes of migration with implications for species' support needs: behavioral plasticity, niche breadth, stopover site fidelity, and connectivity. Behavioral plasticity is characterized as a species' ability to change behavior to cope with habitat disturbance from natural (e.g., fire) or anthropogenic (e.g., habitat degradation, movement barriers, light or noise pollution) sources. Niche breadth describes the diversity of resource use by a species, ranging from a generalist (wide niche) to a specialist (narrow niche). Stopover site fidelity refers to the consistency with which SMS return to the same sites across years. Connectivity refers to the species' ability to successfully move through the migratory medium (e.g., terrestrial, aquatic, or aerial). These migration attributes vary across species and also along a single species' migratory path, which implies that different mechanisms may be appropriate at different locations for a given species. We distill these four attributes into two key ecological characteristics — *route plasticity* and *resilience* — that are used to evaluate which mechanisms best meet the unique needs of an SMS 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). High route plasticity means that the species' movements –

spatial and temporal – between summer and winter grounds can vary considerably in response to stochasticity and to disturbances on their route. Variation in migration timing can be triggered by many factors, including local weather (Horton et al. 2020), resource phenology (Geremia et al. 2020), and photoperiod (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 SMS migration.

Resilience is the combination of behavioral plasticity and niche breadth, indicating the ability to adapt to available resources and cope with habitat disturbances (Figure 1). Low behavioral plasticity precludes the ability to respond to shifts or disturbances by changing temporal migration decisions, and narrow niche breadth 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.

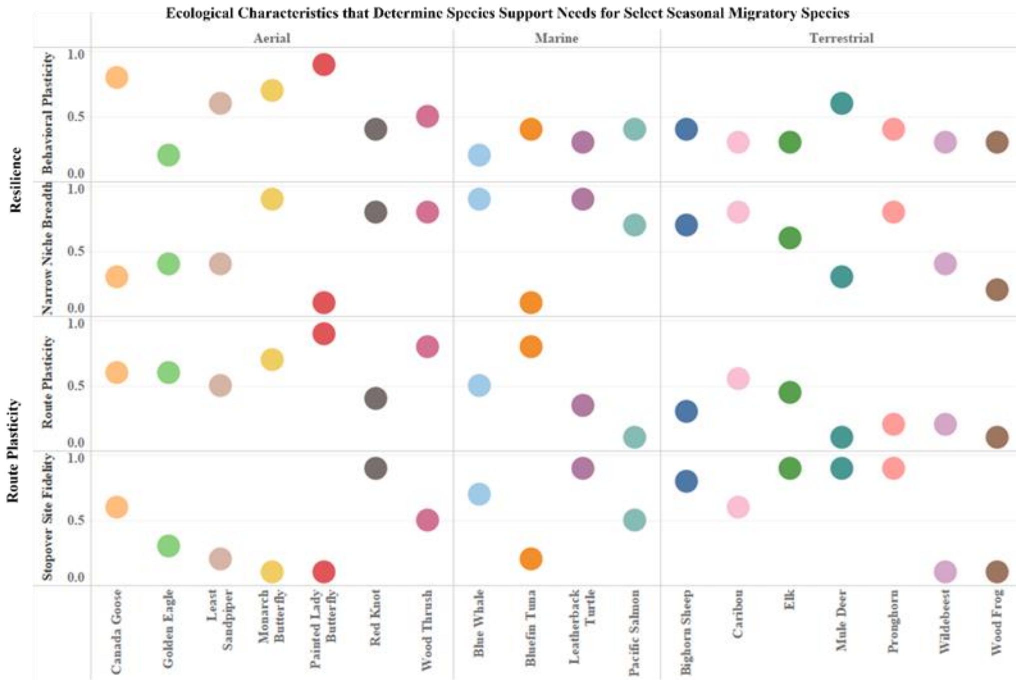


Figure 1. The relative importance of resilience and route plasticity, and their underlying ecological attributes, for various SMS. Species are listed on the horizontal axis. Circles indicate the relative importance of each attribute, with one indicating that the attribute is a critical feature during migration. See supplement for methods and sources used to develop these rankings of resilience and route plasticity.

