Conservation of declining migratory animals: An interdisciplinary analysis of biology, sociology, and policy

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***Abstract** - Migratory animals are imperiled worldwide. Because they cross geopolitical boundaries and rely on diverse habitats and resources, conserving migratory populations presents many challenges. We assess conservation policy for migratory animals and identify multiple scales at which analysis and action are needed: 1) local- and landscape-scale conservation policy based on the movement and habitat requirements of species, 2) targeted mitigation of anthropogenic stressors that impact multiple species and contribute to regional environmental degradation, and 3) a critical dialog about the role of societal economic growth and material consumption on the grand conservation challenges. Our arguments are illustrated through the case of monarch butterflies and generalized to diverse migratory animals. To be effective, international law and policy efforts must be binding within countries, address broad-scale drivers of environmental degradation, and target interventions based on developments in the science of migratory connectivity that span periods of breeding, migration, and overwintering.*

Introduction

Having celebrated the 100th year anniversary of the Migratory Bird Treaty, it is important to recognize successes in conserving flagship migratory species, including gray whales and bald eagles. At the same time, society must confront the remarkable global convergence of migratory species declines, from ungulates and fish, to birds, bats and butterflies (Harris et al. 2009, Bowlin et al. 2010) (Figure 1). In response to habitat loss, food subsidy, barriers to movement, and climate change, some migrations have disappeared altogether (Wilcove and Wikelski 2008), and others have shifted in timing, distances, and routes travelled (e.g., Visser et al. 2009, Pulido and Berthold 2010). The loss of migratory animals and their spectacular international movements reduces ecosystem function and diminishes the values humans derive from nature (Bauer and Hoye 2014). Their loss is also part of a class of complex, large-scale, multi-jurisdictional environmental problems the global community must address to advance biodiversity conservation (Leadley et al. 2014).

By definition, migratory animals have geographically distinct breeding and non-breeding phases that are connected by long-distance migrations. A key issue for migratory species is their tendency to migrate and breed (or overwinter) in large numbers, with high abundances needed to successfully navigate and avoid predators (Wilcove and Wikelski 2008). At the same time, their widespread annual ranges make migratory species highly susceptible to multiple biotic and abiotic stresses, including shifting patterns of resource exploitation by humans (Webster et al. 2002). To succeed in protecting migratory species, scientists, conservation practitioners and policy makers must develop trans-boundary solutions and engage in international cooperation to fill knowledge gaps and overcome institutional barriers to conservation.

Although each animal migration is unique, there are common biological and social threads. Here we identify three levels of analysis and action necessary to reverse migratory species declines: (i) expand the science of migratory connectivity to identify the times and locations where individual species are most vulnerable, (ii) address how multiple anthropogenic stressors, including land use change, pesticide application, and the proliferation of invasive species are impacting animal migrations and their population sustainability, and (iii) recognize

Figure 1. Crossing boundaries in animal migration (Figure 1). In the four panels depicted here, individual animals make their annual (or longer) round-trip journey. a) The likely nocturnal migration routes of Bogong moths (*Agrotis infusa*), a generalist noctuid, in Australia. In spring (September – November) moths move from Queensland, New South Wales and Victoria, to caves in the Australian Alps (December – February). The moths leave the caves at the end of the summer and remigrate (March – April) along similar routes as in spring to their breeding grounds (May – August). Migration journeys have been confirmed with vertical radar, long-term light trapping and careful observation (Warrant et al. 2016).

b) Mature Atlantic bluefin tuna (*Thunnus thynnus*) undergo two types of migrations: a foraging migration to the North Atlantic Ocean and a trans-Atlantic migration to spawning areas in the Mediterranean Sea. Movements of this single individual were documented with implanted archival light-level geolocators that provide light-level data to estimate geographic position and sea surface temperature to help improve latitude estimates.

c) Leatherback sea turtles (*Dermochelys coriacea*) travel great distances between nesting and feeding grounds. The path of an individual of the western Pacific population travels from nesting sites in Indonesia to foraging grounds in the western US and back to nesting sites upon reaching sexual maturity. Satellite tags attached to the carapace of the turtle transmit to Argos satellites when the animal is at or near the surface.

d) The classic migration of Wildebeest (*Connochaetes taurinus*) from the Serengeti in Tanzania to Kenya's Maasai Mara and back. In August, wildebeest migrate towards the Maasai Mara, where they remain until the rains begin in the southern Serengeti (November) and then migrate south. The herds remain in the southern Serengeti until April for calving season, then head northwest to western and northern Serengeti (May – July) (adapted from Musiega et al. 2006). Tracking has been conducted with a combination of radio transmitters followed with fixed-wing aircraft and satellite tags on collars.

Data for panels b and c were accessed from the U.S. Animal Telemetry Network Data Assembly Center. 2016.

<http://oceanview.pfeg.noaa.gov/ATN/#>. Basemap sources: Esri, DigitalGlobe, Earthstar Geographics, CNES/Airbus DS, GeoEye, USDA FSA, USGS, Getmapping, Aerogrid, IGN, IGP, and the GIS User Community.

that, at the largest scale, material consumption is the ultimate driver of ecosystem degradation and the loss of migratory species. We review past international agreements and national policies targeting migratory species conservation, and we outline how future commitments should incorporate scientific understanding of declining species and also integrate socioeconomic and ecological impacts of interventions. We illustrate each of these points through the well-publicized case of North American monarch butterflies. Specifically, we focus on scientific efforts to better understand their movement ecology and population threats, and on conservation initiatives to restore and protect their spectacular tri-national migration.

