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Animal migration in the Anthropocene: threats and mitigation options

Steven J. Cooke[1,*], Morgan L. Piczak[1], Navinder J. Singh[2], Susanne Åkesson[3], Adam T. Ford[4], Shawan Chowdhury[5,6,7], Greg W. Mitchell[1,8], D. Ryan Norris[9], Molly Hardesty-Moore[10], Douglas McCauley[10], Neil Hammerschlag[11], Marlee A. Tucker[12], Joshua J. Horns[13], Ryan R. Reisinger[14], Vojtěch Kubelka[15] and Robert J. Lennox[16]

[1]*Department of Biology and Institute of Environmental and Interdisciplinary Science, Carleton University, 1125 Colonel By Dr, Ottawa, Ontario K1S 5B6, Canada*
[2]*Department of Wildlife, Fish and Environmental Studies, Faculty of Forest Sciences, Swedish University of Agricultural Sciences, Umeå 90183, Sweden*
[3]*Department of Biology, Centre for Animal Movement Research, Lund University, Ecology Building, Lund 22362, Sweden*
[4]*Department of Biology, University of British Columbia, 1177 Research Road, Kelowna, British Columbia V1V 1V7, Canada*
[5]*Institute of Biodiversity, Friedrich Schiller University Jena, Dornburger Straße 159, Jena 07743, Germany*
[6]*Department of Ecosystem Services, Helmholtz Centre for Environmental Research – UFZ, Permoserstr, 15, Leipzig 04318, Germany*
[7]*German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Puschstr, 4, Leipzig 04103, Germany*
[8]*Wildlife Research Division, Science and Technology Branch, Environment and Climate Change Canada, 1125 Colonel By Dr, Ottawa, Ontario K1A 0H3, Canada*
[9]*Department of Integrative Biology, University of Guelph, 50 Stone Rd. E, Guelph, Ontario N1G 2W1, Canada*
[10]*Department of Ecology, Evolution, and Marine Biology and Marine Science Institute, University of California, Santa Barbara, Santa Barbara, CA 93106, USA*
[11]*Atlantic Shark Expeditions, 29 Wideview Lane, Boutiliers Point, Nova Scotia B3Z 0M9, Canada*
[12]*Radboud Institute of Biological and Environmental Sciences, Radboud University, Houtlaan 4, Nijmegen 6525, The Netherlands*
[13]*Department of Biology, University of Utah, 257 South 1400 East, Salt Lake City, UT 84112, USA*
[14]*School of Ocean and Earth Science, University of Southampton, National Oceanography Center Southampton, University Way, Southampton, SO14 3ZH, UK*
[15]*Dept of Zoology and Centre for Polar Ecology, Faculty of Science, University of South Bohemia, České Budějovice, Czech Republic*
[16]*Ocean Tracking Network, Faculty of Science, Dalhousie University, 1355 Oxford St, Halifax, Nova Scotia B3H 3Z1, Canada*

ABSTRACT

Animal migration has fascinated scientists and the public alike for centuries, yet migratory animals are facing diverse threats that could lead to their demise. The Anthropocene is characterised by the reality that humans are the dominant force on Earth, having manifold negative effects on biodiversity and ecosystem function. Considerable research focus has been given to assessing anthropogenic impacts on the numerical abundance of species/populations, whereas relatively less attention has been devoted to animal migration. However, there are clear linkages, for example, where human-driven impacts on migration behaviour can lead to population/species declines or even extinction. Here, we explore anthropogenic threats to migratory animals (in all domains – aquatic, terrestrial, and aerial) using International Union for the Conservation of Nature (IUCN) Threat Taxonomy classifications. We reveal the diverse threats (e.g. human development, disease, invasive species, climate change, exploitation, pollution) that impact migratory wildlife in varied ways spanning taxa, life stages and type of impact (e.g. from direct mortality to changes in behaviour, health, and physiology). Notably, these threats often interact in complex and unpredictable ways to the detriment of wildlife, further

* Author for correspondence (Tel.: +1 613 867 6711; E-mail: steven_cooke@carleton.ca).

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complicating management. Fortunately, we are beginning to identify strategies for conserving and managing migratory animals in the Anthropocene. We provide a set of strategies that, if embraced, have the potential to ensure that migratory animals, and the important ecological functions sustained by migration, persist.

Key words: conservation, animal movement, phenology, natural resources management, wildlife biology, biodiversity.

CONTENTS

I. INTRODUCTION

Animal migration involves the generally synchronous and directional movement of individuals of the same species between distinct environments. If such migrations are not undertaken, individual fitness is typically compromised (Dingle & Drake, 2007). Some migrations are of short distance and duration (e.g. salmon alevins migrate from the substratum to the water surface to fill their swim bladder, often a distance of just a few centimetres) whereas other migrations involve traversing ocean basins, continents, or even hemispheres over months or years (e.g. the remarkable migrations of petrels, terns or shorebirds across thousands of kilometres or the inter-generational migration of monarch butterflies *Danaus plexippus*). Migration occurs in diverse taxa that range in size from microscopic zooplankton to massive marine mammals, and occurs on or in land, water (marine and fresh water), and air (Joly *et al*., 2019). Although there are obvious costs of migration, they are balanced against fitness-related benefits, which include access to habitats that provide nutritional resources, favourable environmental conditions for a given life stage (e.g. for growth or reproduction), and higher survival (Dingle, 1996). Migration is a phenomenon that has captured the attention of scientists and the public alike for centuries. For millennia, Indigenous peoples have forged deep spiritual, ceremonial, and nutritional connections to migratory wildlife. The ecosystem services generated by migratory wildlife are immense (Lopez-Hoffman *et al*., 2017) and it is becoming evident that migratory animals couple biodiversity and ecosystem function at various scales including at a global level (Bauer & Hoye, 2014).

Yet migratory animals are also often among the most threatened groups on the planet (e.g. Harris *et al*., 2009; Rosenberg *et al*., 2019). Recent studies on the status of migratory species have found significant declines for mammals, birds, and fishes, with much still to be learned about these groups as well as other migratory taxa. Migratory bird populations have declined on average more than non-migratory birds, and migratory seabirds and migratory birds in the Palearctic face the highest extinction risk as compared to other birds (Hardesty-Moore *et al*., 2018). Functional connectivity of migratory habitat for birds has declined since 2001, and the loss of functional connectivity is a significant predictor of migratory bird population decline (Xu *et al*., 2019). Migratory mammal populations overall do not seem to be in greater decline than non-migratory mammals according to *Living Planet Index* data, but migratory mammals face the highest extinction risk [based on International Union for the Conservation of Nature (IUCN) threat categories] when compared to birds and fishes and have experienced significant range contractions (Hardesty-Moore *et al*., 2018). The movement of migratory mammals has been reduced by up to one half in regions with a higher human footprint as compared to regions with a lower human footprint (Tucker *et al*., 2018). The status of migratory fish is heavily dependent on region and system (marine *versus* freshwater). Migratory freshwater fish are at greater risk of extinction than migratory marine fish, and migratory freshwater fish have declined globally by an

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average of 76% (Deinet *et al.*, 2020). Migratory freshwater fish in Europe and the Caribbean have experienced the greatest declines (93 and 84%, respectively; Deinet *et al.*, 2020). Migratory marine fish populations in the Pacific Ocean experienced greater declines than non-migratory populations in the same region (Hardesty-Moore *et al.*, 2018). Overall, many migratory fish have experienced significant range contractions (Hardesty-Moore *et al.*, 2018). Collectively, these examples highlight the precarious state of migratory wildlife.

