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REVIEW

Toward a new framework for restoring lost wildlife migrations

Kristin J. Barker | **Wenjing Xu** | **Amy Van Scoyoc** | **Mitchell W. Serota** | **Jessie A. Moravek** | **Avery L. Shawler** | **Rachael E. Ryan** | **Arthur D. Middleton**

Department of Environmental Science, Policy, and Management, University of California—Berkeley, Berkeley, California

Correspondence
Kristin J. Barker, Department of Environmental Science, Policy, and Management, University of California—Berkeley, 130 Mulford Hall #3114, Berkeley, CA 94720.
Email: kristinjbarker@gmail.com

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Abstract

Global declines in wildlife migrations have prompted new initiatives to conserve remaining migratory behaviors. However, many migrations have already been lost. Important attempts have been made to recover extirpated migrations, and our understanding of restoration remains narrowly confined to these particular species and landscapes. Here, we examine diverse restoration efforts through the unifying lens of behavioral ecology to draw broader inferences regarding the feasibility and effectiveness of restoring lost migrations. First, we synthesize recent research advances that illuminate key roles of exploration, learning, and adaptation in migratory behavior. Then, we review case studies to identify common themes of restoration success across four major vertebrate groups: fish, birds, mammals, and herpetofauna. We describe three broad strategies to effectively restore lost migrations: reestablishing migratory populations, recovering migratory habitats, and reviving migratory behavior itself. To guide conservation and research efforts, we link these strategies with specific management techniques, and we explore the biological mechanisms underpinning the success of each. Our work reveals a previously underappreciated potential for restoring lost migrations in terrestrial and freshwater vertebrates, and it provides guidance on whether and how conservation practitioners, researchers, and policymakers can work to restore the valuable migrations we have lost.

KEYWORDS
behavioral ecology, conservation, migration, restoration, vertebrates, wildlife

1 | INTRODUCTION

Migration is a widespread behavioral adaptation that has evolved in every major vertebrate group and affects ecosystems and societies across the world (Bauer & Hoye, 2014). Migratory wildlife provide seasonal influxes of food that support species in higher trophic levels, from Pacific salmon (*Oncorhynchus spp.*) sustaining populations of grizzly bears (*Ursus arctos horribilus*) in North America (Hilderbrand et al., 1999) to dusky rats (*Rattus colletti*) driving seasonal abundance of water pythons (*Liasis fuscus*) in Australia (Madsen & Shine, 1996). Meanwhile, nitrogen deposited by dead and defecating migrants fuels plant growth and nutrient cycling in systems ranging from the

Mara River of the Serengeti (via wildebeest [*Connochaetes taurinus*], Subalusky et al., 2017) to the salt marshes of eastern Canada (via lesser snow geese [*Anser caerulescens caerulescens*], Cargill & Jefferies, 1984). In addition to contributing to ecosystem function, migrants also contribute economic inputs (Gislason et al., 2017) and cultural services (López-Hoffman et al., 2017) to human societies.

In recent decades, changes in climate, vegetation, biotic communities, and human influences have altered some migrations to the point of complete loss (Harris et al., 2009). Migrations may be lost due to population extirpation, as when the introduction of a predatory nonnative trout caused the local extinction of migratory long-toed salamanders (*Ambystoma macrodactylum*, Pearson et al., 2003). In other cases, a migration remains intact, but the migratory population is so depleted that it no longer supports related ecosystem functions—for example, when overhunting and habitat loss reduced migratory whooping cranes (*Grus americana*) to fewer than 15 individuals (Glenn et al., 1999). Alternatively, migration can be lost when a previously-migratory population becomes nonmigratory, like the anadromous alewives (*Alosa pseudoharengus*) that evolved resident freshwater traits after dams blocked passage to estuarine habitat for hundreds of years (Reid et al., 2020). Such losses have recently prompted efforts to conserve migration at the international, national, and local levels (e.g., International Convention on Migratory Species, Harris et al., 2009; Global Initiative for Ungulate Migration, Kauffman et al., 2021; US Department of the Interior Secretarial Order 3362, Middleton et al., 2020; Wyoming Migration Corridor Executive Order 2020–1, Gordon, 2020).

With attention focused on conserving existing migratory behaviors, a critical question has been mostly overlooked: Once a migration has been lost, how can it be restored? Some research casts strong doubt on the potential for restoration, highlighting migrants' reliance on particular environmental or social conditions (Jesmer et al., 2018; Brooks et al., 2019). Other research, however, suggests more restoration potential by highlighting plasticity in some migratory species (Xu et al., 2021).