The Science of Migratory Connectivity

Knowledge of where animals go throughout their annual cycles, and at what points they are most vulnerable to environmental change (Bowlin et al. 2010, Runge et al. 2014) is crucial to predict reproductive success and mortality rates of migratory species. Comprehensive ecological data on most animal migrations covering both breeding and non-breeding areas remain elusive, in part because many animals are difficult to follow, and data collection is challenging and expensive. As cases in point, migratory routes and ecologies are largely unknown for insects such as dragonflies and for nocturnal animals such as tree bats. Scientists have documented basic range distributions for most migratory species, but better information on the geographic links (termed *migratory connectivity*) and the demographic connections (termed *seasonal interactions*) between stages of a migratory animal's annual cycle (Webster et al. 2002) is crucially needed (Figure 2).

Anthropogenic forces, including climate warming and changes to resource distributions, have changed the timing and extent of many seasonal migrations (e.g. Fiedler 2003, Hurlbert and Liang 2012, Satterfield et al. 2018). Research on migratory connectivity and seasonal interactions can advance population models to explain and predict these changes in migratory species abundance and distribution (Marra et al. 2015). For example, winter habitat quality can influence spring arrival date on the breeding grounds, which can in turn affect reproduction, including the number of successful broods and total young fledged, as has been demonstrated for American Redstarts (Norris et al. 2004). Similarly, changes in resources in breeding habitats or stopover sites can affect migratory success or winter survival. In some cases, the removal of physical barriers (e.g., dams, highways), or targeted habitat restoration, can help restore migratory populations, as demonstrated for Pacific salmon and other fish species (Meixler et al. 2009). In other cases, more expansive habitat modifications and the removal of threats across multiple stages of the migratory cycle are needed for populations to recover (e.g., Martin et al. 2007).

In fast-reproducing species like most insects, populations have the potential to recover from temporary reproductive failure or mass mortality through high fecundity and quick turnaround of multiple generations. Conversely, for most vertebrates, individuals typically make the annual migration one or more times before reproducing; thus failure to complete the cycle can have substantial impacts on population viability. For example, breeding failure in black-legged kittiwakes altered schedules of migratory transitions and locations of overwintering (Bogdanova et al. 2011). Although the impacts of these shifts for population dynamics are unclear, the result underscores the reciprocal importance of population abundance for migratory success (Wilcove and Wikelski 2008).

Figure 2. A conceptualization of the annual cycle representative of many migratory animal species, illustrated through the American Redstart (*Setophaga ruticilla*). The redstart breeds in the northern part of eastern North America and western Canada between May and July, and overwinters in Central America and northern South America from September to March. Key food resources and habitats are small insects in open mature woodland habitats. Spring and fall migrations can require up to two months of travel with frequent stopover. Critically, the science of migratory connectivity has a focus not only on the distinct stages of an annual migratory cycle, but also the “seasonal effects” which carry over from one stage to the next. For American Redstarts, key insights are summarized in the figure below (based on research in Norris et al. 2006).

The need for information on migratory connectivity has led to innovative approaches for tracking animal movements in recent years, including the use of citizen science observations, satellite GPS transmitters, miniaturized archival geolocators, and isotopic investigations of animal origins (e.g., Hobson et al. 2014, Fraser et al. 2016, Fudickar and Ketterson 2018) (Supporting Information, Table S1). Deploying these technologies is needed to inform modeling approaches, including stage-to-stage transitions and migratory flow networks (Taylor et al. 2016), with the goal of understanding migratory connectivity and stressors across the annual cycle (Hostetler et al. 2015, Taylor et al. 2016). Insights from these analyses can help establish protected areas, advance targeted restoration, regulate human activity, and advance public awareness of sensitive places and critical times. For example, beginning in 2014, an innovative program spearheaded by The Nature Conservancy used knowledge of the geography of shorebird migration collected by citizen scientists to advance just-in-time conservation (Robbins 2014, Reynolds et al. 2017). They paid California farmers to leave specific rice fields flooded for relatively short intervals, providing stopovers for migratory birds threatened by severe drought during their southern migration.

The pathway forward for migratory species conservation rests on integrating advances in the science of migratory connectivity into more effective conservation strategies that address threats throughout the annual migratory cycle. From the perspective of conservation planning, it is critical to know where interventions are likely to be most cost effective. Spatially explicit data on population sensitivity needs to be overlaid with spatially explicit data on costs of conserving particular habitats. Scaling up from studies of individual species, migration studies can also highlight systemic threats to biodiversity and build the case for action on larger-scale issues, as discussed after the monarch case is introduced below.