An important paper by Wilcove & Wikelski (2008) with the poignant title 'Going, going, gone: is animal migration disappearing?' alerted the masses to the various issues facing migratory wildlife. However, as early as the 1990s researchers had mused that migration as a phenomenon was at risk of 'extinction' (Brower & Malcolm, 1991). The reasons that migratory wildlife populations are disproportionately threatened are multifaceted, but at the core is the fact that animals traverse various environments and multiple jurisdictions where they encounter a greater diversity of threats than resident animals. Moreover, anything that prevents a migratory organism from getting from one location to the next may negatively affect fitness, with consequences for population growth (Runge *et al.*, 2014). Further, migratory animals must transition between many life-history stages within their annual cycle relative to resident species, imposing severe time constraints (Wingfield, 2008). These time constraints may make them more susceptible to carry-over effects (*sensu* Harrison *et al.*, 2011) or alter migratory phenology (Lennox *et al.*, 2016). For example, perturbations that delay the transition between two life-history stages (e.g. post-breeding moult and migration in birds) or that result in reduced condition, can ultimately result in delayed transition into the next life-history stage or transitioning in sub-optimal condition, therefore affecting future performance and ultimately fitness (e.g. Legagneux *et al.*, 2012; Catry *et al.*, 2013). In short, the complexity of migration as a behaviour that has evolved to reap fitness benefits from a complex and dynamic environment is now contributing to the demise of migratory wildlife as a result of rapid human environmental change and exploitation (Shaw, 2016). We have now entered an Epoch distinct from the Holocene (i.e. the Anthropocene) defined by the dramatic impact of humans on the planet (Crutzen, 2006) emphasising the fact that life is not getting easier for migratory wildlife with more potential for mortality or fitness impairments (Hardesty-Moore *et al.*, 2018). Early treatments of this topic were brief (e.g. Wilcove & Wikelski, 2008) or focused more towards lay audiences (Wilcove, 2010). More recent syntheses (including some that are quantitative) have been either taxon specific (Malcolm, 2018; Kauffman *et al.*, 2021; see examples in previous paragraph), regional/realm specific (Kubelka *et al.*, 2022), or focused on a single threat [usually climate change (Robinson *et al.*, 2009; Seebacher & Post, 2015)], rather than a broader threat matrix.

There has been considerable focus on the effects of anthropogenic impacts on the numerical abundance of species/populations, whereas there has been relatively less attention on key life-history activities such as migration (Chowdhury *et al.*, 2021). There are clear linkages, for example where impacts or changes in migration behaviour can lead to population/species declines or even extinction. The objective of this paper is to explore animal migration in the Anthropocene with a focus on threats and threat mitigation. This is not a systematic review but rather a selection of examples intended to highlight some of the ways in which various threats interact with migratory wildlife. We are strong advocates for evidence-based approaches to conservation and encourage rigorous evidence synthesis at the level of a specific threat, taxon, or conservation measure to guide decision-makers. Our goal here is to provide an overview of the ways in which threats potentially impact migratory wildlife to draw attention to the threats they face. To achieve our objective, we first consider the ways in which common anthropogenic threats alter (or have potential to alter) the fitness of migratory animals. We also discuss the evolving threat landscape and strategies for conserving and managing migratory animals in the Anthropocene. Our approach is inclusive, covering diverse taxa from various ecosystems, realms around the globe, and encompassing multiple threats. The authorship team includes experts working on a variety of taxa and problems in various regions and systems, using different methods.

II. IUCN THREAT TAXONOMY

Here we use the IUCN Threat Taxonomy (https://www.iucnredlist.org/resources/threat-classification-scheme) to frame our analysis (Fig. 1). The Taxonomy encompasses 12 threats that are directly linked to IUCN threat assessments: a globally accepted framework for considering the status of a population or species (Rodrigues *et al.*, 2006). We exclude the Threat Taxonomy category 'geological events' (e.g. earthquakes, volcanic eruptions) in that they are not caused by humans and likely are not more prevalent in the Anthropocene than in previous epochs. We also excluded the 'other' category given that the Taxonomy adequately covered relevant threats. For the category 'Climate change and severe weather' we focus on weather events that are mediated by humans as a result of climate change (e.g. storms increasing in frequency or intensity).

(1) Residential and commercial development

Anthropogenic activities including residential and commercial development have contributed to massive alterations in habitats across the globe through removal of natural habitats and creation of food subsidies (Oro *et al.*, 2013). Broadly, changes in habitat can be grouped into three categories: habitat loss, deterioration or improvement (i.e. quality; Sutherland, 1998), fragmentation (Liu, He & Wu, 2016), or creation of predictable and attractive food subsidies that may have unintended consequences

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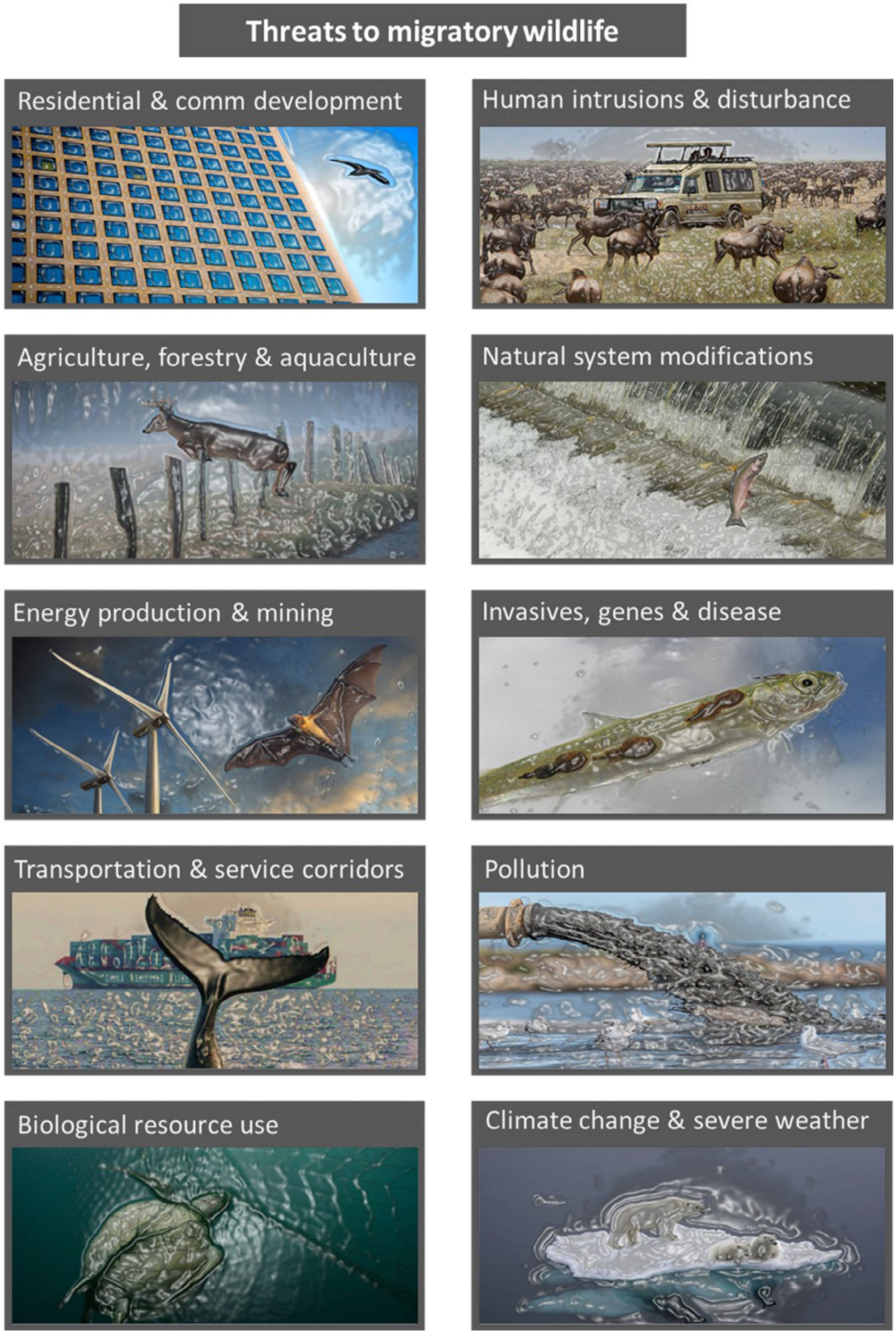

Fig. 1. Threats to migratory wildlife arising from various anthropogenic activities according to the IUCN Threat Taxonomy; Comm, commercial.