The levels of these two characteristics determine the conservation needs for SMS throughout migration. Species displaying low route plasticity require support in particular locations, requiring coordination across space and time. Species displaying high route plasticity create opportunities for species-support benefits in many locations and times, because species experiencing this characteristic have the ability to adjust to disturbances and to take advantage of alternative routes. Species displaying low resilience require species support to protect particular habitats in the species' niches and at specific times of species' use. Species displaying high resilience possess a great ability to adjust to disturbance by changing migration timing or accessing other resources, which provides more flexibility in the location and timing of beneficial species-support actions.

Whether actions are permanent or temporary interacts with these characteristics. If low resilience occurs due to narrow niche breadth, satisfactory habitat along the migratory route may be rare and its disruption quite costly. In this case, permanent species-support actions that mitigate the risk of such critical habitat disappearing are preferred. That preference for permanence is compounded when the required habitat cannot be quickly replaced, as with a narrow niche that requires mature habitat. One-time permanent actions that generate enduring habitat benefits and improve connectivity can be beneficial to all combinations of resilience and route plasticity, with caveats that low route plasticity and low resilience require those actions to occur along a particular route. In contrast, with high resilience and high route plasticity, SMS are better able to take advantage of temporary actions that create temporary habitat (e.g., flooding agricultural fields for migratory waterfowl) or reduce risk during migration (e.g., turning out lights along flyways) across a broad range of locations. Such temporary actions will only be useful for species displaying low resilience and low route plasticity if the actions lead to suitable temporary habitat along the typical migratory route because those characteristics prevent species from seeking out alternatives.

The duration of temporary species-support actions interacts with the uncertainty about migration timing. The length of time commitment required for species-support actions can either include several migration periods (e.g., habitat conservation or restoration that occurs over a period of years) or be limited to periods of active migration (e.g., a matter of hours, days, or weeks). The efficacy of species-support actions associated with high time commitment and duration is relatively unaffected by uncertainty in the timing of annual migrations because the duration of these commitments dwarfs the possible range of species arrival times and length of stay. With shorter time commitments, the impact of temporal uncertainty on the efficacy of species-support actions increases.

Implications for Mechanism Choice

Interactions between route plasticity and resilience determine the actions required to support SMS and the precise challenges that mechanisms will face in achieving these actions. Resilience and route plasticity interrelate to determine conditions that are suitable for SMS support (Figure 2a) and how these needs translate into key challenges for mechanisms to overcome (Figure 2b). Here, we use these relationships to define a framework for evaluating the potential of specific mechanisms to motivate species-support actions for migratory wildlife based on resilience – route plasticity space (Figure 2). Using the four quadrants of resilience-route plasticity space as our evaluation framework, we consider how migratory characteristics inform mechanism choice and related challenges. Then, we discuss the additional challenges of transboundary coordination.

Quadrant I: High Resilience and High Route Plasticity

When SMS display high route plasticity and high resilience, programs can be effective without many restrictions about where, when, and how actions need to be taken. Without the need for specific locations and configurations, 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 on other people's SMS-support actions along those substitute routes.

Given this free-riding challenge, program participation is critical to success, and mechanisms that provide incentives for SMS support are likely important. Conservation auctions are appropriate in these settings, but to be effective at achieving widespread participation, the bidding process must be simple and streamlined. If the auction is too complicated, it will not be well-suited to achieve species support over a large area, due to the challenge of bid formation (Banerjee and Conte 2018). In practice, high transaction costs, such as those associated with program enrollment and bid formation, can limit participation in auctions (Rolfe et al. 2018; Palm-Forster et al. 2016). Although traditional mechanisms that offer financial incentives for SMS support are appropriate here, such extrinsic motivation can reduce voluntary provision by crowding out the intrinsic motivation to contribute to the public good (e.g., Reeson and Tisdell 2008). In the case of SMS support, if individuals willing to support SMS in the absence of regulation demonstrate high levels of intrinsic motivation, their contributions will be susceptible to crowding-out concerns.

Signaling can be an important element of social norm establishment that is helpful in achieving the high levels of participation needed in this setting. Credible signals allow individuals to be recognized for their actions, which encourages participation (Dessart at al. 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.

