Seasonal Animal Migrations and the Arctic: Ecology, Diversity, and Spread of Infectious Agents

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1 Introduction

Long before humans started travelling long distances, many animals have been on the move. Through long-distance migrations, animals move year after year and in relatively predictable manners, between regions, continents, and hemispheres. Migrations come in many forms and fascinate people far beyond the biologists that study them. Many migrants and migrations are iconic, such as the European eels (*Anguilla anguilla*) that after born in the Sargasso Sea find their way to lakes and waterways in Europe, grow up there, and return as adults, for the eels a once in a lifetime trip (Righton et al. 2016). Another example is the common cuckoo (*Cuculus canorus*), which spends the non-breeding season south of Sahara and whose return to Europe is one of the distinguished signatures of spring at northern latitudes (Willemoes et al. 2014). Prominent examples also include migrations to Arctic regions, such as the Arctic tern's (*Sterna paradisaea*) annual move between the Arctic and the Southern Ocean (Hromádková et al. 2020). Well-known are also the abundant and highly visible goose migrations, from temperate wintering grounds to Arctic breeding grounds—a phenomenon seen around the entire northern hemisphere (CAFF 2018). Clearly, migrants are actors in multiple ecosystems through the year and through their life, and they connect very different parts of the planet (Bauer and Hoye 2014).

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Why have seasonal migrations evolved? Migrants exploit spatially and temporally varying resources by inhabiting multiple habitats, often far apart, at different times of the year, and movements between them have in many cases clearly been favoured over stationary (or resident) strategies. That is, migrations have allowed growth, survival, and reproduction to be combined in ways that lead to higher fitness than for the resident alternative (Fokkema et al. 2020). Seasonal food availability is a major selection pressure favouring seasonal migrations (Alerstam et al. 2003; Varpe 2017), but similar variations in predation risk, infection risks, or abiotic environmental conditions can be underlying drivers too. The main costs of migrations are high energy requirements of movement and the need to undergo physiological or morphological changes of operating in different environments (e.g. anadromous fish inhabiting fresh and salt water). Costs also include the need for sophisticated navigation and orientation capacities as well as mortality risk from encountering predators along the migration routes. For broader and more complete coverage of migrations and their evolutionary ecology, see (Alerstam et al. 2003; Dingle 2014; Hansson and Åkesson 2014; Milner-Gulland et al. 2011).

Migrations come in many forms (Chapman et al. 2014) and have been categorized, e.g. according to the distances, timescales or habitats covered, the proportion of a population migrating, or the existence and use of intermediate feeding locations. In this chapter, we focus on *seasonal migrations*, where individuals move between areas on an annual basis, with the movement part usually happening during well-defined and relatively brief time windows and hence with distinct phenology. For species that are long lived and reproduce multiple times through life (iteroparity), an individual performs such seasonal migrations repeatedly. Some migrations take place over particularly long distances, either in the absolute sense or relative to the body size of the migrant, and can be termed *long-distance migrations* (Alerstam et al. 2003), in contrast to *short-distance migrations*. Many migrations cross continents, and in the case of birds, major corridors and routes have emerged that are referred to as flyways (e.g. Wauchope et al. 2017). Clearly, there are also shorter migrations, where some individuals just move a little, typically to lower latitudes. It is a gradient, from the longest migrations to permanent residency. The variety of environments visited during migration is of particular relevance in relation to infections with parasites and pathogens. Some migrations take place as one long move (*non-stop migrations*) with limited interactions with the interjacent environments, whereas most migrants stop over to rest and refuel (*stop-over migrations*) (Alerstam and Bäckman 2018; Hedenström 2010). Finally, there may be variation in the proportion of a population that migrates, i.e. some individuals may be year round residents, whereas others migrate (*partial migration*) (Chapman et al. 2011).