(Satterfied *et al.*, 2018). Taken together, alterations to habitat (e.g. through human development) remain the greatest threat to biodiversity (Brooks *et al.*, 2002) with one reason being that animal migration is impacted (Fahrig, 2007). Specifically, habitat loss at key locations (e.g. stopover sites for migratory birds) could contribute

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to decreased populations by limiting migration preparedness owing to limited food resources (Studds *et al.*, 2017). For example, habitat loss due to human settlement has contributed to the loss of migratory behaviour in two ungulate species, the Mongolian gazelle (*Procapra gutturosa*) (Lhagvasuren & Milner-Gulland, 1997) and mule deer (*Odocoileus hemionus*) (Bertram & Rempel, 1977). Habitat degradation occurs when the habitat still exists but its quality has decreased (thus impacting organismal health, condition, and fitness), which can occur due to urbanization (Sutherland, 1998). Similar to habitat loss, habitat degradation can have a negative impact on migrations (Chowdhury *et al.*, 2021). For example, neotropical migrant birds were more negatively impacted by decreases in habitat quality associated with urbanization relative to resident species (MacGregor-Fors, Moralez-Pérez & Schondube, 2010). Habitat fragmentation occurs when a large area of habitat is transformed into smaller patches consisting of less area (Wilcove, McClellan & Dobson, 1986). Habitat fragmentation can result in patches becoming more isolated and therefore harder to access for migrating animals, resulting in decreased immigration and emigration and hindering the maintenance of gene flow (Couvet, 2002). In Wyoming, USA, residential developments resulted in fragmentation by reducing the size of a pre-existing migration bottleneck for two species of migratory ungulates: mule deer and pronghorn (*Antilocapra americana*) (Sawyer, Lindzey & McWhirter, 2005). Despite the relative importance of migration habitat including biodiversity maintenance, population support, and connections across ecosystems, these habitats are often not conserved (Bolger *et al.*, 2008). That said, habitat alterations, such as urbanization, that introduce food subsidies could attract migratory animals, altering natural behaviour and nutritional physiology/energetics [e.g. sharks (Hammerschlag *et al.*, 2022*a*); birds (Oro *et al.*, 2013)].

(2) Agriculture, forestry and aquaculture

Agriculture, forestry and aquaculture are practices that modify or convert major land and sea areas. Agriculture not only demands area, but also local resources such as water for irrigation (Lemly, Kingsford & Thompson, 2000) that can contribute to droughts and affect the conditions encountered by migratory animals such as fish (Moyle, Hobbs & Durand, 2018). One of the major changes associated with agricultural land conversion and clearcutting in forestry is the establishment of supranormal densities of monoculture species, usually, timber, food crops or pastoral animals. Nutrient subsidies are provided to sustain high densities on the farms and monocultural forest stands (Jefferies, 2000; Fohringer *et al.*, 2021*b*). These nutrient subsidies may spill over to wild animals, altering the ecosystem, the habitat use of animals in several ways, and their population demography. First, farms can provide a resource subsidy that enhances the abundance and aggregation of migratory species; such is the case for species of geese and cranes that decimate fertilised croplands and whose populations increase due to these farmland subsidies (Jefferies, 2000; Nilsson *et al.*, 2016; Tombre *et al.*, 2022). These subsidies may alter the timing of migration or even allow migratory animals to persist without migrating by altering the costs and benefits of migration (Allen *et al.*, 2017). Alternatively, food waste from farms can be capitalised on by predators (Callier *et al.*, 2018); in Norway, open-net pen salmon farms aggregate Atlantic cod (*Gadus morhua*) and pollack (*Pollachius virens*) (Uglem *et al.*, 2014) that are predators of migrating wild Atlantic salmon (*Salmo salar*), sea/brown trout (*Salmo trutta*), and Arctic charr (*Salvelinus alpinus*). There are also indirect effects of farming (including from domestic livestock) on migratory species, such as disease risk, which is increasing in northern areas due to climate change (Khanyari *et al.*, 2021). For example, high densities of organisms in farms create ideal conditions for the reproduction of pathogenic bacteria, viruses, and protists, which can spill over from farms to wild populations (Krkošek *et al.*, 2011). Finally, farms create barriers or even traps for migrating species. Fences around farms can constrict the landscape, forcing migrations through narrow corridors or onto suboptimal habitat. In a particularly incredible example, Fjelldal *et al.* (2021) found wild Atlantic salmon and sea-run brown trout smolts had entered experimental fish farms during their seaward migration and become trapped, growing up in the farm until it was emptied. Similarly, Losey, Rayor & Carter (1999) showed that genetically modified maize plants expressing crystalloproteins from the soil bacterium *Bacillus thuringiensis* increased mortality of monarch butterfly larvae by 44%.

(3) Energy production and mining

Energy production and mining involve the physical alteration of landscapes (e.g. removal of materials, construction of infrastructure) and include elements of disturbance (e.g. noise, presence of humans and machinery) and pollution (e.g. leakages, emissions) that can individually or collectively impact the migration of diverse types of wildlife (Fohringer *et al.*, 2021*a*). For example, oil and gas drilling impacts have been studied for mule deer where tracking studies revealed that rates of travel and migration timing were affected by natural gas development, which could affect birthing rates and stress levels (Lendrum *et al.*, 2013). In oceans, seismic exploration surveys have been shown to alter the behaviour of migrating marine mammals (altered trajectories and speeds; Castellote *et al.*, 2009) and exclude them from key stopover (e.g. feeding) sites (e.g. Richardson, Miller & Greene, 1999). Mining comes in many forms. Terrestrial mining facilities have been shown to alter the migration of ungulates and the traditional livelihoods that depend upon them (e.g. Fohringer *et al.*, 2021*a*) whereas river sand mining has negative effects on migratory fish through silt plumes and changes in river processes (Koehnken *et al.*, 2020; Mingist & Gebremedhin, 2016; Mensah, 1997). Pollution from mining can lead to immediate mortality (e.g. cyanide from gold mines killing migratory birds; Henny, Hallock & Hill, 1994) or contribute to accumulation of

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contaminants (from active or decommissioned mines) with subsequent unknown impacts when animals reach breeding grounds (Durkalec *et al.*, 2022). Even 'greener' renewable energy development often involves use of wind or water to turn turbines which can yield mortality of migratory animals *via* turbine strikes (e.g. turbines have been major contributors to the mortality of migratory American eel (*Anguilla rostrata*) *en route* to oceanic spawning grounds; Pracheil *et al.*, 2016). However, sublethal impacts are also possible. For example, wind turbines have altered the behaviour of migratory mammals [bats (Horn, Arnett & Kunz, 2008); reindeer (*Rangifer tarandus tarandus*; Skarin *et al.*, 2015); pronghorn (Milligan *et al.*, 2023)] and birds (Plonczkier & Simms, 2012), while dams associated with hydropower development have impacted river connectivity and altered river flows and thermal conditions to the detriment of migratory wildlife (e.g. Anderson *et al.*, 2018*a*; Geist, 2021), including extirpation of fish populations in some instances (e.g. Zeug *et al.*, 2011). There are some inherent differences in wind energy *versus* hydropower in that wind infrastructure tends to be less of a physical barrier than a hydropower dam but there is increasing diversity of water-based electricity generation *via* tidal power, instream hydro-kinetic turbines, or run of the river systems that are more like wind turbines in that they do not fully block migrations.

(4) Transportation and service corridors

Transportation and service corridors are ubiquitous around the globe, enabling the movement of people and delivery of materials including goods, utilities, and services. Roads and railways have long been known as direct mortality vectors given collisions with migratory animals ranging from butterflies (Malcolm, 2018), to amphibians (Beebee, 2013), to herpetofauna (Piczak, Markle & Chow-Fraser, 2019) to large mammals (Kušta, Ježek & Keken, 2011). However, roads and railways also impact migratory animals by severing or impeding migration routes as do utility rights-of-way and corridors (Andrews, 1990). Dickie *et al.* (2023) showed that linear habitats in northern Canada affected predator encounters for migratory woodland caribou (*Rangifer tarandus caribou*), a consequence of installing roads and pipelines in the boreal forest. In some cases, it is not the fragmentation but rather the traffic noise that impacts wildlife, as has been documented for frogs engaged in breeding migrations (Tennessen, Parks & Langkilde, 2014). Although often thought of in terms of terrestrial impacts (e.g. Rytwinski & Fahrig, 2015), roads and railways also impact aquatic systems by blocking migration of aquatic animals at improperly designed or installed culverts (Januchowski-Hartley *et al.*, 2014). In aquatic systems, shipping lanes can impede migration of aquatic life through injury and mortality [e.g. vessel strikes of marine mammals (Schoeman, Patterson-Abrolat & Plön, 2020) and sharks (Womersley *et al.*, 2022)] and avoidance of ship noise (Erbe *et al.*, 2019). Shipping activity is increasing in the Arctic with vessel traffic in the same areas frequented by a variety of migratory marine mammal species (Hauser, Laidre & Stern, 2018). However, the impacts associated with shipping also extend to terrestrial mammals such as caribou that have been observed to delay migration due to sea-ice breaking activities conducted with ice-breaking vessels (Dumond, Sather & Harmer, 2013). Increasingly, roads and railway tracks serve as attractive resource habitats for migrating predators to look for scavenging opportunities from the traffic-killed wildlife, thereby functioning as potential ecological traps (Etienne, 2020). Air travel has also impacted migratory wildlife through bird collisions (Sodhi, 2002; Thorpe, 2016).