Monarch Butterfly Migration: Threats and Strategies for Protection

The promises and limitations of migratory species science and conservation can be highlighted through the case of monarch butterfly (*Danaus plexippus*) migration in eastern North America. Monarchs span three countries and travel several thousand kilometers throughout their annual cycle (Figure 3). During the spring and summer, monarchs fly north over multiple breeding generations across the U.S. and southern Canada, laying eggs on milkweed host plants as their larval food. Butterflies that emerge in late summer migrate south to overwintering sites in high altitude fir forests in the neovolcanic mountains of central Mexico.

Since the discovery of the monarchs' overwintering grounds in Mexico in 1975, conservation concerns have been raised, especially because of the narrow geographic location and specific habitat requirements of the overwintering sites (Brower et al. 2012, Vidal et al. 2014, Agrawal 2017). In 1983, the IUCN designated the monarch migration as a threatened phenomenon, noting that although monarchs are widespread globally and not likely to go extinct as a species, the North American migration was at risk, mainly owing to threats from logging at the overwintering sites (Brower et al. 2002). Despite further efforts to protect the monarchs' winter forests, which include designation of the Monarch Butterfly Biosphere Reserve as a UNESCO World Heritage Site (2008), estimates of overwintering monarchs have declined dramatically since the late 1990s, with the lowest numbers recorded in 2012-2015 (Figure 4). This trend required two decades of monitoring to resolve, owing to historically strong population fluctuations both within and between years (Brower et al. 2012).

Figure 3. Annual migratory cycle and key risks identified to date for North American monarch butterflies.

1. Monarchs overwinter from November to March in high elevation fir forests in Central Mexico (red circle) that have been protected by Mexico since the mid-1980s, and became UNESCO World Heritage Sites in 2008. Logging operations, including small scale subsistence logging and larger harvesting, continue to degrade the sites, although careful monitoring of forests, stronger protections from federal police and reforestation efforts have increased in recent years.

2. The spring migration and recolonization starts in mid to late March each year and spans 2-3 generations as monarchs move northward. Only recently has the US Fish and Wildlife Service encouraged habitat restoration and protection in the south-central US (including Texas) during the first spring generation.

3. Widespread discussion about the role of habitat quality and milkweed abundance in monarch **summer breeding range**, which spans across the central and eastern US and southern Canada, has prompted analysis of citizen science data, modeling efforts, and habitat restoration of milkweed plants in the Midwestern and Northeastern USA. US Fish and Wildlife Service and Forest Service are engaged in developing conservation plans, but these are not legally binding.

4. A role for the **fall southern migration** (dashed arrows), which extends from late August to early November, in the decline of monarchs has been hypothesized, but few data are available on habitat needs and migratory mortality, and no protections for migrating monarchs in the US or Canada are in place.

Since 2011, scientific focus on the causes of monarch declines shifted to milkweed host plant declines throughout the breeding range, in large part owing to widespread spraying of herbicides and the planting of herbicide tolerant crops in the U.S. (Flockhart et al. 2015, Inamine et al. 2016). This attention has motivated recent efforts to increase monarch breeding habitats by planting milkweed and nectar resources, especially in the central U.S. (Lewandowski and Oberhauser 2016). Other possible threats, including those during the monarchs' fall migration, remain relatively unexplored, and comprehensive analyses of existing data and integrative modeling approaches are needed to understand migratory connectivity and identify where in their annual cycle conservation efforts will have the greatest impact (Flockhart et al. 2015, Inamine et al. 2016, Oberhauser et al. 2017, Agrawal and Inamine 2018). In the absence of data, some current modeling efforts rely heavily on "expert opinion" to define key parameters such as migratory mortality (Flockhart et al. 2015, Oberhauser et al. 2017, Thogmartin et al. 2017a).

Data from multiple citizen science monitoring efforts at continent-wide scales could be used to document shifts in monarchs' migration patterns, and to resolve the absence of a strong signal of decline at some points in the monarchs' annual cycle. As a case in point, controversy was sparked in 2012 when an analysis of two citizen science fall migration census programs at northern stopover sites *en route* to Mexico revealed no evidence of decline (Davis 2012). Subsequent analyses of butterfly count data on the summer breeding grounds also showed no consistent downward trend (Ries et al. 2015), and an assessment of connectivity between the successive stages did not point to milkweed limitation during the breeding season as a cause of declines in the wintering population (Inamine et al. 2016, Agrawal and Inamine 2018). Rising levels of monarch disease over the past two decades were recently reported from a North American monitoring program, and this has now been included in modelling population trends (Thogmartin et al. 2017b). Despite the assumption that restoring and protecting breeding habitat in the Midwestern U.S. is key to sustaining monarch reproduction, a long-term analysis of natal origins of overwintering monarchs showed that nearly two thirds of monarchs in central Mexico originate from other parts of North America (Flockhart et al. 2017), suggesting that reversing habitat loss in the Midwest will not protect the majority of the migratory population. Future modeling efforts, novel approaches to historical data, and assessment of monarch mortality during migration are especially needed to resolve the apparently contradictory trends in monarch abundance data (e.g., Flockhart et al. 2017, Oberhauser et al. 2017), and to better integrate the roles of lesser-appreciated threats to monarchs (e.g., droughts, snowstorms, roadside mortality, insecticides, and disease).