Migrations have many ecological consequences and influence ecosystem functions and the structures of ecological communities. Importantly, migrants are living links, or vectors, between ecosystems (Bauer and Hoye 2014); hence, a meta-ecosystem perspective is required (Loreau et al. 2003; Varpe et al. 2005). Migrants transport energy and nutrients, primarily through defecation, offspring (such as eggs), and the death of individuals. The offspring produced by migrants may be placed in a different system than where the resources for their production were obtained, such as fish feeding in the open ocean and spawning in coastal ecosystems (Varpe et al. 2005; Willson and Womble 2006). Some migrants such as several salmon species have a strategy where death follows reproduction (semelparity), and individuals hence become a resource for scavengers and decomposers (Finney et al. 2000; Naiman et al. 2002). Part of the matter transported can be pollutants that have accumulated in the organism, particularly so for lipid rich migrants high in the food chain (Krümmel et al. 2003). An individual is also a whole ecosystem with many other smaller species inhabiting its interior as well as its exterior. Some of these are, for instance, symbionts in the gut, but many are also parasites and infectious agents that travel with the migrants and may jump on or off along the route (Viana et al. 2016). Consequently, parasites and infectious agents are dispersed between systems through migrants, a central element of this chapter and the whole book. When migrations change, these changes will have ramifications for the spread of infectious agents.

This chapter focuses on seasonal migrations to and from, or within, the Arctic and sub-Arctic regions, to form an ecological and evolutionary basis about migrations that a One Health perspective on Arctic ecosystems can build on. We cover the particular aspects of migrations to these northernmost areas of the planet, such as the pronounced seasonality of the environment, the oftentimes highly synchronized migrations, and the large aggregations of a diverse range of animals in the Arctic summer, arriving there from many different parts of the world. This melting pot effect seems particularly interesting from the perspective of infectious agents and the diseases they may cause. We give ecological background on the linkages between migrants and disease, both more generally, and with respect to the particular migrations we see in the Arctic. Overall, we advocate a meta-ecosystem perspective where places and environments are connected through organisms whose migrations and other behaviours may change, sometimes rapidly through phenotypic plasticity and other times more slowly through evolution. As a consequence, a dynamic perspective is needed when interpreting ecological consequences of migrations and the interplay between infectious agents, migratory hosts, and changing environments.

2 Arctic Migrations

2.1 A Seasonal Environment

The fundamental cause of seasonality is the tilted axis of the earth and the resulting seasonal pattern of irradiance experienced at all places on the planet. This seasonality, however, increases with latitude and is therefore particularly pronounced in high-latitude Arctic and sub-Arctic regions (and similarly so at equivalent southern hemisphere latitudes). The seasonal light and heat fluxes affect a range of derived physical variables, such as air and water temperatures, snow cover, sea ice cover, freshwater availability and run-off from land to sea, and so forth. These direct and derived abiotic variables have many consequences for biological processes and, in particular, for primary producers dependent on light for photosynthesis. The primary production in the Arctic is highly seasonal, both on land (Zeng et al. 2011) and in water (Ji et al. 2013), and basically divides a year into a productive and an unproductive period. A range of adaptations to this seasonality follows among grazers and for consumers higher up in the food chain (Varpe 2017). One such adaptation is the capacity to move to the Artic when the productivity is high and leave when it is low, through seasonal long-distance migrations (Alerstam et al. 2003).

Importantly, food availability is about more than the seasonal timing of photosynthesis. For plant material fed on by herbivores, some of the resources produced during one productive window remain in the environment, such as in roots or seeds, and can be fed on through the winter as well as next spring. Arctic year-round residents such as reindeer (*Rangifer tarandus*) and the rock ptarmigan (*Lagopus muta*) would do so. Physical conditions may also constrain access to food. For instance, anadromous arctic char cannot leave the lake for the ocean before the connecting river or creek is open and with water flowing (Gulseth and Nilssen 2000). Similarly, migrating birds arriving early to a snow covered and frozen Arctic have little or no food (Ebbinge and Spaans 1995; Grabowski et al. 2013; Prop and de Vries 1993), and the feeding season in the Arctic can be short, impacting breeding, moulting, and migration schedules (Holmes 1972). In the marine environment, many species cannot access their feeding environment if it is covered by sea ice, such as in seabirds where the extent of sea ice near the breeding colony may impact breeding phenology and success (Chaulk and Mahoney 2012; Gaston et al. 2005). Also, because of sea ice, most estuaries are only accessible to shorebirds well into the summer and during the autumn (Churchwell et al. 2016; Taylor et al. 2010). Furthermore, marine mammals need to surface for air and cannot swim far into ice covered areas (Brierley et al. 2002) unless there are open leads. As sea ice also blocks most of the surface light from entering the water column, it makes it harder for visually searching predators, such as fish and birds, to detect prey (Langbehn and Varpe 2017). Little light during the winter will also make visual search difficult on land. Finally, food availability is further impacted by seasonal trophic interactions, such as competition (DuBowy 1988) and kleptoparasitism (Varpe 2010).