(5) Biological resource use

The most obvious and direct impact on migratory animals is harvest *via* fisheries (e.g. nets, hooks, traps), hunting (e.g. firearms, bow and arrow) or trapping (e.g. leg-hold traps). Such equipment is often deployed in areas that exploit knowledge of the cyclical (in time and space) and concentrated (i.e. spatial) nature of migrations. Examples range from salmon migrating upstream that have been captured at river constrictions for millennia for subsistence by Indigenous peoples (Johnsen, 2009), to illegal hunting focused on migratory wildebeest (*Connochaetes* spp.) in Africa as animals attempt to hydrate at watering holes (Foley & Foley, 2015), to historical whale exploitation along known transit routes (Weller *et al.*, 2002), to highly regulated hunts for migratory waterfowl that cross international boundaries at known times (Anderson *et al.*, 2018*b*). Taken together, humans have continuously shown themselves to be formidable predators of migratory species. Exploiting migratory species has both ecological and evolutionary consequences (Hard *et al.*, 2008). When predator–prey imbalances occur, there is potential for unanticipated effects: for example grizzly bear (*Ursus arctos horribilis*) and wolf (*Canis lupus*) extinction had negative consequences for neotropical migrant birds by enabling moose (*Alces alces*) populations to expand unchecked, with this altering ecosystem structure and feeding opportunities for birds (Berger *et al.*, 2001). Beyond the immediate impacts on abundance, exploitation of wild animals is typically selective (i.e. removing the largest or fastest growing individuals) such that there is potential for evolutionary impacts that can impact migration timing and contribute to mismatches in resource availability (e.g. Jørgensen *et al.*, 2008; Allendorf & Hard, 2009). Some impacts are more indirect where animals are perhaps not removed (e.g. catch-and-release fisheries; bycatch discards) and survive, yet their subsequent migratory behaviour is altered (Wilson *et al.*, 2014). In some instances, the biological resource use is focused on non-animal taxa such as plants, resulting in both direct and indirect effects on the fitness of migrants (see Section II.2). Forestry activities have long been known to impact migration of terrestrial mammals (Blagdon & Johnson, 2021) and birds (Buler & Moore, 2011). Complex interactions may also occur where exploitation (e.g. hunting)

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and forestry intersect to magnify impacts on migratory wildlife (Naranjo & Bodmer, 2007).

(6) Human intrusions and disturbance

The presence and activities of humans in ecosystems can result in a variety of disturbances that negatively impact migratory wildlife. Recreational activities involving powered machines have been demonstrated to alter migration paths. Studies of migratory waterfowl have revealed that power boating disturbed migration (Kahl, 1991) and that such disturbances impact the energy expenditure of some waterfowl species (Schummer & Eddleman, 2003). In winter conditions, Borkowski *et al.* (2006) determined that use of snowmobiles altered the behaviour of bison (*Bison bison*) and elk (*Cervus elaphus*) in Yellowstone Park although it was unclear if those impacts extended to migratory consequences. Large-scale events such as the Winter Olympics can result in significant high-intensity and localised disturbance that presumably impacts all wildlife, including migratory species (May, 1995). Even superficially benign individual activities such as hiking, mountain biking, camping, and bird-watching can negatively impact wildlife although much of this literature is not specific to migratory species (Monz *et al.*, 2021). However, a body of research on bird-watching ecotourism in coastal New Jersey revealed changes in the distribution of some migratory species and raised concerns about potential changes in energy intake that could impact subsequent migrations and breeding (Burger, Gochfeld & Niles, 1995). Disturbance from fireworks has been documented to increase the distance and height of flight for four species of migratory wild geese in Europe with compensation in subsequent days by less movement and more feeding activity demonstrating prolonged consequences (Kölzsch *et al.*, 2022). Noise pollution from coastal music festivals can alter the adjacent underwater soundscape and elevate stress hormones in fish (Cartolano *et al.*, 2020). Modern warfare (including training and routine patrols in non-conflict zones) has manifold effects on biodiversity (Lawrence *et al.*, 2015) although there are few studies specific to migratory animals. In one of the few examples, nocturnal migration of songbirds was altered in the presence of military-related noise disturbance (Larkin, 1978). Some species of migratory birds were extirpated from Midway Island, USA during World War 2 (Fisher & Baldwin, 1946), although it is difficult to decouple human disturbance from massive habitat alteration. Finally, use of drones for recreation or military purposes presumably could impact animal migration based on a growing number of studies that demonstrate behavioural and physiological responses (Mulero-Pázmány *et al.*, 2017), although we are unaware of any research specific to migration impacts.

(7) Natural system modifications

Natural system modifications include actions that degrade habitat for the benefit of humans in efforts to manage natural systems. These threats include modifications involving fire (e.g. increases in fires and/or fire suppression), hydrology (e.g. dams), and other ecosystem alterations (e.g. beach development). Wildfires and wildfire management/suppression can have wide-ranging impacts that are often compounded by the world's changing climate. Specifically, the frequency, size, and severity of wildfires have increased recently. Wildfires have been shown to displace migratory species such as mule deer (Brazeal, Sollmann & Sacks, 2021) and even bird species (tule geese, *Anser albifrons elgasi*), and can disrupt migratory behaviour, and increase both energetic demands and mortality risk (Overton *et al.*, 2022). On the other hand, fire suppression can result in changes to habitat structure such as increased density of tree stands and understory (Gilliam & Platt, 1999). These changes in habitat structure caused by fire suppression can also disrupt migrations. For example, gopher frogs (*Rana capito*) avoided areas that were fire suppressed and selected for fire-maintained habitats during emigration from ponds (Roznik & Johnson, 2009). Dams and water management have significant adverse impacts on migrating aquatic species (e.g. salmonids) by obstructing migrations and altering habitat from lentic to lotic (Liermann *et al.*, 2012). The habitat fragmentation caused by dams can decrease access to important habitats that support spawning, refuging and/or foraging opportunities for migratory species including diadromous (e.g. Atlantic salmon) and potamodromous fishes (e.g. piramutaba, *Brachyplatystoma vaillanti*), and crustaceans (e.g. long-faced shrimp, *Xiphocaris elongata*) as well as freshwater mussels (e.g. ebonyshell, *Fusconaia ebena*) that depend on migratory fish for dispersal of young. Other modifications to hydrology can include the abstraction of surface (e.g. for human consumption) and groundwaters (e.g. for crop production), which can decrease the available habitat, resulting in fragmentation such as reduced wetland habitat available for migratory birds (Benstead *et al.*, 1999). Other ecosystem modifications can include shoreline alteration (e.g. hardening), channelization, vegetation succession, erosion, sedimentation, beach development, removal of natural habitat structure (e.g. snags) or bottom trawling.

(8) Invasive and other problematic species, genes and diseases

Biological invasions are widely considered to be one of the most extreme threats to global biodiversity (Pyšek *et al.*, 2020). Invasions have largely been facilitated by the propensity for people to promote propagule pressure of alien species *via* economic introductions or inadvertent transportation of particles (e.g. in ballast water). Invasive plants often provide habitat for migratory species, especially birds that roost and forage in trees. Although invasive trees have been speculated to be of lower quality for migratory birds. Owen, Sogge & Kern (2005) found no evidence that willow flycatcher (*Empidonax trailliiextimus*) using invasive tree stands were in poorer condition than those in native habitat. However, Faldyn, Hunter & Elderb (2018) found an interaction between climate change and foraging on an invasive milkweed (*Asclepias curassavica*) by monarch butterflies, such that

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the invasive plant decreased survival and growth in future climatic scenarios, which are also projected to reduce migration performance. Invasive species can also create conditions that alter the nutrient balance in systems. For example, pink salmon (*Oncorhynchus gorbuscha*) that have been established in Russia and Norway from the Pacific have increased nutrient concentrations in oligotrophic northern rivers, thus fundamentally changing water quality (Dunlop *et al.*, 2021) and their massive biomass may impede the migration of endemic species such as Atlantic salmon (Lennox *et al.*, 2023). Invasive parasites (e.g. Sandodden *et al.*, 2018) and predators have a strong role in altering fitness of migrating animals, for example the introduction of Wels catfish (*Silurus glanis*) in France led to increased pre-spawn mortality of salmon trying to use a fish ladder to reach upstream spawning areas (Boulêtreau *et al.*, 2018). The spread of non-endemic diseases is also presenting an urgent threat to migratory species; chronic wasting disease, a transmissible prion disease in ungulates (Edmunds *et al.*, 2018), and avian influenza A ('bird flu'; Olsen *et al.*, 2006), are growing focal points of research on migratory animals that may threaten future viability of many species. In some cases, non-native genetic material is introduced (usually *via* stocking) in an effort to supplement natural populations. This can contribute to introgression and inbreeding depression such that migratory performance and success is impaired, as has been observed for native pink salmon populations in Alaska (Reisenbichler & Rubin, 1999). Little has been done to understand how parasites affect the partial migration of species either by disrupting their energetics or by altering their cognition to affect their movements.