CBC is also consistent with intrinsic motivation for SMS support. Given the reliance on community, CBC may be useful for species with migratory routes that cover relatively limited distances in a small number of jurisdictions. CBC may also be appealing when species-support actions are temporary, because stakeholder knowledge of local habitat conditions can reduce the uncertainty and transaction costs associated with species-support actions to reduce the intensity of disturbance. Given the reliance on the salience of the SMS for behavioral nudges, success will correspond to the value of the species in that community, which could be high when species display high resilience, because they may have higher populations, although the lack of scarcity of species displaying this trait could also make them 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 CBC 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. Requesting actions with low opportunity costs, such as temporary actions, may generate greater participation in efforts to support SMS. Greater participation can improve cost-effectiveness of SMS support as long as low-cost efforts provide adequate habitat in terms of quality, composition, and structure. Participants in PES programs have a preference for actions with low net private costs, which might result from significant private benefits of conservation (Vukina 2008). However, if participants seek out the lowest-cost actions that generate few social benefits, cost-effectiveness is eroded. Preferences for low-cost actions may also result in 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.

The above possibilities suggest that species-support actions with low opportunity costs may still have high total costs due to high transaction costs associated with monitoring and enforcement to ensure increased provision of SMS support. The need for repeated program enrollment will also increase the transaction costs associated with programs targeting temporary species-support actions. Using programs with low transaction costs (e.g., 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. The responsiveness of species displaying high resilience to temporary species-support actions necessitates attention to temporal coordination as well. While strategic holdouts are a concern with species exhibiting low route plasticity, the availability of a variety of credible species-support actions may help to mitigate the importance of this challenge to mechanism cost-effectiveness.

For holdout concerns to be significant, relevant stakeholders must be aware of the importance of their behavior to the species-support efforts. Given that migration is a landscape-level process, this awareness may not exist at the onset of SMS support efforts, especially with a range of commitment times associated with targeted species-support actions. Then, policy makers face a choice about how much information to share with relevant stakeholders as they balance the desire to target particular areas for participation while navigating potential strategic behavior by stakeholders. Although temporary conservation actions are useful in high resilience settings, they could serve to inform stakeholders of the importance of their behavior and increase the long-run holdout problem if they are motivated via repeated enrollment in programs reliant on voluntary mechanisms.

When a species displays low route plasticity, there is a requirement to motivate species-support actions at particular locations on the landscape. An agglomeration bonus, whether offered in addition to a uniform payment or incorporated into a spatial conservation auction, rewards the coordinated adoption of conservation actions across properties. The viability of temporary SMS-support actions suggests that there might be benefits of such bonuses in the temporal dimension as well, with additional payments available for long-term commitments to provide temporary SMS 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 serve as a signal to property owners of 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 actions, which allows procuring agencies to balance procurement of the most-cost effective parcels with concerns about rent-seeking (Conte and Griffin 2017.)

With these issues, strategic holdout threats may lead to a preference for DRI over voluntary mechanisms reliant on extrinsic motivation for species support. Seasonal closures and/or use restrictions in key nesting grounds for SMS (e.g., migratory shorebirds along the Atlantic and Pacific coasts of North America) are examples of DRI to support migratory species. Under the United States Endangered Species Act, DRI has conserved habitat on private lands through temporary and permanent land use restrictions (Innes and Frisvold 2009).

Alternatively, collective action of multiple stakeholders at the community level may be of use to 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 CBC, including trust among stakeholders.

Due to the need for connectivity in low route plasticity settings, SMS support is an example of weakest-link supply. With the level of the public good provided 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

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

Strategic holdouts present a primary challenge when a species displays these characteristics, requiring particular species-support actions in particular locations. Given the weakest link characteristic and this location-specific SMS support need, 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 et al. 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 her 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 non-resident SMS could prove challenging and eminent domain for temporary periods appears rare, suggesting the use of this threat point only when the risk of holdout is large.

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 SMS support.

In such settings, mechanisms like conservation easements or the establishment of protected areas through DRI are helpful. Agency transaction costs of DRI can be high in terms of the cost of monitoring and enforcing protections. Although transaction costs are lower when agencies or private organizations use conservation easements or buy critical land parcels, transaction costs of one-time purchases can still be significant, which implies that the cost-effectiveness of mechanisms that change property rights increases with contract length (Schöttker and Wätzold 2018). The flexibility in contract design afforded by conservation easements is appealing as it can accommodate shifts in needed restrictions on use to achieve species-support goals.

Also supporting species with particular habitat needs, PES programs can target funds to locations and actions that achieve the desired habitat and configuration. Species displaying low resilience, notably, may benefit from results-based (pay-for-performance) 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, and 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.