Efforts to restore lost migrations have been reported in all major vertebrate taxa (e.g., Figure 1), but the success of existing attempts remains highly idiosyncratic. Species in unrelated taxonomic groups can display remarkably similar responses to restoration, while animals of the same species do not. For example, removing barriers to movement allowed both bull trout (*Salvelinus confluentus*) and zebras (*Equus burchelli antiquorum*) to swiftly restore lost migrations on their own (Bartlam-Brooks et al., 2011; Quinn et al., 2017). Yet the construction of passage structures around dams did not restore fish migrations in South America as it had in North America (Oldani et al., 2007). Likewise, elk (*Cervus canadensis*) transplanted into the American Midwest did not migrate seasonally like their montane counterparts (Wichrowski et al., 2005). These inconsistencies suggest a need to synthesize lessons learned across varied case studies to elicit more general insights.

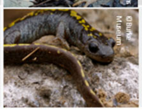
Here, we assess the prospects for restoring lost vertebrate migrations worldwide, defining migration broadly as synchronized movement between seasonal ranges (Dingle & Drake, 2007). First, we introduce key recent advances in the study of wildlife migrations that reveal opportunities for restoration. Next, we bring together case studies of restoration attempts across four major taxonomic groups (fish, birds, mammals, and herpetofauna) to synthesize common themes influencing restoration success among terrestrial and freshwater vertebrates. From this evaluation, we develop a conceptual framework to help inform restoration efforts across taxa. Our review reveals three broad strategies comprising seven specific techniques capable of effectively restoring lost migrations, and we explore the biological mechanisms that underpin their potential for success. Finally, we discuss how the work of researchers, conservation practitioners, and policymakers can directly influence restoration efforts.

2 | RECENT DEVELOPMENTS IN MIGRATION ECOLOGY

Innovations in animal tracking equipment, remote sensing technology, and computing approaches now allow us to link animals' behavioral choices and fates more effectively to environmental attributes. The resulting advances in our understanding of migratory behavior now inform prospects for restoring migrations by revealing migrants' capacities for learning, exploring, and adapting to changing environments. These advancements include increasing recognition of (1) variation among individual-level behaviors, (2) variation among population-level behaviors, (3) the role of cultural knowledge in perpetuating behaviors, and (4) the scale and predictability of relevant environmental variations.

2.1 | Migratory behavior varies among individuals

The ability to radio track more animals over longer time spans and at finer temporal resolutions has uncovered far more variation in individual behavior than previously recognized. Whereas early research posited that characteristics of individual movements remained fixed (Farner, 1950), contemporary studies find that many animals alter

	Species & Location		Pre-restoration status	Restoration technique*	Post-restoration status**
Fish	American shad (*Alosa sapidissima*), Susquehanna River, New England, USA		Effective loss of population by 1928 due to construction of multiple hydroelectric dams	2, 3, 4	*Partially restored*: Human-operated lifts at dams provide fish passage; pollution reduced; hatcheries still supplement juvenile population [1, 2]
	Bull trout (*Salvelinus confluentus*), Elwha River, Washington, USA		Complete loss of migration to estuary due to blockage by dam	4	*Fully restored*: Dam removal resulted in re-establishment of migratory life history strategy [3, 4]
Bird	Whooping crane (*Grus americana*), North America		Fewer than 15 wild adults by 1938 due to hunting and habitat loss	1, 2, 3, 4, 5, 6, 7	*Partially restored*: More than 600 individuals; individuals can migrate on their own but require human assistance with reproduction [5, 6]
	Siberian crane (*Grus leucogeranus*) and other species, Poyang Lake Ecosystem, Jiangxi, China		Drastic decrease of bird species diversity and population sizes due to conversion of overwintering habitat	3	*Partially restored*: Increased number of species and population sizes recorded anecdotally after wetland size recovered (lack of explicit pre-treatment counts) [7, 8]
Mammal	Bighorn sheep (*Ovis canadensis*), western United States		Some populations extirpated due to disease and overhunting; others reduced to point of high risk of migration loss	1,7	*Partially restored*: Some, but not all, translocated individuals migrated. In successful cases, individuals learned from historic migrating populations how to track environmental cues [9]
	Zebra (*Equus burchelli antiquorum*), Botswana		Historic migration fully lost due to construction of veterinary fence	4	*Fully restored*: Historical migration that had not occurred from 1968-2004 was completely restored four years after fence removal [10]
Herpetofauna	Agile frog (*Rana dalmatina*), Channel Island of Jersey, United Kingdom		Critically Endangered; population limited to a single 10-ha area by 1988	2, 3	*Partially restored:* Two new migratory sites established; evidence of wild breeding in new areas; principal breeding sites protected [11]
	Long-toed salamander (*Ambystoma macrodactylum*), Waterton Lakes National Park, Alberta, Canada		Strong decline in migratory population; 10% mortality of migrants yearly due to road crossings	4	*Partially restored*: Installation of roadside fences and underpass tunnels reduced migrant mortality during road crossings to fewer than 2% [12]