(9) Contamination and pollution

Diverse forms of pollution occur in air, water, soil, and plants with many documented impacts on animals yet there is comparatively less known about these impacts on migratory species. Runoff from urban and agricultural areas, particularly during flood conditions, can suspend sediments, change water temperatures, and mobilise chemicals and nutrients that can collectively impact upriver migration of fish (e.g. McIntyre *et al.*, 2018). Even though effluents with high levels of nutrients can stimulate food growth and attract migratory birds, this also comes with the potential to accumulate chemicals (Alves, Sutherland & Gill, 2012). Pesticides have been implicated in impairments in migration and mortality of bats (Geluso, Altenbach & Wilson, 1976), while herbicide levels in migratory amphibians have been found to be coincident with application levels (Berger *et al.*, 2018). Oil spills directly impact the flight performance (Perez *et al.*, 2017) and migratory ability of oiled birds (including the possibility of immediate mortality; Piatt *et al.*, 1990), but latent effects on migrant species may be observed that cascade across ecosystem types (Henkel, Sigel & Taylor, 2012). Migratory marine mammals tend to avoid areas with oil on the surface (Kent, Leatherwood & Yohe, 1981), which itself can impede migration routes and alter timing (Helm *et al.*, 2014). Garbage dumps can serve as ecological traps for migratory vultures (Buechley *et al.*, 2018) and alter natural feeding regimes for a variety of birds (Tortosa, Caballero & Reyes-López, 2002). Plastic debris such as lost fishing gear has been observed to entangle migratory wildlife such as humpback whales (*Megaptera novaeangliae*; Gregory, 2009) and the Critically Endangered North Atlantic right whale (*Eubalaena glacialis*; Knowlton *et al.*, 2022), while plastics (micro and macro) may be ingested by a variety of taxa creating bezoars that impact nutrition and eventually can result in inability to migrate (or death; Lusher *et al.*, 2022). Compared to the obvious negative effects of macroplastics (de Stephanis *et al.*, 2013; Cartarud *et al.*, 2019), the consequences of microplastics on migratory birds are unclear despite evidence that they are common (Hoang & Mitten, 2022). Light pollution arising from urban centres is greatest in migratory passage areas for nocturnally migrating birds (Cabrera-Cruz, Smolinsky & Buler, 2018) and fish (Riley *et al.*, 2012), with alarming evidence of behavioural alterations across a range of bird species (La Sorte *et al.*, 2017). Noise pollution on land can alter migratory behaviour of frogs (Engbrecht *et al.*, 2015) whereas in marine systems, noise arising from various activities is particularly problematic for marine mammals (Erbe, Dunlop & Dolman, 2018). Finally, activities such as hunting using lead (Pb) ammunition generate toxic food subsidies in the form of lead-infested offal, and predators (e.g. golden eagles, *Aquila chrysaetos*) may learn to match their migration timings and aggregation to these subsidies with consequences for their fitness (Singh *et al.*, 2021).

(10) Climate change and severe weather

Climate change and severe weather (mediated by humans) impact migratory animals in diverse ways, with such impacts expected to become more frequent and intense reflecting International Panel on Climate Change projections in environmental chaos (Pörtner *et al.*, 2022). In a review of global warming impacts on migratory species, Robinson *et al.* (2009) mused about mistimed migrations, declines in animal condition (energy), and decoupling of animal–environment interactions as temperatures exceed thresholds. Today, those impacts are being observed, particularly in northern clines (Kubelka *et al.*, 2022). For example, narwhals (*Monodon monoceros*) in the Arctic are keeping pace with phenology changes through behavioural adjustments to migration timing but that is exposing them to other stressors during prolonged summer residency in shipping channels (Shuert *et al.*, 2022). Ocean warming has altered the distributional range and timing of tiger shark (*Galeocerdo cuvier*) migrations in the Western North Atlantic, which as a consequence has decreased their spatial protections from commercial fishing (Hammerschlag *et al.*, 2022*b*), The migratory saiga antelope (*Saiga tatarica*) in central Asia have undergone substantial range shifts and changes in abundance linked to climate change and severe weather events, along with human land use, over the last several decades (Kock *et al.*, 2018). Birds are exhibiting advances in spring migration (Bates *et al.*, 2022), but such patterns are more varied for the autumn migration with growing evidence of wind being more important than temperature (Haest *et al.*, 2019). Climate change is impacting food supplies and their availability for migratory birds, especially at Northern latitudes, and when a reproduction event is not synchronized well with the peak in food supply trophic/phenological mismatch can occur, resulting in malnutrition and reduced offspring survival (Gilg *et al.*, 2012; Kubelka *et al.*, 2022). Moreover, climate change can alter whole trophic food webs, disrupting predator–prey interactions and increasing predation pressure (e.g. on nests of migrating shorebirds with cascading negative effects throughout Arctic ecosystems) (Kubelka *et al.*, 2018).

Exposure of migrants to warm temperatures (especially for ectotherms) can accelerate energy use and disease development, and if temperatures exceed thresholds that lead to aerobic collapse, migration failure (i.e. mortality) is inevitable. This has been observed for Pacific salmon leading to major conservation concern for some populations (Cooke *et al.*, 2012). Human-mediated floods can lead to stranding of migratory fishes (Thomas *et al.*, 2013), while drought can impede migration of fish in rivers due to lack of water for swimming (Lennox *et al.*, 2019) and mammals in terrestrial landscapes *via* decreased availability of water and food (Donaldson *et al.*, 2020). Winter is also notably different (less severe) in some regions, leading to some instances of animals ceasing migration, with ecosystem-level impacts across broad geographic scales as has been observed in migratory mammals and birds (Ng *et al.*, 2022), and resulting in changes to thermoregulation patterns and movement behaviour. Catastrophic weather events such as hurricanes are increasing in frequency and intensity and have been observed to alter space use of some migratory sharks (Gutowsky *et al.*, 2021), while storm events (presumably the wind) have been responsible for high mortality of hoverflies (Fisler & Marcacci, 2022). Notably, climate change and severe weather will occur in combination with other stressors (outlined above) which has the potential to magnify impacts on migratory wildlife and generate more uncertainty and mass-mortality events (Robinson *et al.*, 2019; Wilkening *et al.*, 2022).

III. SYNTHESIS: THE EVOLVING THREAT LANDSCAPE FOR MIGRATORY ANIMALS

As evident from the diverse examples provided above, animal migration in the Anthropocene is certainly a phenomenon under threat that could lead to the extirpation or extinction of species and populations with wide-ranging consequences for general biodiversity. In that sense, we amplify the conclusions of Wilcove & Wikelski (2008), however, our assessment extends well beyond climate change (recognizing that climate change will disruptively amplify and extend the impacts of other threats). Some threats are well documented, with examples spanning multiple populations, taxa, and realms, while for others the evidence base is weak. Gaps in the evidence base do not mean that there is 'no impact', rather, those impacts have not been studied or are indirect and challenging to demonstrate with the available information about the species and its environment. Studying the biology of migratory animals is challenging under the best of circumstances (Bowlin *et al.*, 2010) and researchers investigating migration often end up studying single populations (Dingle & Drake, 2007; Nathan *et al.*, 2008). However, understanding if human activities or infrastructure impact migratory animals requires knowledge of the baseline conditions and demonstration of an active interaction with human-modified habitats. In some instances, we are too late to obtain baselines in that the world has already changed so much. Nonetheless, there is much room for experimental approaches with relevant comparators and replicates to understand the mechanistic basis for human impacts on migratory animals (Birnie-Gauvin *et al.*, 2020). Studying stressors or challenges that face wild animals is inherently difficult (albeit, new methods are improving our ability to do so), particularly when it is not possible to isolate the effects of different stressors.