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 the social value of SMS support by a particular stakeholder is not sufficiently high or the costs of coalition formation are sufficiently high.

The SMS' 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 required by SMS. 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 SMS, 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, DRI and CBC may be effective with low resilience.

Transboundary Coordination

Transboundary coordination can heighten the challenges of temporal and spatial coordination for SMS with migration routes that cross international boundaries, especially when there is low route plasticity. Because low route plasticity means species do not change their route in response to a nation's lack of action, it creates a weakest-link provision technology, in which unilateral actions do not benefit species. This support provision leads to a coordination assurance game to avoid unilateral actions, and there is a preference to cooperate given that other nations act in the same way (Touza and Perrings 2011). For "weakest-link" supply, nations prefer not to contribute unless they expect contributions from a substantial coalition of other nations, and, in this situation, nations may take the lead in enacting species-support actions if there are sufficiently strong expectations that other nations will follow (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 facing the prospect of forgoing the benefits of the transboundary public good. Unilateral provision of SMS support associated with "weaker-link" supply technology of high resilience SMS 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 SMS that can benefit from temporary species-support actions (e.g., temporary flooding of fallowed agricultural fields for migratory shorebirds).

Uncertainty about how various species-support actions in a range of locations contribute to overall SMS 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, that uncertainty complicates the process whereby nations identify the likely behavior of others to determine their best responses, which shapes equilibrium strategies. That challenge may influence the transaction costs of such international environmental agreements across resilience and route plasticity space, 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 DRI or voluntary mechanisms with extrinsic motivations to provide species support within their borders. Depending on the relationship between the involved nations CBC could be effective in changing norms for relevant stakeholders across borders in order 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 SMS, as nations typically only join and comply with such agreements when the agreement makes them better off (Barrett 2003).

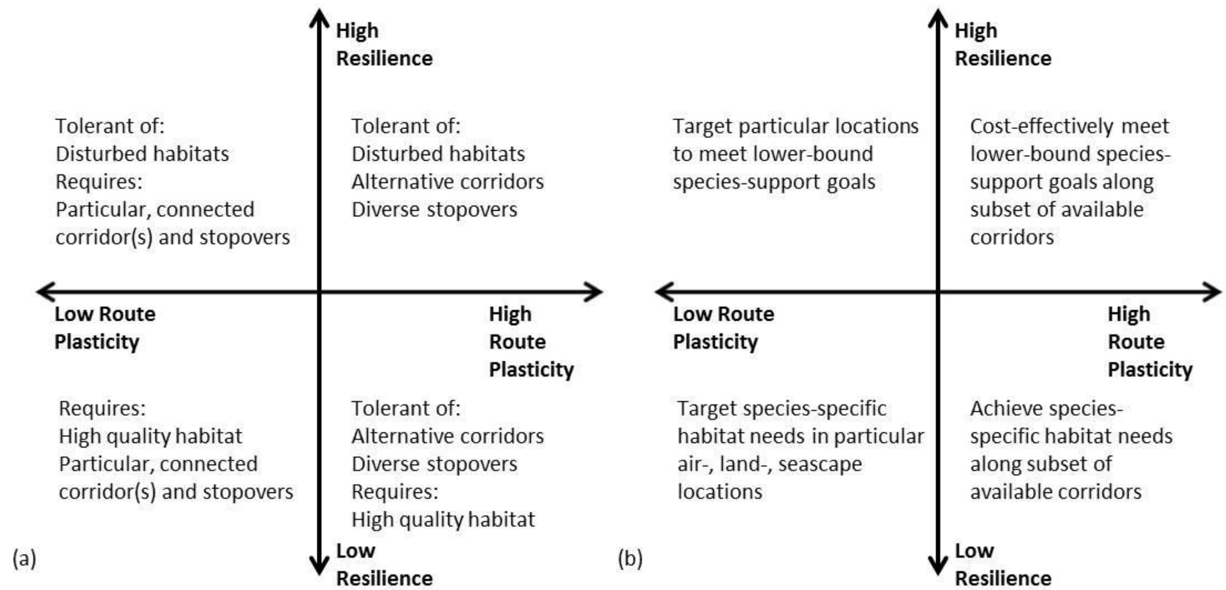
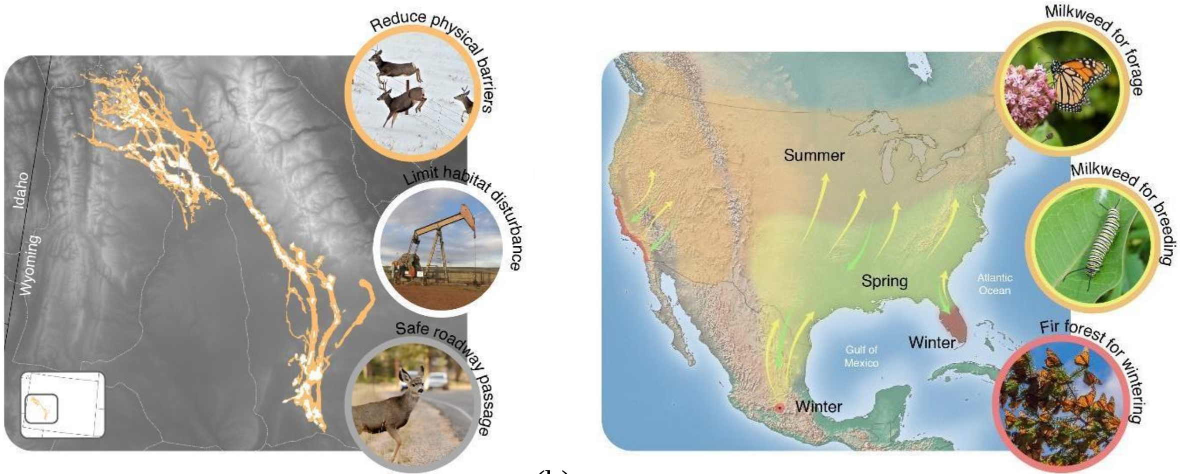