* 1) Translocate wild animals, 2) Release captive-bred animals, 3) Restore seasonal habitat, 4) Improve connectivity, 5) Restore stopover sites, 6) Teach via human intervention, 7) Facilitate social learning (as in Fig. 2)

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FIGURE 1 Key examples of efforts to restore lost migrations across four major vertebrate groups

the timing, direction, and duration of yearly migrations in response to environmental fluctuations. Such flexibility occurs across diverse vertebrates including fish (Meager et al., 2018), birds (Fraser et al., 2019), mammals (Xu et al., 2021), and herpetofauna (Jourdan-Pineau et al., 2012). Perhaps more surprisingly, all taxonomic groups include some individuals that go so far as to alternate between migratory and nonmigratory behavior (e.g., striped bass [*Morone saxatilis*], Secor et al., 2020; wood storks [*Mycteria americana*], Picardi et al., 2020; spotted salamanders [*Abystoma talpoideum*], Kinkead & Otis, 2007; and elk, Eggeman et al., 2016).

Such behavioral flexibility reveals considerable potential for individuals to naturally restore lost migrations under appropriate conditions. In species that alternate behaviors between years, for instance, individuals not currently migrating but retaining relevant knowledge or genetics can resume the behavior in future years if conditions prove beneficial and the cues of movement remain intact. Yellow-bellied toads (*Bombina variegata*), for example, can forego yearly migrations but resume them if rainfall again becomes sufficient to support breeding (Cayuela et al., 2014). Additionally, species that alter aspects of migratory behavior in response to environmental fluctuations can naturally restore migrations under suitable external conditions. For instance, eight waterfowl species rerouted migrations to recolonize historic seasonal habitats after environmental conditions improved (Fang et al., 2006), thereby restoring migrations that had been functionally lost from the area.

2.2 | Migratory behavior varies among populations

Partial migration—in which only part of a population migrates—has long been acknowledged, but more nuanced studies now reveal that partial migration does not manifest as a simple dichotomy of migration vs. residency. Rather, migration is best conceived as a continuum that also includes intermediate movement tactics (e.g., making multiple trips; moving for abbreviated times or distances; Boel et al., 2014). This population-level variation in behavior has proven far more diverse than previously recognized, and populations even within the same species and geographic area can exhibit markedly different variations (Barker et al., 2019; Weimerskirch et al., 2017).

Populations with a higher diversity of individual behaviors often prove more resilient to variable environmental conditions, because different individuals can prosper under different conditions (i.e., the portfolio effect, Schindler et al., 2010). Therefore, diversity in population-level behavior suggests considerable potential for restoring migrations amid changing environments. Indeed, translocating behaviorally diverse source populations of fish was more effective at long-term restoration of migration than translocating less-diverse populations (Waldman et al., 2016). Furthermore, diverse extant populations may naturally reestablish extirpated local migrations, as when individuals from a genetically diverse population of Canada geese (*Branta canadensis*) colonized a new seasonal breeding range in Greenland (Scribner et al., 2003). Of course, environmental fluctuations beyond the scope of variations historically experienced by a population may still result in permanent migration loss if the range of behavioral diversity does not allow adaptation to the new conditions.

2.3 | Cultural knowledge perpetuates migratory strategies

Recent work highlights the role of cultural knowledge transmission in maintaining migration across taxa including mammals (Festa-Bianchet, 2018), birds (Mueller et al., 2013), and fish (Brown & Laland, 2003). Translocated moose and bighorn sheep, for instance, adopted the migratory behavior of their new population rather than retaining that of their natal population, revealing that social learning had a stronger influence than genetic encoding in driving migratory behavior in these species (Jesmer et al., 2018).

Social migratory animals with knowledge of past behaviors may naturally restore lost migrations if conditions again become beneficial, whereas loss of cultural knowledge can impede or eliminate the possibility of reestablishing migrations (Jesmer et al., 2018). Alternatively, if knowledge of migration has been lost from a population or species but retained by humans, it may be possible to reteach animals to migrate, as demonstrated by pioneering work in which researchers led Canada geese along historic migration routes with ultralight aircraft (Lishman et al., 1997). Although research on social learning has historically focused on birds and mammals, reptiles and fish also demonstrate proclivities for communication and learned behaviors (Brown & Laland, 2003). Bearded dragons (*Pogona viticeps*), for example, can learn to open trap doors by mimicking conspecifics (Kis et al., 2015), and archer fish (*Toxotes jaculatrix*) learn to hunt simply by observing others (Schuster et al., 2006). If the learning of behavior extends to space use and seasonal movement, species in these taxa may be capable of learning migration from conspecifics as well.