In the real world, multiple stressors are the norm and animals have evolved physiological systems and behavioural responses to detect stressors and maintain homeostasis (Folt *et al.*, 1999; Boonstra, 2013). Despite using a well-established threat taxonomy that is used to categorise threats for the IUCN *Red List*, we still noted much overlap between categories and connections among threats. For example, military activities require development of infrastructure, use of various vehicles, vessels, aircraft, and munitions that make noise (e.g. explosions), create disturbance, and generate pollution (Lawrence *et al.*, 2015). This example is not intended to single out warfare, but rather to emphasise that threats are interconnected. A migratory bird or whale transiting a military training range may be exposed to legacy pollutants, noise disturbance, altered landscapes, and so on. Similar suites of multiple threats may be experienced as a result of energy development and tourism. In other words, a single human activity may yield many different challenges.

An individual animal (for our purposes consider a sockeye salmon; *Oncorhynchus nerka*) will undoubtedly interact with a variety of threats over its life, spanning life stages and geographic locations and ecosystems (Hinch *et al.*, 2005). As sockeye migrate from spawning grounds to rearing lakes to the high seas and then back to natal rivers they face a gauntlet of challenges as they grow from <1 g to several kilograms (Hinch *et al.*, 2005; Fig. 2). In addition, those challenges can interact in complex ways. For example, when sockeye begin their upriver migration there is a well-documented interaction where warm water temperatures related to climate change increase energy expenditure and accelerate the development of emerging pathogens and make it more difficult for salmon to contend with fisheries interactions (even when released) (Cooke *et al.*, 2012; Miller *et al.*, 2014). In other words, the stressors can compound and interact (e.g. synergistically) to make things even worse (Johnson

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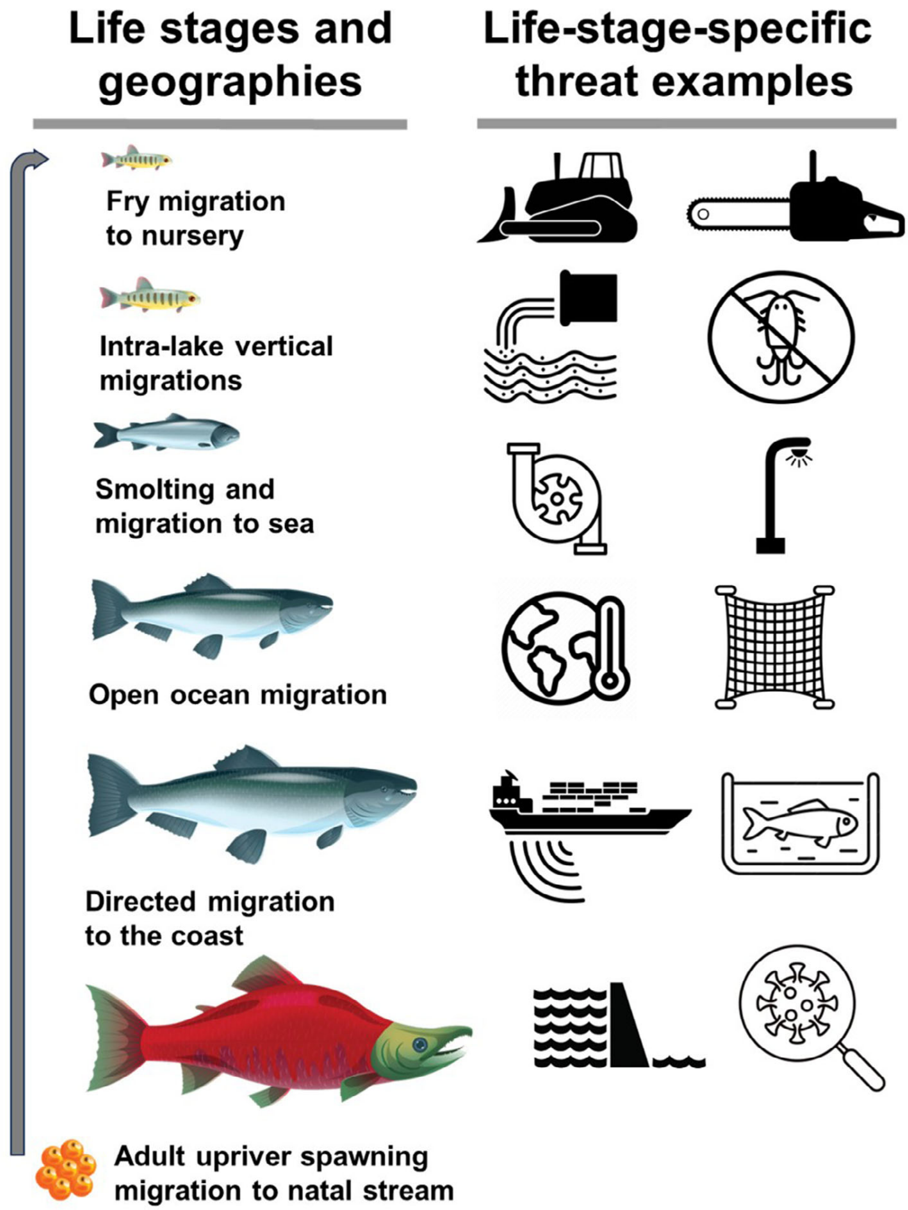

Fig. 2. Examples of threats faced by animals across life stages and geographies/ecosystems using sockeye salmon (*Oncorhynchus nerka*) as an example (two examples of threats are shown for each phase/stage). Sockeye salmon have complex life cycles that involve distinct migratory phases that take them from inland/upriver areas to the high seas and back (Hinch *et al.*, 2005). Here we visualize six key phases: (*i*) fry migration to nursery lake; (*ii*) intra-lake vertical migrations; (*iii*) smolting and migration to sea; (*iv*) open ocean migration; (*v*) directed migration to the coast; and (*vi*) adult upriver spawning migration to natal stream. Upon hatching, sockeye fry migrate from the spawning grounds to nursery lakes. During that period they have to contend with altered habitat from various types of development and resource extraction (e.g. forestry) and avoid invasive predators. Once in rearing lakes they need to undertake vertical migrations to feed, with altered water quality and ecosystem structure (from development) and the presence of invasive species influencing such migrations. When sockeye smolt and migrate to sea, they encounter hydropower infrastructure (e.g. turbines, bypass channels), invasive predatory fishes, degraded water quality (e.g. from agricultural runoff), parasites from fish farms, light pollution from urban areas, and a cocktail of contaminants. Once (if) they reach the high seas they must navigate in an uncertain space attempting to feed in a dynamic environment that is altered in yet unknown ways by climate change while avoiding fish capture gear (with potential for harvest or bycatch). When they migrate to the coast in preparation for spawning migration they may face fishing gears, boat transportation corridors, offshore wind installations, contaminants, noise and light pollution, aquaculture net pens, and disease/pathogens. Once they initiate upriver migration, other challenges present themselves including climate-change related warm waters, lower flows due to less snowpack (another climate change impact), emerging pathogens, confusing odour cues arising from hydropower diversion projects as dams obstruct migration pathways or alter water flows, and more. This incomplete summary is intended to emphasise the multiple IUCN Threat Categories and stressors that a single individual may face during its lifetime on top of the inherent ecological and environmental challenges that already exist for migratory animals.

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et al., 2012). Some stressors are virtually omnipresent such as climate change and pathogens (Altizer, Bartel & Han, 2011) with potential to impact migratory animals in all environments and migratory phases. Thus, migratory wildlife can face interacting and overlapping challenges that take very different forms and act on different parts of the biology of an animal. Given the incredible coupling of behaviour and physiology that defines migration (Jachowski & Singh, 2015; Birnie-Gauvin *et al.*, 2020), and the temporal constraints associated with transitioning between life-history stages (Wingfield, 2008), it is not surprising that migratory organisms are particularly susceptible to threats that disrupt various biological processes and systems.