Seasonality also impacts food independent processes such as environmental temperature and access to breeding habitat. The ground must typically be snow-free and relatively dry before birds establish their nest and lay eggs (Hendricks 2003; Holmes 1966; Prop and de Vries 1993). For instance, many species in Greenland recently experienced reproductive failures due to unusually much snow during winter and a subsequently delayed melt during the summer (Schmidt et al. 2019). Furthermore, low temperatures may prevent egg laying and lead to a skipped breeding season, as suggested for Brant geese (*Branta bernicla*) in the Canadian Arctic (O'Briain et al. 1998), or add costs that may have most severe consequences in species where only one of the parents is incubating, such as in some sandpipers (Meyer et al. 2021).

2.2 Why Migrate to the Arctic?

The cost-benefit analyses for Arctic migrations typically involve the same variables as for other regions, but their seasonality aspect is more distinct. Historically, high food availability and long days (24 h daylight for long parts of the summer) have been argued to be the main benefit of migrating to the Arctic to breed. This is a key selection pressure in many taxa (Alerstam et al. 2003; Corkeron and Connor 1999; Schekkerman et al. 2003), but additional benefits have also been highlighted. Notably, an experiment with artificial eggs across a latitudinal gradient documented lower predation risk for ground nesting birds the higher north (McKinnon et al. 2010), suggesting that predator avoidance could also be key to why breeding in the Arctic is beneficial. Similarly, the Arctic tundra ecosystem may be regarded parasite-poor, which would make low parasite pressure a potential benefit to spending parts of the year in the region (Piersma 1997).

From a cost perspective, arriving too early, or not being ready to leave in time in the autumn, may lead to costs and mortality. There is a rapid transition both from winter to spring and from autumn to more winter-like conditions. Low temperatures, frozen ground and seas, and little food are all among the challenges involved if arriving too early or staying too long. Similarly, arriving too late may have costs such as too little time to successfully raise young or failure to compete for and occupy the best breeding sites. Consequently, selection pressures on the timing of migrations and subsequent breeding seem particularly strong for breeding migrations to the Arctic (Burr et al. 2016; Holmes 1966; Love et al. 2010; van Gils et al. 2016).

2.3 Diversity of Arctic Migrations

Long-distance seasonal migrations to breed in the Arctic are particularly common in birds, both in seabirds and terrestrial birds. Some of these species are also extremely abundant and therefore constitute considerable biomasses (Fox et al. 2019; Gonzalez-Bergonzoni et al. 2017). The migration routes and modes of bird migrations to the Arctic are also very diverse (Fig. 1, Table 1). Some cover long non-stop flights and cross large oceans, whereas others stop frequently and have complex routes with intermittent resting and refueling. Furthermore, other organisms such as some fish and marine mammals primarily migrate to the Arctic to feed while they reproduce further south. These marine migrants often combine seasonal migrations with energy storage which in turn allow for reproduction at times of the year and at places where food availability is not necessarily high, but where it is beneficial to spawn or give birth (Fokkema et al. 2020; Varpe 2017). Breeding based on such reserves is referred to as capital breeding (Jönsson 1997; Stephens et al. 2009; Varpe et al. 2009).

Below, we provide four exemplary cases to illustrate the diverse migration patterns and selection pressures. Our cases are chosen to include some of the particularly abundant groups of migrants that breed on the arctic tundra, notably