2.4 | Migration relies on predictable resource variation at appropriate spatiotemporal scales

Whether individuals move based on social cues, past experience, or fixed internal mechanisms, recent studies reveal that migration typically occurs where variable resource patches are aggregated at broad spatial scales and where resources vary predictably each year (Barker et al., 2019; Bastille-Rousseau et al., 2017). Predictability is important not only for animals that track resources in near real-time but also for those that migrate in anticipation of future resources. For example, barnacle geese (*Branta leucopis*) are more likely to arrive at stopover sites during peak forage conditions if climatic conditions vary more predictably (Kölzsch et al., 2015). Relatedly, reticulated flatwoods salamanders (*Ambystoma bishop*) can fail to reproduce when high environmental stochasticity disrupts the relative timing of male and female arrival on seasonal breeding grounds (Brooks et al., 2019).

Restoring a lost migration is therefore most likely where resources vary predictably enough that migrants can effectively track, and benefit from, seasonal changes. Evaluating the variability and distribution of resource patches across biologically relevant spatial scales may help inform feasibility of restoration. For example, facilitating movement across broad spatial scales was more effective than local habitat restoration in maintaining resilience of migratory fish species in Australia (Marshall et al., 2016). Temporal scales of variation also influence the feasibility of reestablishment. For instance, if the cues triggering migration no longer align temporally with seasonal resource benefits, long-term restoration of migration is unlikely. Such phenological mismatches have already reduced population sizes of migratory birds unable to adjust the timing of seasonal movements to match climate-driven changes to seasonal breeding or brood-rearing habitats (Saino et al., 2011). Ongoing climate change will likely exacerbate mismatches for such species and may contribute to further declines of extant migrations.

3 | EFFECTIVE MEANS OF RESTORING LOST MIGRATIONS

Given the recent advances in our understanding of migration ecology, it is timely to explore whether, when, and how lost migrations can be restored. To provide a foundational understanding of the prospects for restoring lost migrations worldwide, we review and synthesize insights from case studies of restoration across four major vertebrate groups—fish, birds, mammals, and herpetofauna (e.g., Figure 1). We focus on terrestrial and freshwater vertebrates due to a relative dearth of research on restored migrations in marine species, which are likely limited by technical and logistical constraints. Because the field of migration restoration lacks consistent terminology that would allow for a systematic search of the literature, and because many restoration efforts are described in technical reports rather than peer-reviewed scientific journals (e.g., Brink et al., 2018; Soorae, 2016), our review was more opportunistic than exhaustive. We located key examples of both successful and unsuccessful restoration attempts by (a) searching peer-reviewed literature in Google Scholar and Web of Science for relevant taxa, species, and all forms of the keywords "migration," "restoration," "recovery," "reestablishment," and "recolonization," and (b) following threads of citations through relevant publications.

From our review, we identify three nonmutually exclusive strategies encompassing seven specific techniques capable of effectively restoring lost animal migrations (Figure 2). First, lost migratory populations can be reestablished (via techniques of either translocating wild animals or releasing captive-bred animals). Second, lost habitats can be recovered (by techniques aimed at restoring seasonal ranges, reestablishing habitat connectivity, or restoring stopover sites). Third, lost behavioral patterns can be revived (using techniques involving teaching animals or facilitating social learning). We discuss each strategy below, combining lessons learned from case studies with those gleaned from behavioral and ecological theory to illuminate the biological mechanisms underlying the success of each.

3.1 | Reestablishing migratory populations

Several case studies demonstrate that when migration is lost due to extirpation of a migratory population, releasing either wild or captive-bred individuals into a previously occupied seasonal range can result in restored migratory behavior (Figure 2, techniques 1 & 2, respectively). Successful examples exist in all major vertebrate groups and include wild alewives translocated into historic spawning lakes (Reid et al., 2020), captive-bred loggerhead shrikes (*Lanius ludovicianus migrans*) released into areas where wild populations had become endangered (Imlay et al., 2010), and wild-born but captive-reared agile frogs (*Rana dalmatina*) released into historic breeding ponds (Figure 1; Ward et al., 2016). In addition to underlying biological considerations, this strategy should be considered along with relevant aspects of the habitat restoration strategy to ensure adequate habitat exists to support a restored population.

Biologically, the success of population reestablishment in a target area hinges primarily on mechanisms of movement that are often genetically controlled. For example, some species will readily migrate to and from a release site (e.g., Asian houbara bustard [*Chlamydotis macqueenii*], Burnside et al., 2020), whereas others appear genetically predisposed to return to their birth site or other nontarget area (e.g., cuckoos [*Cuculus canorus*], Thorup et al., 2020). Genetics may also determine whether an individual will migrate at all, though the immediate trigger of movement typically consists of complex interactions between internal and external mechanisms (Kendall et al., 2015), and some genotypes considered migratory or nonmigratory may in fact display the opposite behavior (Kelson et al., 2019). Understanding the genetic basis of migration is important for understanding where and whether translocated animals will migrate, as well as for deciding whether wild or captive-bred