To develop effective conservation actions, it is necessary to identify the mechanisms and levers that contribute to population declines (Allen & Singh, 2016; Cooke *et al.*, 2023). Such information enables practitioners to make good decisions about how to allocate limited resources and where to place conservation efforts. However, the fact that migratory animals face numerous overlapping and intersecting threats either simultaneously or in sequence (as they transition among locations and life phases; see sockeye example above and in Fig. 2), creates additional challenges (Shuter *et al.*, 2011). There may be instances where the stressor experienced by one threat is not manifested until months later, perhaps on a different continent. So-called 'carry-over effects' (Harrison *et al.*, 2011; O'Connor *et al.*, 2014) greatly complicate conservation (O'Connor & Cooke, 2015). This has been well documented for migratory birds (Norris & Taylor, 2006) and salmon (e.g. Ross *et al.*, 2013; Burnett *et al.*, 2014). However, threats facing migratory wildlife may have systems-level effects that extend well beyond a focal migratory animal; Allen & Singh (2016) presented a framework for developing this. For example, the Deepwater Horizon oil spill in the Gulf of Mexico impacted migratory shorebirds through local impacts on health and condition (Henkel *et al.*, 2012). The absence of shorebirds capable of migration or impaired upon arrival at stopover sites and at their Arctic breeding grounds could have ecosystem-level consequences. In that sense, migratory animals serve as systems-level integrators connecting individuals, populations, communities and ecosystems in space and time. Putting migratory animals in a proverbial 'black box' to study them will result in under-appreciation of the direct and indirect ways threats impact migratory wildlife and will ensure that management efforts fail. In such cases, it is often crucial to focus on threat management instead of focal species.

IV. THE CONSERVATION AND MANAGEMENT OF MIGRATORY ANIMALS IN THE ANTHROPOCENE

Despite the numerous and unique threats facing migratory animals (Shuter *et al.*, 2011; Horns & Şekercioğlu, 2018), there is evidence that with targeted and thoughtful management interventions, promise exists for migratory animals in the Anthropocene. For all biodiversity we are at a turning point where there is an urgent need to invest in management measures that work. We are learning more about the type of interventions that benefit migratory species/populations (Table 1). However, we also need to ensure that management efforts are fit for purpose and clearly defined. Management may also differ between resident and migratory species, populations or individuals. Notably, an understanding of how and why migratory animals of a given population or species are distributed in space and time and the threats driving their distribution in their seasonal ranges or life-cycle stages are prerequisites to being able to develop effective conservation or management strategies (Martin *et al.*, 2007; Allen & Singh, 2016).

For almost all of the examples provided in Table 1, there is a substantial body of research on a specific population or species, often tailored to a specific location, that has enabled the development and implementation of mitigation measures. Applying an effective management effort that does not consider the requirements of the organism or is provided in the wrong location may simply fail. For example, placement of wildlife underpasses for turtles should consider the specific requirements of those species and understand movement trajectories and habitat preferences to provide a suitable structure that they are able to use in a useful location where mitigation (e.g. passage or exclusion fencing) is needed (Markle *et al.*, 2017). Even management measures that on the surface appear to be suitable, may not be sufficient to protect migratory species. For example, consider a scenario where a population is protected across 99% of its range and during 99% of the year. If an animal is a facultative migrant and must travel between protected habitats along well-defined migration corridors to complete its life cycle, targeted exploitation or the imposition of a barrier or disturbance (e.g. a dam on a river) could nullify other protections. Thus, protections for migratory species and populations need to consider their entire life history (Allen & Singh, 2016; Schuster *et al.*, 2019; Kubelka *et al.*, 2022). Moreover, management actions need to consider that there is already evidence of distributional changes and phenology of migration – management is a moving target especially in the context of climate change (Singh & Milner-Guilland, 2011; Allen & Singh, 2016). Therefore, dynamic management strategies (e.g. dynamic protected areas that move with the animals and their life-cycle events; Maxwell *et al.*, 2015) may be necessary for migratory species (Reynolds *et al.*, 2017; Bull *et al.*, 2013). However, in some cases we are too late – migrations have been lost. Restoring migrations is an emerging area of research and practice that will unfortunately become increasingly necessary (Barker *et al.*, 2022). Ensuring connectivity for previously fragmented systems that impede migration (e.g. in rivers) is perhaps one of the most obvious examples where there has been success as a result of dam removal and construction of fish passage facilities (Thieme *et al.*, 2023).

Given that wildlife ignores geopolitical boundaries, efforts to mitigate threats means that different jurisdictions need to

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Table 1. Mitigation opportunities associated with various threats facing migratory wildlife that can be employed by conservation decision makers and other relevant stewards. For each threat we provide three diverse examples of potential mitigation opportunities that have been used to address the threats as summarized in the IUCN Threat Taxonomy.

IUCN Threat category	Mitigation opportunity examples
Residential and commercial development	– Delineation of wildlife corridors through and around urban areas (Ford *et al.*, 2020; Adams *et al.*, 2021) – Use of window treatments to reduce window collisions in birds (Riggs *et al.*, 2022) – Providing natural areas within urban centres that can serve as stopover habitat for birds (Homayoun & Blair, 2016)
Agriculture, forestry and aquaculture	– Create and manage wetlands in agricultural landscapes to provide habitat for migratory birds (Li *et al.*, 2013 Lehikoinen *et al.*, 2017) – Support farmers with efforts to increase plant diversity in an effort to enhance stopover habitat for migratory birds (Blount *et al.*, 2021) – Develop land-based recirculating aquaculture facilities that do not involve use of sea cages to separate cultured fish from wild conspecifics (Frazer, 2009) – Organic farming increases stopover habitat for migratory birds in homogenous landscapes (Dänhardt *et al.*, 2010)
Energy production and mining	– Develop and install 'fish-friendly' turbines that reduce mortality for out-migrating (i.e. downstream) fish (Watson *et al.*, 2022) – Alter wind turbine operational parameters (e.g. activity, lighting) and siting to reduce mortality for migratory bats and birds (Baerwald *et al.*, 2009; Marques *et al.*, 2014) – Increase gas flare boom height on oil and gas platforms in the sea above mean altitude of migrating birds to reduce chances of incineration (Day *et al.*, 2015)
Transportation and service corridors	– Engage in spatial planning to position shipping lanes and design vessel speed regulations that reduce vessel–whale interactions (Petruny *et al.*, 2014) – Install wildlife crossings on roads to enable safe passage of taxa such as mammals (Clevenger & Waltho, 2000) and herptiles (Woltz *et al.*, 2008) on key migratory corridors – Reduce vehicle speeds during migratory periods, manage roadside vegetation, or use deflection barriers to reduce collision risk along roads for migratory butterflies (Mora Alvarez *et al.*, 2019)
Biological resource use	– Apply knowledge of sea turtle migration routes to inform the deployment of fishing gear to reduce turtle bycatch (Fossette *et al.*, 2014) – Apply herd-based protection zones (i.e. mobile protected areas) for wide-ranging animals like barren ground caribou (Taillon *et al.*, 2012) – Enhance enforcement to reduce illegal capture and trade of migratory birds, offering legal protection *via* quotas or prohibition of capture (Nijman & Nekaris, 2017; Lees & Yuda, 2022)
Human intrusions and disturbance	– Install exclusion fencing and minimum offset of recreation trails to reduce disturbance and perceived habitat quality for migratory birds (Martín *et al.*, 2015) – Prohibit use of motorized recreation vehicles and/or limit speeds in key migratory corridors (Olson *et al.*, 2017) and along shorelines of waterbodies (Rodgers & Schwikert, 2002) – Limit military training activities (e.g. weapons ranges, fighter jet training) during sensitive migration periods for priority species (Eberly & Keating, 2006) – Dynamic conservation through allocation of protection efforts from rangers at calving aggregation areas (Bull *et al.*, 2013)
Natural system modifications	– Conduct restoration that provides access to essential habitats along migration corridors such as has been done for zebra in Botswana (Bartlam-Brooks *et al.*, 2011) – Remove dams that block migration routes for migratory animals that use riverine systems (Katopodis & Aadland, 2006) – Ensure adequate faunal refuges in fire-prone landscapes or when conducting prescribed burns (Robinson *et al.*, 2013)
Invasive and other problematic species, genes and diseases	– Limit release of captive-reared butterflies to maintain natural genetic variation in migratory population and limit pathogen spillover and/or rear under natural conditions to maintain migratory phenotype (Oberhauser, 2019; Tenger-Trolander *et al.*, 2019) – Ensure that captive-reared fish are not released into nature *via* escapes or stocking to maintain a healthy gene pool and fitness of wild migrants (O'Sullivan *et al.*, 2020) – Ensure judicious use of antibiotics to treat disease in wild migrants given potential for such animals to disperse antimicrobial-resistant microbial communities elsewhere (Arnold *et al.*, 2016)
Contamination and pollution	– Select light bulbs (wavelengths and intensities) optimized to reduce impacts of light pollution on migratory wildlife (Gaston *et al.*, 2012) – Develop and enforce regulatory restrictions and application guidelines for pesticides that are known to disrupt migration as has been observed for common toads in vineyards (Leeb *et al.*, 2020)