The record low monarch numbers observed at overwintering sites between 2012-2015 engendered an immediate response from the public and generated high-level attention from North American leaders on a level that has never been seen for other declining insects (Diffendorfer et al. 2014). Leaders of Mexico, US and Canada created domestic task forces to address the problem. Current recovery efforts span federal and state government agencies and include action plans by NGOs, schools, and individuals. In the U.S., a petition to list monarchs as threatened under the Endangered Species Act in August 2014 has further thrust monarchs into view as a species in need of immediate action. The U.S. Fish and Wildlife Service is currently conducting analyses of population trends and migratory connectivity, and the agency is required by law to reach a decision about federal protection by June 2019.

The monarch enjoys iconic status premised on decades of scientific study, educational programming, and popular engagement (Gustafsson et al. 2015). Yet the future of their migratory cycle remains in doubt, even though the species itself is unlikely to go extinct. Growth in global

Figure 4. The population decline of monarch butterflies as measured by hectares of forest occupied in the highlands of Central Mexico during overwintering (data courtesy of WWF Mexico). This pattern of decline has not been strongly observed at other stages in the annual migratory cycle, such counts of summer adults in the breeding range or fall migration counts at northern stopover sites.

demand for agricultural products, intensification of corn and soybean production and pest control, and land use change linked to urbanization and infrastructure reflect economic growth and expanded demands on ecosystem processes. Thus, despite the monarch's status in our collective consciousness and the 1996 chartering of the Trilateral Committee for Wildlife and Ecosystem Conservation and Management between Canada-US-Mexico, declines have continued. The monarch case suggests that sustained scientific engagement and the mobilization of conservation responses ranging from raising the awareness of generations of schoolchildren, organization of vast citizen science networks, and public statements of cooperation among the political leaders of North America is not enough to address the population decline. Below, we outline several approaches at the science-policy interface that could show promise for conserving the migrations of monarchs and diverse other species.

Moving forward with integrating science into policies

The case of the monarch butterfly highlights multiple challenges that migratory species face. Even when seasonal movements are well-known, movement across national borders, and a multitude of threats, introduce a need for cross-jurisdictional cooperation. Differences between countries in conservation goals, laws and governance capacity pose particular challenges to cross-boundary conservation. Easing the diverse stresses in multiple locations and stages of the migration will be critical for monarch conservation, and could benefit a large number of other species including insect pollinators, wildflowers and birds. In what follows, we explore examples of international conservation initiatives and the implications and limitations of migratory science for enhancing their effectiveness (see Supplemental Information, Table S2). These ongoing efforts address (i) direct threats during species' annual cycles, (ii) systemic threats to regional or global ecosystems, and (iii) pervasive political and economic drivers underlying biodiversity declines.

International Policies Targeting Species-level Conservation

The emerging science of migratory connectivity, particularly understanding detailed migratory pathways and demographic perturbations, can improve the effectiveness of international efforts to prevent direct threats at the species level, including overharvesting and habitat loss. Treaties aimed primarily at restricting harvesting, including international trade, are among the earliest and most common international conservation efforts. Examples of treaties aimed directly at lowering the harvest of wildlife include the Northern Fur Seals Agreement (fur seals), the Migratory Bird Treaty of 1916 (migratory birds) and the International Whaling Convention (whales) (see Table S2). These treaties have been fairly effective in reducing the mortality of species that cross international borders.

The global Convention on International Trade of Endangered Species (CITES, 1987) does not prohibit the harvesting of species directly, but instead restricts the *international trade* in threatened or endangered species or their parts. A benefit of CITES is that countries that sign the treaty pledge to pass domestic legislation and train enforcement officers, and violating countries may be subject to sanctions (Vasquez 2003). A recent case involving Saiga antelope (a highly mobile nomadic species) exemplifies how CITES pressured China and other countries trading in

Saiga horns towards enforcement against poaching (Von Meibom et al. 2010). Saiga also benefit from a cross-convention collaboration between CITES and the Convention on Migratory Species (see below). Additional high profile examples of protection under CITES include efforts to conserve elephants, birds in the pet trade, and sea turtles.

If the major driver of migratory species decline is over-harvesting, a policy response that restricts or prevents harvesting at vulnerable times or locations is relatively simple and can be straightforward to enforce, depending on the motivation for harvesting. For some species, recovery can be significant (Table S2). For many other species such as the monarch butterfly discussed above, habitat loss, appears to be a major cause of declines. In these cases, other initiatives have aimed at protecting habitats of high conservation value. For example, the Convention on Wetlands of International Importance Especially as Waterfowl Habitat (Ramsar Convention) is designed to provide international support for protecting wetlands that support significant populations of migratory waterfowl. Parties designate wetlands for inclusion on an internationally recognized list that makes them eligible for financial and other support. Currently, the Ramsar Convention covers 2,288 wetland sites (totaling nearly 221 million hectares) in 169 countries. The Convention both explicitly and implicitly considers migration in its activities. The same basic approach, without a specific focus on migration, leads to the listing and protection of some high value natural sites under the UNESCO Convention Concerning the Protection of the World Cultural and Natural Heritage (the “World Heritage Convention”). Indeed, as noted above, the monarch butterfly’s wintering grounds were listed on the World Natural Heritage List, but this added protection did not stem the decline, in part due to threats outside the protected area, illegal logging that continued within the protected area, and other potential stressors such as climate change, pesticides and disease.