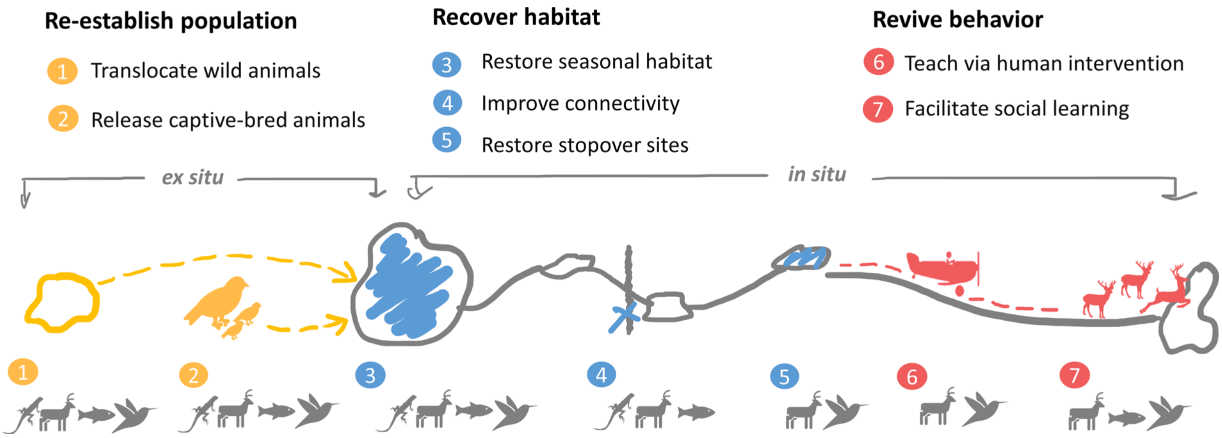

FIGURE 2 Lost migrations can be restored ex situ or in situ using three broad strategies: reestablishing populations (yellow), recovering habitats (blue), and reviving behaviors (red). Each strategy encompasses multiple techniques (numbers 1–7) that have proven effective for terrestrial and freshwater vertebrates. Animal icons represent taxa in which the restoration technique has been successfully applied (herpetofauna, mammals, fish, and birds)

individuals will be the most effective source population for restoration.

In addition to genetic traits of individuals, population-level genetic diversity also influences effectiveness of efforts to reestablish migratory populations. Low genetic diversity caused unsuccessful restoration of Atlantic salmon migrations (*Salmo salar*, Fraser et al., 2007), whereas retention of diverse native genetic traits allowed successful restoration of migratory rainbow trout (*O. mykiss aquilarum*, Carmona-Catot et al., 2012). Even where temporary local-scale restoration remains feasible, lack of genetic diversity can limit the ability to restore a sustainable metapopulation. For instance, efforts to reestablish Atlantic salmon migration in Canada were thwarted when immigration from nearby populations could not compensate for lack of genetic diversity in the released population (Fraser et al., 2007). Potential hybridization between released and extant individuals constitutes another important genetic consideration. Limited existing work suggests hybrids sometimes prove less adept at migrating (e.g., Reid et al., 2020), though results may be specific to species or areas. Opportunities to restore migratory populations may be limited where genetic diversity has already been lost, for instance if changing anthropogenic influences or environmental conditions have selected against the more migratory genotypes.

Characteristics of the area into which animals are released can also influence the success of reestablishment. Because animals often migrate to access temporally variable resources, reestablishing populations in resource-limited habitats is most likely to result in migration because such areas become seasonally less hospitable. For example, trumpeter swans reintroduced into their migratory summer range naturally restored migrations out of necessity when ponds froze during winter (Baskin, 1993), and European bison (*Bison bonasus*) reintroduced into forested areas migrated to open grassland to take advantage of the higher forage availability during the growing season (Kowalczyk et al., 2013). Moreover, the habitat into which animals are released must provide adequate resources for continued seasonal use. For instance, American shad (*Alosa sapidissima*) introduced into high-quality breeding grounds above dams consistently returned to their release sites each year (Figure 1; Brown & Pierre, 2001), whereas giant kokopu (*Galaxias argenteus*) released into a stream with suboptimal water flow moved to other drainages rather than reestablishing historic migrations in the release area (Soorae, 2016).

3.2 | Recovering migratory habitats

Habitat loss and barriers to movement rank among the most common causes of migration loss (Wilcove & Wikelski, 2008). Provided the fitness benefits of migration remain intact, simply removing physical barriers between seasonal habitats or otherwise reestablishing habitat connectivity (Figure 2, technique 4) can allow species across taxa to naturally restore migration (e.g., dam removal for bull trout, Quinn et al., 2017; fence removal for zebras, Bartlam-Brooks et al., 2011; highway crossing structures for salamanders, Pagnucco, 2010; Figure 1). In addition, recovery efforts can improve fitness benefits provided by seasonal habitats or along migration routes (Figure 2, techniques 3 and 5, respectively). However, some recovery efforts prove insufficient to restore behaviors, as when alewives landlocked for centuries evolved freshwater-specific traits rendering them unable to restore historic seaward migrations (Reid et al., 2020). Effectiveness of habitat recovery therefore depends not only on the quantity and quality of the restored habitat but also on the ability of animals to discover and use restored areas.