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Table 1. *(Cont.)*

IUCN Threat category	Mitigation opportunity examples
	– Growing Arctic settlements need proper waste disposal systems to avoid supplemental feeding of generalist predators which can impact the breeding productivity of migratory birds (Kubelka *et al.*, 2022)
Climate change and severe weather	– Forecast alterations in migration patterns and proactively adjust protected areas to match (Hazen *et al.*, 2018; Reisinger *et al.*, 2022)
	– Maintain and restore networks of habitat refugia where organisms can seek temporary refuge during migration (Stralberg *et al.*, 2020; Friggens & Finch, 2015)
	– Regulate water-taking efforts from lakes and rivers to ensure they do not exacerbate climate-induced drought conditions for freshwater fish (Crook *et al.*, 2010)

work together in a coordinated manner. There is a need for local actions in relevant locations that target specific threats but also more coordinated 'big picture' protections that involve multi-national collaborations [e.g. international bodies collaborating on the development of global policy instruments like the Convention on the Conservation of Migratory Species (De Klemm, 1989; Lyster, 1989) plus many others (see Shuter *et al.*, 2011)]. At the international level, trade agreements between countries can be used to establish environmental protections during the negotiation process and through side agreements. For example, the Commission for Environmental Cooperation (CEC) was formed under the North American Agreement for Environmental Cooperation (NAAEC) between Mexico, the USA, and Canada, which acts at a continental scale and was formed as a side agreement to the North American Free Trade Agreement signed in 1994 (http://www.cec.org/about/agreement-on-environmental-cooperation, accessed Feb 6 2023). The CEC continues to work to promote collaboration on environmental issues at a continental scale, including conservation challenges facing migratory animals, under the United States–Mexico–Canada Agreement. Details on other such side agreements that result from trade agreements are scarce, but we emphasise that they provide one more tool for conservation practitioners both to conserve and to raise awareness about the decline of migratory animals with decision makers at the national level.

An excellent example of how these international instruments and cooperation work in practice can be derived from monarch butterfly conservation efforts in North America. The eastern migratory monarch butterfly population has declined by ~80% since monitoring began in 1994–1995 (Fig. 3). The lowest population observed occurred in the winter of 2013–2014, representing a decline of 95% from the peak abundance observed in 1996–1997. In response, the governments of Canada, the USA, and Mexico agreed to an evidence-based shared tri-national recovery target and formed the Tri-national Monarch Conservation Science Partnership (TMCSP) to identify conservation priorities and knowledge gaps, share and disseminate new knowledge, and work collaboratively towards recovery (Diffendorfer *et al.*, 2023). The TMCSP is comprised of scientists from government, academia, and environmental non-government

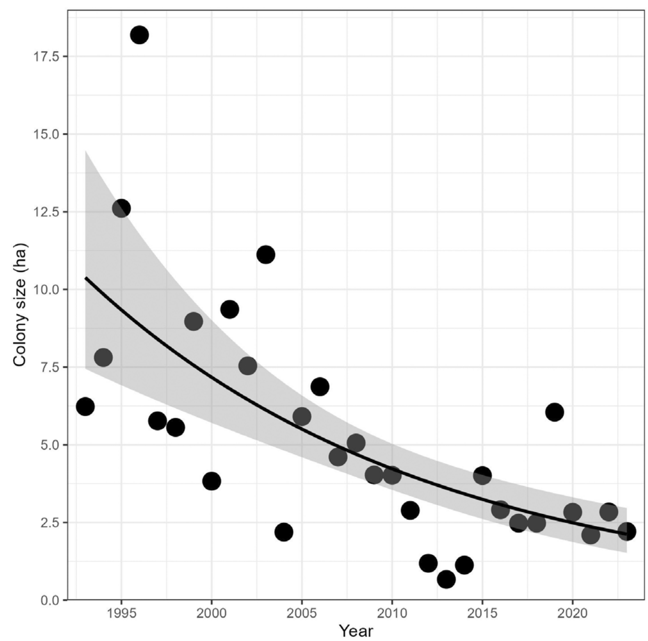

Fig. 3. Population trend of monarch butterflies (*Danaus plexippus*) from their wintering grounds in Central Mexico. Population size is measured as the area occupied by the butterflies over the same period of time each year (CEC, 2017); area is measured as opposed to counting individuals (which can number in the millions). Dots represent the annual measurements obtained from Monarch Watch 2022 and the trend line was fitted with generalised linear model with a gamma family and log link function. The shaded area represents the standard error of the fitted line.

organizations and received funding and logistical support both federally and through the Commission for Environmental Cooperation. Together, scientists from the TMCSP worked to establish a new monitoring program for the breeding grounds, set habitat restoration targets, identify threats, and gain a better understanding of migration through Northern Mexico (e.g. Semmens *et al.*, 2016: Thogmartin *et al.*, 2017*a*,*b*; Castañeda *et al.*, 2019; Cariveau *et al.*, 2019). Importantly, citizen/community and professional scientists and policy makers continue to rally around the monarch butterfly through habitat restoration and re-evaluation of

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population trends and threats *via* monitoring and data analysis. Frequent communication and cooperation with scientists and policy makers across international and domestic borders continues to be invaluable and allows for adaptive management at a scale that encompasses the entire annual cycle.

We also emphasise the need to consider diverse knowledge systems including Indigenous science. There are several good examples of Indigenous knowledge holders informing the design of shipping activity in the Arctic to benefit wildlife (including many migratory species; Dawson *et al.*, 2020). Unfortunately, there are relatively few other examples where Indigenous science or ways of knowing has been used to inform contemporary management or threat abatement of migratory species. Clearly Indigenous knowledge systems have much to offer, including baseline information and observations on impacts of threats to migratory animals (and the consequences of those changes on their peoples). For example, Reid *et al.* (2022) collated Indigenous elder knowledge on the state of Pacific salmon migrations, creating a baseline and revealing changes over the last half century. However, if such knowledge is shared by rights holders it will need to be done in a way that respects data sovereignty and privacy [e.g. following the OCAP principles (Mecredy, Sutherland & Jones, 2018) – as was done in Reid *et al.* (2022)].

V. CONCLUSIONS

(1) Animal migration is a remarkable phenomenon that has captured the imagination of scientists and the public alike. Yet, the complexity of migration as a behaviour with associated fitness benefits from a mosaic of dynamic environments, is contributing to the demise of migratory wildlife as a result of rapid human environmental change and exploitation (Shaw, 2016). Declines in migratory wildlife have been observed in a wide range of animal taxa. Life for migratory wildlife in the Anthropocene is getting harder (Hardesty-Moore *et al.*, 2018).

(2) Here we used the IUCN Threat Taxonomy to consider both the diverse ways in which various threats impact migratory wildlife and the ways in which those threats can be mitigated. Understanding how threats, singularly and in combination, impact migratory wildlife and the ecosystems that they transit will help to reduce uncertainty for decision-makers (Wilkening *et al.*, 2022).

(3) At present, most mitigation measures that have been applied have been implemented in a tactical and localised manner, so it remains unclear if they will be transferable. The examples we have highlighted serve as useful cases where successes have been achieved and as the evidence base grows it is our hope that we will be able to identify more generalizable and broadly applicable measures that can be implemented to benefit migratory wildlife, ecosystems, and humans that depend on them. The strategies for managing migratory wildlife identified here require careful evaluation to enable an evidence-based approach to the conservation of migratory animals.

(4) Shuter *et al.* (2011) eloquently note that the challenges underpinning the sustainable management and conservation of migratory wildlife are substantial yet the benefits of doing so are immeasurable. We concur and submit that if the strategies for mitigating threats and managing migratory wildlife identified herein are embraced, we have the potential to ensure that migratory animals and the important ecological functions sustained by migration persist in the Anthropocene and beyond.

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VII. AUTHOR CONTRIBUTIONS

S.J.C. and R.J.L. conceived the idea. All coauthors contributed to writing and editing.

VIII. REFERENCES

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