Arguably the most comprehensive framework for addressing migration, including both overharvesting and habitat loss, is the Convention on Migratory Species (CMS, Table 2). The CMS provides a framework for developing treaties and other initiatives tailored to specific species or groups of species, and could eventually promote the conservation of a wide range of migratory species across diverse taxonomic group and habitats used. It currently consists of seven binding agreements and 19 memoranda of understanding. Countries that join one of the agreements (and contain part of the range of endangered migratory species) are expected to prohibit the taking of that species, conserve and restore its habitat, and reduce other threats facing the species’ existence. Non-migratory species that have transboundary distributions can also be protected under the CMS. Thus, the CMS focuses the attention of the conservation community on species that require international agreements for their protection, and assigns responsibility for conservation to specific countries (Hensz and Soberón 2018).

The impact of the CMS is currently constrained by a lack of resources for enforcement, and because participation by key countries such as the United States remains limited (Marra et al. 2011). Another major shortcoming of the CMS is the limited number of species for which agreements have been negotiated; only a small number of species are covered, and sometimes only for part of their range. Nonetheless, CMS is gaining greater acceptance and provides a framework to fill crucial conservation gaps, but this depends on enhanced scientific understanding of migration and engagement of relevant countries. Beyond strengthening the CMS, the Ramsar Convention (noted earlier) could be used as a model through which science can inform conservationists about protecting critical migratory hot spots for species other than waterfowl.

Recruiting more Western Hemisphere nations to join existing conventions remains a high priority, but it is also only a first step. Care should be taken to not let international agreements legitimate what could be seen as superficial conservation strategies. Domestic legislation that binds nations to action consistent with the treaties is typically lacking under these global agreements (except CITES discussed above), and enforcement is highly uneven, producing significant failures of implementation. For example, the existing Trilateral Committee engaged in monarch conservation has yet to influence major policy decisions and legal enforcement across Canada, USA, and Mexico. Conservation commitments could be targeted at a broad array of sectors, including regulation and investment applied to transportation, public lands management, and agriculture.

Within countries or political unions, major legislation has had some success, but for migratory species, success is constrained by geopolitical boundaries. For example, the Endangered Species Act (ESA) of 1973 protects threatened and endangered species in the USA without limitation to specific causes of species decline or methods of protection. Successful protections have improved populations of several migratory species, including the bald eagle, impacted by DDT, as well as the more recent increase in the Kirtland's warbler population. Lack of funding and the resulting listing backlog at the U.S. Fish and Wildlife Service, combined with the limited regulatory reach outside the USA, reduce the ESA's effectiveness, especially for migratory species. Current efforts to diminish legislated protections for species under the ESA is particularly worrying, as this development highlights the weak political consensus for combatting extinction. The European Union Birds Directive (EUBD), a legal act of the EU, similarly compels member nations to achieve broad scale conservation goals. A recent study addressed bird population trends of species protected by the EUBD versus unprotected birds, including migratory species (Sanderson et al. 2016). Although protected species showed more positive population trends than unprotected species, this difference was absent for long-distance migrants. The models evaluated by Sanderson et al. (2016) suggested that protections resulting from the EUBD produced some protection in the face of climate change, but it remains unclear as to why migratory species were consistently less positively impacted by the regulation.

Regional-scale Policy Responses to Systemic Stresses

As a complement to species-specific and place-based conservation efforts, interventions focused around broader-scale threats to biodiversity, including species invasions and habitat loss, are critical to reducing stresses on migratory species. Such threats can be especially harmful for migratory animals that encounter a wide variety of environments and potential stressors throughout their annual cycle (Opdam and Wascher 2004). The primary response to land conversion is either to zone off some areas from conversion or to mitigate the impacts of intensified use. However, this patchwork approach to habitat conservation efforts is particularly ineffective at countering the threat of widespread land conversion, and less than 7% of terrestrial land is set aside for protection at a global scale. Many non-treaty initiatives have tried to address the patchwork problem by expanding the geographic scope of conservation efforts. For example, the Yellowstone-to-Yukon Conservation Initiative represents an ambitious and innovative approach to trans-boundary science, environmental management, and policy (Graumlich and Francis 2010). Globally, the Aichi targets (<https://www.cbd.int/sp/targets/>) under the Convention on Biological Diversity aim to increase conservation areas to 17% of land and 10% of oceans by

2020. More ambitious still is the Half Earth goal championed by E.O. Wilson, which calls for the protection of half of the earth to maintain most of the life forms. Migratory connectivity science, in addition to other approaches (e.g., Redding et al. 2015), could be useful to prioritize the highest value regions and to support the creation of conservation corridors linking larger scale efforts. Beyond regulating land use and land cover change in conservation corridors and pursuing habitat restoration, it is possible to imagine targeted efforts in these zones focused around reductions in pesticide use, control of invasive species, and reductions in mortality linked to infrastructure such as roads and building strikes.