The scale of required habitat recovery can vary widely, from spanning multiple continents to discrete localized areas, depending on the distance across which the species ranges, the portion of the historic range across which restoration is desired, and the nature of threatening habitat characteristics. Habitat recovery areas are best identified based on their ability to provide the fitness benefits afforded by the original migratory habitat. In addition to determining which habitat type across the potential migratory range has limited behavior (i.e., seasonal ranges vs. migration paths vs. stopover sites), habitat recovery efforts must identify and ameliorate the specific habitat characteristic(s) threatening migration. Considerations should extend beyond physical aspects of the habitat (e.g., connectivity; invasive species; Randall et al., 2016) to include ecological processes on which migrants also rely (e.g., river runoff regimes, Travnichek et al., 1995). Where limiting aspects are uncertain or complex, adaptive management strategies can help discern whether recovery efforts are effectively addressing the initial cause of migration loss.

The primary biological mechanism underpinning the success of habitat recovery efforts is the capacity of animals to perceive and respond to changing external conditions rather than relying on memory of past experiences. Examples of species rapidly colonizing new habitats occur in all major vertebrate groups, revealing considerable promise for naturally restoring migrations. Great crested newts (*Triturus crisatus*) took less than 3 years to discover and use seasonal ponds constructed to mitigate construction impacts (Jarvis et al., 2019); Atlantic salmon and alewives recolonized upstream areas within 2 years of dam removal (Hogg et al., 2015); and reed warblers (*Acrocephalus scirpaceus*) established a sustainable breeding population in a new habitat within 2 years of its restoration (Sætre et al., 2017).

A particular benefit of habitat recovery is the potential to restore multiple migrations simultaneously without directly manipulating wild populations. For example, habitat restoration projects in the central Yangtze River allowed at least eight waterfowl species to reestablish use of historic wintering grounds (Figure 1; Fang et al., 2006), and enhancing a flow regime doubled the diversity of fish species downstream of the Thurlow Dam in Alabama (Travnichek et al., 1995). Thus, identifying shared species requirements on which to base habitat recovery goals can provide a relatively high return on project investment. Additionally, knowledge of species' responses to degraded environmental conditions can help determine the most effective habitat recovery technique. For instance, songbirds successfully migrating through corridors where recent hurricanes had significantly depleted food and shelter (Lain et al., 2017) suggest that habitat recovery efforts for such species may be more effective if focused on seasonal breeding grounds rather than stopover sites along migration corridors.

3.3 | Reviving migratory behavior

In some cases, existing habitat can support migration, and migratory species remain present, but animals no longer move seasonally. For species in which migration is learned rather than strictly inherited, case studies reveal that lost behaviors can be restored by either facilitating learning among conspecifics or teaching behavior to remaining individuals (Figure 2, techniques 7 and 6, respectively). In perhaps the most well-known example of a restored behavior, researchers taught Canada geese to migrate between Ontario and Florida (Lishman et al., 1997), a story adapted into the major motion picture *Fly Away Home*. The most successful examples of revived behavior across taxa capitalize on cognitive capacities of the target species by focusing on when, what, and from whom animals most readily learn to migrate. Underlying cognition of migratory behavior is therefore the primary biological mechanism influencing success of this restoration technique.

Though most migrants accumulate experiential and cultural knowledge as they age, they typically learn the basics of migration during early life stages. One restoration effort learned this lesson the hard way, when the majority of translocated adult elk returned to the areas from which they were captured. The subsequent translocation of yearlings proved far more successful as the younger animals more readily learned to migrate in novel environments (Allred, 1950). Similarly, lesser spotted eagles (*Clanga pomarina*) that learned as juveniles from experienced conspecifics were more likely to migrate along the correct flyway than translocated juveniles that did not learn appropriate behavior during their first migration (Meyburg et al., 2017). Though migration-focused studies of social learning in fish remain rare, existing evidence similarly points to a heightened propensity for learning in juveniles relative to adults (Brown & Laland, 2003).

In addition to learning migration during the most beneficial life stage, individuals must also learn the most beneficial type of migratory behavior. Successful restorations typically entail animals learning not to migrate along a fixed path at a predetermined time, but rather to actively perceive and respond to their environment. Translocated bighorn sheep and moose, for example, tracked seasonal changes in forage more optimally the longer they lived in novel areas, and extant native populations tracked forage most optimally (Figure 1; Jesmer et al., 2018), suggesting that accumulated knowledge of flexible behavior improves fitness of migrants and contributes to sustainable restoration. Similarly, young whooping cranes migrated more efficiently and effectively when they learned flexible behaviors from more experienced conspecifics (Mueller et al., 2013).