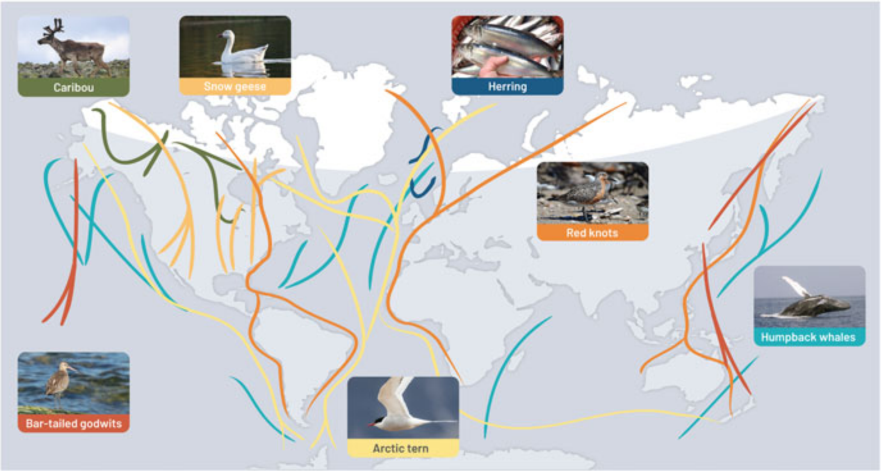

Fig. 1 Long-distance migrations and the Arctic, schematically illustrated through examples covered in the chapter. Migrants connect the Arctic to the rest of the world and make it a seasonal melting pot during the productive summer, when large numbers of organism move in from all over the world, some to breed, others to just feed. For photo credit, see the Acknowledgment

shorebirds and geese. These two groups also differ in a range of attributes related to their biology and migration strategies and thus serve as interesting contrasts. We have also included a case for within-Arctic migrations of the dominant terrestrial ungulate of the Arctic, the reindeer or caribou (*Rangifer tarandus*). Their notable interaction with humans through reindeer hunting and herding, is covered briefly. Finally, we discuss migrations in marine species. We focus these cases on the migrations and interactions with food, predators, and the physical environment. Interactions with infectious agents are covered in Sect. 3.

2.3.1 Shorebirds: Global Distributions and Major Flyways

Shorebirds are small to medium-sized birds that are commonly found along shorelines and mudflats, where they forage on invertebrates in the mud or sand. Of the >200 species worldwide, many shorebird species feature high among the most impressive migrants on earth—the distances they cover annually are simply astounding. For instance, bar-tailed godwits (*Limosa lapponica baueri*) migrate from non-breeding sites in New Zealand and Australia to breeding grounds in Alaska (Battley et al. 2012; Gill et al. 2009), red knots (*Calidris canutus*) migrate from South Africa or Mauretania to the Russian Arctic (van Gils et al. 2016), and Western sandpipers (*Calidris mauri*) migrate from the Pacific coast in North and South America to Alaska or Eastern Siberia (Lank et al. 2003) (Fig. 1, Table 1). However, some shorebird species breeding in the Arctic travel moderate distances, e.g. purple sandpipers (*Calidris maritima*) that winter in temperate areas and migrate to the coasts around the North Sea during their non-breeding season (Summers et al. 2001).

Table 1 Examples of migrations to and from or within the Arctic. Species are selected to illustrate a diversity of migration routes and types

Arctic migrants	Migration route characteristics	Time in the Arctic	Literature
Birds Dominant group of seasonal migrants to the Arctic. Geese, shorebirds, gulls, and auks are particularly numerous			
Arctic tern	Migrate between the Southern and Northern Atlantic ocean. Use prevailing winds and the route is therefore meandering. One-way distance >18,000 km	May–July	Egevang et al. (2010), Hromádková et al. (2020)
Brent goose	Migrate to the Arctic from non-breeding areas in temperate regions of Western Europe via several intermittent stops for resting and refueling to breeding areas in the Arctic	May/June–September	Clausen et al. (2003), Green et al. (2002)
Long-tailed skua	Migrate between the Arctic and the South Atlantic and Indian Ocean. The Grand Banks of Newfoundland appears to be important marine staging areas. Individuals estimated to travel more than 40,000 km over 1 year	June–August	Gilg et al. (2013)
Bar-tailed godwits	Migrate from non-breeding areas in New Zealand and Australia to breeding areas in Alaska and Russian Arctic. Extraordinary long non-stop flights, up to ~11,000 km. Migration routes differ between the way north and south	June–September	Battley et al. (2012), Gill et al. (2009)
Terrestrial mammals One dominant migrant, the ungulate *Rangifer tarandus*. It is an abundant herbivore with circumpolar distribution			
Reindeer or caribou	Migrate within the Arctic. Some herds have among the longest migrations of any terrestrial mammal (annual distance >5000 km for some herds), whereas other herds (for instance, inhabiting islands) are mostly stationary. Distinct calving areas often form key parts of the migration structure	Year round	Fancy et al. (1989), Gunn et al. (2011), Gurarie et al. (2019)