In some locations, habitat restoration and improved management can create and protect crucial resources. As one example, the restoration of prairie potholes and other wetland habitats in the U.S. and Canada offers critical stopover habitat for migratory birds, in addition to conserving biodiversity more generally (Naugle et al. 2001). For monarch butterflies, it has been suggested that nectar resources from flowers may be critically limiting during migration (Inamine et al. 2016), and efforts to promote nectar availability are underway within the migratory flyway. Where changes in land management will disrupt livelihoods and make marginalized people and cultures less secure, prior informed consent and compensation are needed to advance fair conservation arrangements (Kiss 2004).

Bans placed on pesticides such as dichlorodiphenyltrichloroethane (DDT) have been implicated in the recovery of some migratory species (Cade et al. 1988), but differences in pesticide regulation across nations continues to be an issue (Mora 1997). The current rise in knowledge about neonicotinoid insecticides on biodiversity (van der Sluijs et al. 2015, Mitchell et al. 2017) reminds of the importance of continual risk assessments of emerging threats. The emerging science has contributed to the abandonment of several neonicotinoids by countries in Europe and parts of Canada, but not in the United States and Mexico. The US Environmental Protection Agency is currently reviewing evidence of neonicotinoid effects, where tradeoffs between food prices, human health, R&D in the pesticide industry, and the conservation of biodiversity will be considered.

The widespread threats of invasive species (Molnar et al. 2008, Vilà et al. 2011) and climate change (Frost et al. 2016, Sanderson et al. 2016) have been widely recognized for both terrestrial and marine species, but international agreements and national legislation have lagged behind this knowledge. At present, most conservation policies do not mitigate the effects of invasive species and climate change on migratory species, and we believe this to be both a problem and an opportunity. Because interventions targeting such threats can resonate with a wide variety of interest groups (e.g., across taxa, environmental media, and welfare of humans and non-humans) across numerous jurisdictions, organizing them into effective advocacy coalitions is difficult, but with increases in migratory science demonstrating migratory connectivity, the emergence of more robust advocacy coalitions (Sabatier 1988) may be possible. Migratory species conservation is important in and of itself, but advocates for migratory species need to build diverse partnerships to construct and maintain popular and policy salience.

Addressing Global-scale Socioeconomic Drivers of Species Declines

Despite the iconic status of many migratory species, lack of political will in the face of significant economic and political forces limit effective responses to population declines. This suggests that protecting the world's migratory species also requires a renewed conversation

about conservation and the limits of science and policy as currently structured and practiced. Despite promising breakthroughs in conservation science, including in migratory connectivity research, large-scale drivers, such as material consumption and human appropriation of net primary productivity (Krausmann et al. 2013), are swamping our capacity to respond. At this macro-scale, economic policy and practice must better incorporate the inevitable limits to sustainability of our ecological systems.

The implications of the human population and explosive growth in resource consumption for ecology and conservation indicate that novel modes of social regulation of economic activity are crucially needed. Within the fields of environmental social science and humanities, there have been long-standing debates on the potential for transitions to sustainability, and the interplay between technology, politics, and environmental change (Box 1). The complex and indirect nature of connections between material problems of ecology and social responses have been amply discussed yet are difficult to address (Blühdorn 2007). When examined empirically and critically, contemporary conservation policy is essentially not capable of producing major conservation outcomes (i.e., stemming population and extinction of large numbers of species). In this sense, the function of much contemporary conservation policy is to legitimate “business as usual” rather than arrest or reverse degradation. In the language of environmental politics, these policies are “post-ecological” (Blühdorn 2013). It is essential that conservation scientists recognize this perverse dynamic and do not allow their work to legitimize policies and social arrangements that further advance unsustainability.

Globalization of commerce and finance are presenting new opportunities for negotiating conservation impacts in the context of trade agreements. The US-Peru Free Trade Agreement, for example, has a detailed section requiring enhanced forest conservation efforts in Peru. Most international project financing to developing countries now include environmental standards, including some aimed at nature conservation. Leading NGOs are working with multinational companies to introduce rigor and accountability into voluntary standards for sustainable commodity systems and value chains (e.g., palm oil, cocoa) (Carlson et al. 2018). Development banks also have power to impact conservation when they are committed to environmentally responsible guidelines (as recently advanced in the CMS). More generally, concerns about environmental conservation have begun to creep into conversations about economic competitiveness and economic growth. Without engaging dynamics at these higher levels of problem definition and social organization, saving the Earth’s great migrations, together with other efforts aimed at biodiversity conservation generally, will likely fail. Nation states are essential elements of international conservation strategy, but we must also engage economic actors and organizations of civil society operating at larger scales.

Finally, we question the typical invocation of ‘policy’ as a sufficient complement to ‘science’ in guiding conservation efforts. Some analyses suggest limits to the dominant model in which science informs, motivates, and legitimizes policy, and where policy then attempts to control social processes and alter resource flows in a manner that protects ecosystems. A more probing analysis and reconstruction of science-policy-practice interfaces is needed (Weichselgartner and Kaspersen 2010, Gustafsson et al. 2017). New relationships between science, citizens and policy processes could produce novel approaches to advance conservation. While migratory species conservation is a daunting challenge because of the social and geopolitical boundaries that these species cross, the phenomenon of migration and the way it connects humanity across boundaries may provide a catalyst for deeper conversations about sustainability.