Successful restoration efforts also incorporate information about from whom animals learn. Some migrants primarily learn from one closely-related individual (e.g., white-tailed deer [*Odocoileus virginianus*], Nelson, 1995), whereas others learn from multiple unrelated conspecifics (e.g., short-toed snake eagles [*Circaetus gallicus*], Agostini et al., 2016; and sockeye salmon [*O. nerka*], Berdahl et al., 2017). Appropriate teachers can further vary among individuals within populations; for example, great bustards (*Otis tarda*) learn migration only from members of the same sex (Palacín et al., 2011). In many social species, a small number of individuals disproportionately influence population behavior by acting as group leaders (e.g., European bison, Ramos et al., 2015). The importance of individual leadership is increasingly recognized in behavioral ecology (Couzin et al., 2005) and holds particular promise for informing efforts to revive lost migrations. Because leaders tend to be older and more experienced, efforts to retain such individuals in restored populations may help build self-sustaining migrations with minimal management intervention.

4 | KEY CONSIDERATIONS IN RESTORATION DECISIONS

Our work reveals promising avenues for restoring lost migrations, as well as instances in which restoration may not be feasible or desirable. In addition to evaluating which aspect(s) of migration require restoration, decisions related to restoration efforts should consider whether, where, and how migration can effectively be restored (Table 1). Clearly identifying conservation goals associated with restoration initiatives, the threats that originally caused migration loss, and the spatiotemporal scale of required initiatives can help improve the success of restoration efforts.

Importantly, migration is not always vital—or even desirable—for populations in which the behavior has been lost. Individuals may achieve higher fitness by not migrating, as in the blackbirds (*Turdus merula*) whose nonmigratory populations exhibited higher population growth than their migratory counterparts (Møller et al., 2014). Furthermore, migratory animals can transmit diseases across species and habitats, with potentially detrimental effects on the health of both ecosystems and humans (Altizer et al., 2011). Environmental alterations driven by climate change may intensify these and other issues if migrants establish new seasonal ranges and pathways that alter expected ecosystem interactions. Alternatively, a migration that is suboptimal for migratory individuals may still merit restoration to benefit other species or ecosystem functioning—for instance if migrants provide an important food source for predators (Hilderbrand et al., 1999), contribute to nutrient cycling (Subalusky et al., 2017), or shape vegetative communities in seasonal ranges (Cargill & Jefferies, 1984).

Foundational to any successful restoration project is eliminating or reducing the original cause of loss. Acute, easily-manipulatable threats allow for relatively straightforward restoration approaches, whereas chronic or more complex threats prove more challenging to alleviate. Not only the original cause of loss but also potential future threats can affect the feasibility of migration restoration, most notably unpredictable environmental fluctuations and extreme weather events associated with climate change. Considering and integrating elements of adaptability—with respect to both management approaches and animal behavior—can bolster the likelihood of success amid uncertain future conditions.

Successful restoration culminates in the reestablishment of a self-sustaining migratory population. However, many key examples of ostensibly successful restorations rely on continual management intervention to bolster populations or behaviors (Figure 1). Whooping cranes, for example, require artificial insemination to effectively reproduce (Brown et al., 2019); American shad require human-operated lifts to migrate past dams (Pierre, 2003); and northern leopard frogs (*Lithobates pipiens*) require continual reintroductions to reinforce migratory populations (Randall et al., 2016). Thus, restoration projects should be initiated with consideration not only of immediate but also of long-term resource needs to ensure continued viability of migratory populations. Efforts can run the gamut from continually facilitated (e.g., yearly translocations; ongoing habitat treatments) to temporarily facilitated (e.g., population reintroductions across a discrete number of years or areas) to largely unfacilitated (e.g., waiting for animals to naturally restore behaviors after a single habitat restoration). Capitalizing on animals' inherent flexibility may provide the most cost-effective means of restoring migrations with minimal ongoing interventions.

5 | FUTURE DIRECTIONS IN MIGRATION POLICY AND MANAGEMENT

Despite the promising research and applied work we review here, environmental policies and management strategies generally do not include migration restoration

TABLE 1 Decisions regarding whether, where, and how to restore lost aspects of vertebrate migrations can be guided by careful consideration of management goals, species biology and ecology, and logistical constraints