(continued)

Table 1 (continued)

Arctic migrants	Migration route characteristics	Time in the Arctic	Literature
Marine mammals Several species have summer feeding migrations to the Arctic and breed in low-latitude waters, often oligotrophic waters with low food availability			
Grey whale	Feed on Arctic benthos in Bering, Chukchi, and Beaufort Seas. Migrating along the coasts of western North America. Calving areas near Mexico. Migrations segregated with sex, age, and reproductive-stage differences in migration timing	~ half a year during the productive summer season	Guazzo et al. (2019), Rice and Wolman (1971), Swartz et al. (2006)
Humpback whale	High-latitude (e.g. sub-Arctic) feeding grounds and low-latitude (often tropical) breeding and calving grounds. Capital breeding combined with seasonal migrations	~ half a year during the productive summer season	Calambokidis et al. (2001), Clapham and Mead (1999)
Beluga whale	Migrate within the Arctic. As shown for the Pacific Arctic beluga, the timing and spatial extent of the migrations are linked to seasonality in sea ice. Offspring migrate together with their mother, and the migrations are matrilineally maintained	Year round	Colbeck et al. (2013), Hauser et al. (2017)
Fish Several species have seasonal feeding migrations to Arctic and sub-Arctic seas while spawning grounds are located further south. Others have a life and annual cycle that combines life in lakes with feeding migration into the ocean during the productive summer			
Northeast Arctic cod	Feed in the Barents Sea as young. Migrates south to spawn, with areas near Lofoten in Northern Norway being a key spawning area, but a wide latitudinal range of spawning grounds exist, particularly historically. Mature fish live long and will migrate many times between feeding and spawning grounds. Larvae drift northwards from spawning grounds to the nursery area	May–December (for the migratory adult part of the population)	Jørgensen et al. (2008), Ottersen et al. (2014)
Atlantic herring (Norwegian	Planktivorous fish with oceanic feeding migrations that reach sub-Arctic seas	August–October (for the migratory	Claireaux et al. (2020), Dragesund

(continued)

Table 1 (continued)

Arctic migrants	Migration route characteristics	Time in the Arctic	Literature
spring-spawning)	during the later parts of the seasonal feeding migration. Spawning along the coast of Norway and responsible for huge fluxes of biomass from ocean to coast as eggs are placed in distinct areas and at the seabed. Wintering areas have been highly variable. Larvae drift northwards from spawning grounds to the nursery area in the Barents Sea	adult part of the population)	et al. (1997), Varpe et al. (2005)
Arctic char	Anadromous fish with seasonal feeding migrations from lake ecosystems into the ocean and back. Time at sea relatively brief, from weeks to a few months. For some populations, some individuals migrate, while others are stationary and spend the whole year in the lake. The lakes are sometimes very close to the seashore, and the actual migration distance between the systems can be short	Year round	Gulseth and Nilssen (2000), Klemetsen et al. (2003)

With return journeys exceeding tens of thousands of kilometres, shorebirds are truly connecting continents and even hemispheres. As many species rely on specific coastal habitats, e.g. tidal mudflats, for fueling up before and during migration, the availability of these habitats determines overall migration routes and culminates in major flyways (Mathot et al. 2018). Along these flyways, some stopover sites are of particular importance as they are hotspots of productivity (Butler et al. 2001). There, shorebirds find their preferred food in excess, such as bivalves, snails, crustaceans, and polychaete worms, and consequently achieve unprecedented fueling rates (Kvist and Lindström 2003).

Shorebirds species differ in how they move along these flyways depending on how frequently they stop and how much fuel they accumulate: "*hop*" migrants cover short distances between successive sites and accumulate only little extra fuel stores, "*skip*" migrants are intermediate, and "*jump*" migrants accumulate large fuel stores and make long non-stop migrations (Piersma 1987). Although this distinction may seem marginal, how many and which sites migrants use determines migratory connectivity, which has far-reaching implications for individual fitness and population dynamics, gene flow and genetic mixing, the transmission of parasites and other infectious agents, and, ultimately, the conservation of migrants (Taylor et al. 2016; Webster et al. 2002).