Figure 2. Linkages between characteristics of SMS that determine species needs (a) and the resulting prioritized objectives of mechanisms based on these characteristics (b).

VI SMS Examples

We apply our framework to determine the mechanisms best suited to support the migration of two species – mule deer and monarch butterflies (see Figure 3). These species have different resilience and route plasticity characteristics within and across their migratory routes 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.



(a) (b)

Figure 3. Illustrations of the migratory journeys of (a) mule deer and (b) monarch butterflies.

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 by anthropogenic disturbances that fragment the landscape and threaten the connectivity of habitat (WAFWA 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% 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), leading to the use of the same stopovers between seasons and years, with migration corridors generally showing little variation (Merkle et al. 2019). Mule deer migrations are negatively affected by semi-permeable 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. First, mule deer exhibit high stopover site fidelity and require connectivity along corridors, which means that they are unlikely to alter their route. Second, if mule deer can access stopover sites, a variety of forage species are generally sufficiently abundant to meet their needs, indicating their wide niche breadth. In addition, mule deer increase their rate of movement and reduce time in stopovers in response to semi-permeable development, which can reduce population fitness (e.g., Wyckoff et al. 2018).

With their low route plasticity and high resilience during migration, our framework finds that efforts to support mule deer are likely to be confronted by the challenges of holdouts, with some transaction costs issues. Holdouts might recognize the value of their actions and their land given the weakest link characteristic of migration paths due to mule deer's low route plasticity. Because holdouts create a high risk of coordination failure, DRI may be necessary to ensure preservation of a specific mule deer population's migratory route. The large amounts of public land in these migratory routes may limit the amount of DRI on private lands. In addition, the short duration of mule deer migration and mule deer resilience across potentially degraded habitats means that temporary DRI can be beneficial, such as seasonal reductions in activities on energy sites or seasonal dropping of fences on the migratory route. 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.

In non-energy development portions of mule deer migratory paths, ranching communities may value wildlife viewing (e.g., agri-tourism revenues) or have personal value for migrating species, which raises the possibility of both CBC and behavioral nudges as support mechanisms. Either 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 managed and conserved through a coordinated policy across jurisdictions (local, state, federal) nor across annual habitats including the migration routes (Stoellinger et al. 2021). State policies designate migration corridors, bottlenecks, and stopovers to establish conservation measures and coordinate with other departments such as the Department of Transportation (DOT), but pushback from stakeholders occurs. 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 DRI on some critical pieces of private land.

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 wild-life friendly modifications to fences.