Part of the societal response to declining biodiversity must reflect changes in human relationships to nature. This can be aided by further investments in citizen science programs that combine data collection and public education, ecological literacy, and advances in transdisciplinary research. The iconic status of some migratory species, like the monarch butterfly, and their capacity to highlight interdependence among people and places are potent resources for initiating and sustaining dialogue about the value of conserving nature in a time of rapid and uneven economic growth. While migratory animals pose particular conservation challenges, they are often widely recognized and cherished, creating opportunities to place conservation on the policy agenda and to advance public education.

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Box 1. A primer on the environmental sociology of sustainability issues

Within the field of environmental sociology, debate about the interactions between society and environment has been framed as a contest between two contrasting models of human ecology. Both models address prospects for sustainability under capitalism:

- Ecological Modernization (EM) anticipates the progressive restructuring of society such that economic development is decoupled from ecological degradation. EM emphasizes that institutional changes can improve human wellbeing without degrading natural capital (Asafu-Adjaye et al. 2015). Technological innovation and changes in material consumption – as emphasized in Ehrlich and Holdren’s famous IPAT formula - emerge from shifts in governance and culture, specifically new patterns of market competition and new understandings of humans’ dependence on nature (Chertow 2000).
- Treadmill of Production emphasizes structural constraints to sustainability. Competition in markets drives successive rounds of capital investment at the level of firms and nation states, resulting in productivity gains, decreases in costs of finished goods, and expanded opportunities for material consumption by consumers. At the same time, the state fails to impose environmental controls on firms and sectors due to demands from workers and consumers to maintain purchasing power in the face of declining wages and bargaining power in a globalizing economy (Schnaiberg et al. 2002).

More recently, new theory has explicitly engaged with the symbolic dimensions of contemporary environmental politics (Blühdorn 2007) to emphasize the tension between acknowledgement of ecological crisis, on the one hand, and bedrock commitments to liberalism and capitalism, on the other. Faced with limited options, the resulting legitimacy crisis gives rise to gestures and performances of engagement with sustainability by states, markets, and individuals. In this formulation, conservation actions are gestures (including calls for a more authentic dialogue) that serve to legitimate precisely what it is they contest. In other words, applied ecology and conservation of individual species are understood as an essential resource for “sustaining the unsustainable” (Blühdorn 2007). For example, environmental policy and management concepts such as ‘critical minimum habitat’ derive from a scientific foundation that makes it possible to designate and protect habitat in some territory to avoid species extinctions. But even if we were to be persuaded that the habitat and population models (including stressors at all life stages across a migratory cycle) are robust, consideration of ongoing environmental change and issues such as migratory connectivity raise questions about the future of a given species, let alone the countless species at risk for which we do not mobilize a similar effort.

The implications of this analysis of environmental politics is that conservation science risks providing plausible deniability to elected officials, to corporations, and to consumer society. In this context, it is important that conservation science question its role in sustaining business as usual. Acknowledging that such issues are relevant to the discipline represents a first step.

Supporting Information, Table S1. Available technologies that enhance the ability of scientists to track migratory animals throughout their annual cycles.

Tracking Technique	Type of Animal	Minimum Body Size (g)	Cost per Animal	Data Retrieval	Data Type	Data Accuracy	Life
Individual Marking (bands, tags)	Any	None	Low: Close to \$0	Recapture of animal	point location	Exact	years
Passive Integrated Transponders (PIT tags)	Amphibians, birds, invertebrates, fish, reptiles, mammals	0.9	Low: \$2	Recapture or when animal passes antenna	point location	Exact	years
Stable Isotopes (tissues)	Any	None	Low: \$10	Tissue sample collection	latitudinal location	600 km	N/A
Molecular Markers (genetics)	Any	None	Low: \$20	Tissue sample collection	differentiated populations	Broad	N/A
MOTUS Network (nanotags)	Large insects to birds and bats	10	Medium: \$75	Receivers log signals from transmitters when in range	point location	15 km	weeks to months
ICARUS network (International Space Station)	Birds, mammals, aquatic	160	Medium: \$500-700	Signals sent to handheld device or base station	GPS	5 m	>1 year
Light-level Geolocation	Birds, fish	8	Medium: \$200	Archival - requires recapture of animal	light level to infer latitude and longitude	100-150 km	>1 year
GPS Geolocation	Birds, mammals	33.3	Medium: > \$390	Archival - requires recapture of animal	GPS locations	10 m	months
GSM Tags	Birds, mammals, aquatic	566	High: \$2,500-4,000	Uses the cellular network to receive and transmit locations	GPS locations	10 m	months to >1 year
Acoustic Telemetry	Aquatic	16.6	High: >\$3,000	Receivers log signals from transmitters when in range	point location	<1 to >1,000 m	days to >1 year
Radio (VHF) Telemetry	Birds, mammals	6.6	Medium: \$100-200	Antennas and receivers pick up unique frequencies from a distance	point location	10 m	weeks to >1 year
Satellite Telemetry	Birds, mammals, aquatic	116.6	High: \$3,000-7,000	Almost real time locations transmitted to satellites and sent to email, fax, web or software	GPS or other point location	250-1500 m	months to >1 year

Supporting Information, Table S2. Key examples of international initiatives for biodiversity protection with implications for migratory species, and reciprocally, the impact of migratory connectivity research on the conservation potential of these initiatives.