Decision point	Management considerations	Biological influences	Logistical factors
Why restore migration?	• Benefit migratory species • Improve ecosystem function	• Threat types and characteristics • Effect of migration on target populations, other species, and ecosystem processes	• Socioeconomic impacts of migration and of the restoration effort • Current and future manipulability of threats
How can you conduct restoration efforts?	• Ongoing initiatives • Multiple efforts over limited time • One intervention	• Species behavioral plasticity and propensity for learning • Demographic and fitness requirements for a self-sustaining population	• Amount and timespan of funding • Available staff and resources • Quality of sociopolitical support
Where can you restore?	• Historic habitat • New area(s)	• Species flexibility and response to new environments • Quality and manipulability of habitat in target area	• Availability of adequate locations • Likelihood of ongoing suitability for migration
Which aspect(s) of migration have been lost?	• Population	• Relevant genetics and/or memory of migration • Ontogeny: How genes and experience interact to influence migratory behavior	• Source population availability • Moving animals across jurisdictions • Adequate habitat across yearly range
	• Habitat	• Relative importance of seasonal ranges, movement paths, and stopover sites • Selective advantage: How target areas support fitness	• Likely future changes to climate and land use practices • Feasibility of removing barriers to movement
	• Behavior	• Relevant aspects of social learning and knowledge transmission • Control: Trigger of a migratory event	• Regulations allowing manipulation of wild populations • Human knowledge of past migration

as an explicit goal, particularly for terrestrial taxa. Instead, they tend to focus on conservation to prevent further loss of migrations, and on the physical environment rather than species ecology and behavior (e.g., Gordon, 2020; Kauffman et al., 2021; Middleton et al., 2020). The omission of migration restoration as a policy and management goal likely stems in part from a lack of knowledge about, or confidence in, the ability to restore such behavioral phenomena. Our work suggests an important need for governmental and nongovernmental organizations to incorporate restoration of lost wildlife migrations more clearly into policy goals and conservation strategies (Table 1).

Efforts ranging from top-down policy regulations to bottom-up community-led efforts can drive successful restoration initiatives. Policies can promote restoration across broad spatiotemporal scales by ensuring long-term protection for recovering populations, regulating threats to migratory behavior, and addressing issues of environmental justice. Practical examples include strengthening requirements for developers to include migration recovery in mitigation planning; increasing protections for migratory species across historic ranges; requiring infrastructure such as fences and dams to maintain wildlife permeability; recognizing and elevating indigenous rights to wildlife stewardship; and shifting population objectives from being primarily numerical to being more flexible and behaviorally or diversity based (e.g., target percentage of the population migrating seasonally; objective ranges of population-level genetic diversity).

Working in support of or independently from policy requirements, management strategies can effectively restore migrations by directly manipulating wild populations and habitats, building local support for conservation projects, and maintaining flexibility in restoration efforts. Land management agencies, conservation organizations, grassroots groups, tribes, and private landowners can implement habitat improvement projects, remove barriers to animal movement, and establish conservation easements with explicit migration-related objectives (Middleton et al., 2020). Wildlife management agencies, zoos, and museums can use captive breeding programs and research into animal husbandry to provide source animals capable of restoring lost behaviors (Soorae, 2016). Effective management goals incorporate relevant logistical as well as biological considerations (Table 1).

6 | CONCLUSION

Preventing migration loss is likely a simpler and cheaper alternative to restoring lost migrations, yet failing to recognize the potential for restoration needlessly constrains future conservation efforts. Our synthesis of the literature reveals that migrations can be restored across vertebrate taxa and ecosystems, highlighting both opportunities and challenges in recovering lost migratory behaviors and related ecological processes. Popular attention typically focuses on the immediate aftermath of dramatic reintroductions or the human-wildlife relationships on display in the retraining of charismatic megafauna, but we show that restoring migratory behaviors more often requires long-term and painstaking efforts, significant investments, and a wide range of techniques to manage populations, habitats, and behaviors.

Countless opportunities exist to restore lost migrations worldwide. Although no single management technique can reliably restore migrations under all circumstances, explicitly considering each possibility and its potential for success can help guide restoration efforts and direct limited resources. The most successful restoration efforts will likely be those that recognize and facilitate migrants' adaptability, particularly in light of likely ongoing environmental changes. To date, the field of migration conservation has focused primarily on recovering damaged habitats and retaining extant migrations. We now invite conservationists to expand their thinking beyond environmental resources and population sizes to include restoration of large-scale behavioral phenomena.

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AUTHOR CONTRIBUTIONS

KJB, ADM, ALS, and WX conceived the original ideas for this paper. All authors designed methodology and contributed critically to manuscript development. KJB led the writing of the manuscript. WX led the creation of figures.

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The authors declare no conflict of interest.

ORCID

Kristin J. Barker https://orcid.org/0000-0002-1618-7610
Wenjing Xu https://orcid.org/0000-0001-5657-2364
Amy Van Scoyoc https://orcid.org/0000-0001-8638-935X
Mitchell W. Serota https://orcid.org/0000-0002-8885-5577
Jessie A. Moravek https://orcid.org/0000-0003-1938-6962
Arthur D. Middleton https://orcid.org/0000-0003-3887-0434

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