Our framework identifies the potential for short-term permeability-increasing species support. Although no large-scale programs offer incentives to private landowners for "pop-up" 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. Still, several agencies and conservation groups provide education and support for both temporary and permanent changes to fencing that facilitate migrations through private land and DOT construction of wildlife bridges over/under highways, in a form of public good provision for mule deer.

Monarch butterfly

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, up to 99% (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 has 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 thus creating a limiting overwintering habitat requirement. Over three-quarters of the overwintering habitat exists within the Monarch Butterfly Biosphere Reserve (MBBR), a world heritage site near Mexico City (Vidal and Rendón-Salinas 2014). Deforestation and forest degradation in and near these forests, including 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. During most of their migration, monarchs move through breeding grounds: 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 SMS. 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., 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 the 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 can also 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. These efforts manage habitat by planting nectar-rich native plants in critical areas and managing established habitat using butterfly-friendly practices 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 DRI, CBC, and incentives for habitat protection. DRI may be most effective to protect the particular habitat requirements in the monarchs' migratory path that ensures connectivity to overwintering sites. However, DRI may be insufficient if monitoring and enforcement are inadequate or if the government lacks the capacity or authority to protect habitat. Given the existing CBC in this region, incentives for habitat protection (e.g., PES contracts to CBC institutions) and behavioral approaches (e.g., promoting social norms and recognizing stewardship) can be used to support CBC 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 due to deterioration of both overwintering habitat in Mexico and breeding habitat in the US and Canada. Mexico's conservation efforts provide $12 million in cultural benefits to the US and Canada (López-Hoffman et al. 2017). Within the US 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 of monarch populations to communities that face substantial costs associated with monarch conservation.

VII Discussion and Conclusion

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

First, temporary species-support actions can benefit SMS. 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 SMS fitness implications of various species-support actions and the lack of economic understanding of the value of different population levels of SMS, which creates a policy-relevant research agenda. Because temporary actions rely on forecasts of SMS arrival, forecast uncertainty and errors in estimated species arrival time may result in reduced program participation. Work exploring the tradeoffs between forecast lead time and forecast error rate seems essential to boost SMS support. While the low opportunity costs of temporary species-support actions are appealing, the rate of habitat loss and degradation across the world suggests that risks of habitat conversion in the absence of long-term conservation actions reduce cost effectiveness for these actions. 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 species-support actions in contracts of different lengths will provide more evidence about the opportunities for temporary actions to support SMS.

Second, although research exploring mechanisms to aggregate conservation actions across properties has existed for decades, SMS conservation poses additional questions. SMS support can require conservation in particular configurations, not just the need for larger patches of habitat across the landscape, and at particular times, which stretches beyond current knowledge of how existing mechanisms can achieve desired configurations of conservation. An exciting area for future research involves designing mechanism extensions that can address the spatial-temporal aspects of SMS conservation needs through combinations of voluntary and regulatory actions.

Third, although this discussion of conservation mechanisms on a theoretical migratory route assumes property rights are secure, many SMS do not migrate through such landscapes, such as open oceanic waters and many landscapes in developing nations. Property rights are necessary for voluntary mechanisms with extrinsic motivations to be viable. The lack of adequate governance and institutions may also challenge DRI in these locations, especially when SMS 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 SMS 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 CBC and behavioral interventions, would fill this gap.

Fourth, similarly, transboundary coordination to support SMS requires research to determine mechanisms that operate at the international level rather than the individual property rights level. Still, the “weakest-link” supply of SMS 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 SMS support. This motivation for cross-boundary investment, which is needed if efforts to mitigate catastrophic climate change are to be successful, might offer nations opportunities to demonstrate commitment to the common good in ways that spill over to other problems requiring international environmental agreements.

Fifth, coordination among mechanisms appears understudied in the literature but is important for SMS support. The movement of wildlife demands coordination by stakeholders, both spatially and temporally, and the preferred mechanisms may vary over space and time, which calls for more research that combines mechanisms to achieve SMS support. A more detailed investigation of the tensions or synergies, or both, 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.

This framework, focusing on resilience and route plasticity, can be used by researchers and practitioners to identify and modify mechanisms to provide effective SMS 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 DRI, stemming from DRI's lack of susceptibility 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 SMS 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.

Acknowledgements
M.N.C. gratefully acknowledges funding from USDA NIFA award number 2016-67023-2462 and NSF award number 1924378.

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