Threat	Examples of International Initiatives	Primary Policy Response	Strengths and Weaknesses regarding conservation of migratory species	Impact of expanded Migratory Connectivity research
Direct Overharvesting	International Whaling Convention (1948)	Harvest limits and moratorium	Complete ban on commercial harvest; Exceptions for “scientific research” exploited	Population monitoring improved
	US-Canada Migratory Bird Treaty (1916)	Prohibited “take” of most migratory birds	Broad definition of “take”; Implemented by clear national laws in US and Canada; enforcement is limited by resources	Population monitoring improved
	Convention on International Trade in Endangered Species (1987)	Restricts commercial trade of listed threatened or endangered species	Strong ban on commercial trade with focus on enforcement; Only covers species once they are threatened or endangered; No coverage of habitat protection or domestic harvests	Improved scientific basis for listing of species; Improved population monitoring and targeted enforcement
Habitat Loss	Convention on Biological Diversity (1993)	Promotes inventories, protected areas, and conservation generally	Comprehensive in highlighting all threats to biodiversity; No enforcement mechanism; No specific focus on migration	Scientific basis for taking action on a wide range of species
	RAMSAR Wetlands Convention (1975)	Targets protection of wetlands important to migration	Prioritizes protection of habitat areas for migration stop-overs; Limited to wetlands	Scientific basis for listing new wetlands and for enhancing management of existing ones
	Convention on Migratory Species (1983)	Targets conservation of species in full range, including migration	Can include states throughout life cycle, including migration; Limited participation; Limited species covered so far	Identifying conservation priorities given migration paths
	Inter-American Sea Turtle Convention (2001)	Highlights need to protect nesting habitat and to reduce direct exploitation	Has strengthened national commitments to protecting sea turtles; limited protections while sea turtles at sea	Improved scientific basis for protecting animals outside of breeding areas
	UNESCO World Heritage Convention (1975)	Gives international attention to conservation of listed sites	Publicity of listing adds some protection; Limited number of conservation-related sites	Can build the scientific basis for listing sites; Build international support for improved management of sites
	Western-Hemisphere Convention on Nature Protection (1942)	Promotes national parks and protected areas	Highlights need to take measures for migratory birds particularly; no enforcement or implementation infrastructure	Increased attention might build support for modernizing the convention
Chemicals and pesticides	Stockholm POPS Convention (2004);	Bans and regulates pesticides and other chemicals	Complete bans on some of most damaging pesticides; Many chemicals, such as neonicotinoids left to national law and often unregulated	Better understanding about the impacts of neonicotinoids

Invasive Species	Biodiversity Convention Invasive Alien Species Programme (2001)	Provides voluntary guidelines and some financial and technical support for controlling invasive species	Guidelines are voluntary and there is insufficient financial support for effective implementation	Better documentation on threats posed by invasive species throughout life cycles could attract more resources and political commitment to controlling spread of invasive species
Genetically Modified Organisms (GMOs)	Cartagena Biosafety Protocol (2003)	Control trade in GMOs by implementing a system of informed consent	Creates a labelling and information exchange system; Regulation left to national levels	Studies could close gaps in knowledge about potential impacts and provide the scientific basis for regulating certain GMOs
Climate Change	UN Framework Convention on Climate Change (1994) and Paris agreement (2016)	UNFCCC Creates the framework for addressing climate change; Paris Agreement signals long-term switch from fossil fuel use and has prompted nationally determined commitments	Almost all countries are now participating; Ambition gap is still significant between promises and levels needed to avoid severe impacts; some unanticipated consequences from climate policy (e.g., land conversion due to biofuels)	Helps prioritize and build support for where we put climate finance, May also help mobilize people in these areas
	Reduced Emissions from Deforestation and Degradation (REDD) (2009)	Provide incentives to conserve forests as carbon sinks under the climate regime	Links climate mitigation with forest conservation; Less international financial support than expected	Helps prioritize sites with wildlife co-benefits
Macroeconomic growth (trade, investment, finance)	International Financial Corporation's Performance Standards (2012); Equator principles III (2013)	Environmental standards for projects supported with project finance from certain public and private commercial banks	Impacts on migratory species part of impact assessments; some require no net loss of habitat	Improves impact assessments and establishes priorities for offsets and other conservation mitigation measures
	Peru-US Free Trade Agreement (2009) EU Forest law Enforcement, Governance and Trade (FLEGT) Action plan (2003)FLEGT Agreements	Agreements to strengthen sustainable forest management in context of trade agreements	Linking forestry standards to trade agreements can build political will and line up legal trade in forests with sustainability goals. Limited to key natural resource and commodity sectors (e.g., forest conservation in Peru); may have limited impact on the ground	Could build basis for side agreements for increased cooperation in protecting shared resources
Unsustainable Consumption Patterns	Global Supply Chain Sectoral Standards (E.g., FSC, MSC, bird-friendly coffee, RSPO)	Sets standards for certifications, eco-labels, green finance, etc.	Many initiatives in many sectors, often with a focus on reducing land conversion; Most are voluntary and with limited penetration into the market; sometimes weak scientific basis for standards	Improves Scientific basis for standards