Shorebird populations have severely declined over the past decades, such as the species breeding in the North-American Arctic (Smith et al. 2020). In the East-Asian Australasian flyway, even more species are threatened (Clemens et al. 2016; Piersma et al. 2016). Although we still need to fully understand which threats and disturbances impact shorebirds, the rapidly changing climate in the Arctic (see below), human impacts on coastal systems, and hunting and agricultural shifts are among the prime culprits (Colwell 2010; Mu and Wilcove 2020).

One major human-made threat to shorebirds is habitat destruction and alteration. Especially along the East-Asian Australasian flyway, coastal developments over the past decades have resulted in a >50% loss of the coastal wetlands (MacKinnon et al. 2012), notably in the Yellow Sea where 28% of the tidal flats existing in the 1980s have disappeared (Murray et al. 2014). This trend will continue through future reclamation projects such as landfills in estuaries and result in further declines of shorebirds (Studds et al. 2017). Similarly, in North American Delaware Bay, shorebirds feast on energy-rich eggs of horseshoe crabs (*Limulus polyphemus*), but overharvesting of crabs has deprived the shorebirds of much-needed fuel and resulted in strong population declines (Baker et al. 2004).

Also on the list of threats to shorebirds are recent and rapid increases in many goose populations (see below). For instance, snow geese have degraded wetlands along the coast of Hudson bay, a key refueling area (Jefferies et al. 2006), ‘mowed’ down the grass in shorebird breeding habitats, and thus exposed eggs to predators and attracted predators such as Arctic foxes into breeding areas (Flemming et al. 2019; Lamarre et al. 2017).

2.3.2 Arctic Geese: Large Birds and Populations, with Major Ecosystem Signatures

Migratory geese are long-distance migrants that typically spend the non-breeding season in temperate regions. On the way to their Arctic breeding grounds, they use intermittent stopover sites for resting and refueling. Although migration routes are diverse, broad patterns exist with European geese migrating to the Russian Arctic, e.g. Taymyr peninsula, or to Svalbard and Greenland, North-American geese migrating to Canadian Arctic and Alaska, and Asian geese migrating to Siberia or Alaska (CAFF 2018).

Prior to migration and between migratory bouts, geese accumulate body reserves. As body reserves are mainly stored as body fat deposits, they can be relatively easily scored using abdominal profiles (Madsen and Klaassen 2006). Consequently, changes in abdominal profiles over repeated sightings of individually marked (neck- or leg-banded) birds can indicate fundamental energetics, e.g. fueling rates or energy required for a migratory flight bout (Chudzinska et al. 2016). The timing of migration of geese is determined by a combination of cues—with a general cue such as photoperiod indicating time of the year and a more specific cue such as vegetation development for fine-tuning migratory progression to local phenology (Bauer et al. 2008a, 2011). Also, depending on the spatial scales involved, the conditions at one stopover site may be correlated with conditions at the next and hence indicate the conditions the geese will meet on next location (Bauer et al. 2020; Kölzsch et al. 2015; Tombre et al. 2008).

In contrast to most other migratory species, the populations of many migratory goose species have increased tremendously over the past decades: in the Western Palaearctic alone, there are 4.7 million geese from nine species (Fox et al. 2019; Madsen et al. 1999). This upsurge can probably be attributed to two major factors: agricultural change and policy and legislation. In the regions where migratory geese typically spend the non-breeding season, agricultural practices have undergone a major transformation, and many former natural habitats have been converted to farmland. Consequently, food during winter has become a superabundant high-quality resource, sustaining larger populations than ever before (Fox et al. 2005). Increasing goose populations are also a result of effective legislation: International treaties such as the Agreement on the Conservation of African-Eurasian Migratory Waterbirds (AEWA) or the Ramsar convention protect migratory waterbirds and their habitats across Africa, Europe, the Middle East, Central Asia, Greenland, and the Canadian Archipelago (https://www.unep-aewa.org/en and https://www.ramsar.org/). Hunting bans and restrictions as well as the fading popularity of hunting have also reduced mortality.

Another factor contributing to the geese' success story is their social transmission of migration behaviour, i.e. young learn where and when to migrate by accompanying their parents, and therefore, they can respond to environmental changes much faster (than under genetic transmission) (Sutherland 1998). Indeed, over the past few decades, many migratory goose species have changed migration behaviour, e.g. pink-footed geese adjusted migration timing to changes in phenology of vegetation growth (Bauer et al. 2008b) and barnacle geese shifted the spring-staging area northward (Tombre et al. 2019). Barnacle geese have also established new breeding areas, some of them far south of the Arctic, e.g. at the island Gotland in Sweden, and thereby drastically reduced migration distances (Larsson and Forslund 1994; Larsson et al. 1988; Van Der Jeugd et al. 2009). Some barnacle geese have even ceased migrating altogether and live year-round in the Netherlands (Jonker et al. 2012).

Although migrants are generally thought to affect ecosystem functioning and community structure (Bauer and Hoye 2014), this all the more applies to the immense numbers of migratory geese. Their intense and extended herbivory may turn the Arctic from a carbon sink into a carbon source (van der Wal et al. 2007), increase nutrient loading of Arctic freshwaters (Hessen et al. 2017), or lead to near-irreversible shifts in coastal marsh ecosystems (Jefferies et al. 2006). Conflicts with agriculture in temperate non-breeding and stopover areas have also intensified (Bauer et al. 2018; Fox et al. 2017). To alleviate these conflicts while still sustaining migratory wildlife populations as an internationally shared objective, adaptive flyway management plans have been developed for several goose populations over the past years, e.g. (Madsen et al. 2017).

2.3.3 Caribou and Reindeer: Seasonal Movements Within the Arctic

The reindeer (or caribou) inhabit tundra, alpine, and forest regions in Arctic and sub-Arctic ecosystems, with several sub-species identified (Gunn et al. 2011), and with distinct herds within sub-species. Some herds are very abundant, such as the Taymyr reindeer herd in Russia, estimated to around one million individuals (Kolpashikov et al. 2015). Reindeer can be mostly sedentary, such as the Svalbard reindeer (Tyler and Øritsland 1989) and the Peary caribou (Gunn et al. 2011), whereas many perform seasonal migrations, including several North American sub-species and herds (Gunn et al. 2011). The migrations are truly astonishing and among the longest of any terrestrial mammal (Berger 2004). Individuals in the Porcupine and Central Arctic herds cover more than 5000 km per year (Fancy et al. 1989). Reindeer and caribou migrations are typically between distinct calving areas, sometimes in coastal areas, and larger and more interior feeding areas during winter, on the tundra or in forest environments (Gunn et al. 2011; Nicholson et al. 2016). Some herds also cross long stretches of sea ice both during their spring and autumn migration, such as the herds calving and spending the summer on Victoria Island in the Canadian Arctic (Poole et al. 2010). Reindeer rarely swim long distances and, if possible, circumvent open water along their tundra routes (Leblond et al. 2016).

Migration patterns of caribou may vary between years, such as the large variability recently analyzed for the Riviere-George (RGH) and the Riviere-aux-Feuilles (RFH) herds (Le Corre et al. 2020), where wintering areas in different years may be situated several hundred kilometres apart. Individuals were more likely to change migration route and wintering area when the population size was large, suggesting competition for food, also between the herds, to be the underlying reason for the plasticity in migration movements (Le Corre et al. 2020).

Many Arctic and sub-Arctic people interact closely with reindeer and their annual cycle and migrations. Some are primarily hunting them (Kolpashikov et al. 2015), whereas others, such as many Saami in northern Fennoscandia, keep reindeer as their property and are involved in reindeer husbandry (Weladji and Holand 2006). Reindeer kept by herding communities are considered semi-domesticated and this reindeer husbandry exists among several people throughout northern Eurasia, for instance, by the Nenets. A nomadic lifestyle and seasonal migrations are often integrated in this interaction, where reindeer and people move together through the landscape. For instance, in Finnmark (Northern-Norway), it is common practice to move the reindeer between coastal calving and summer pastures and winter feeding grounds in the interior where the climate is colder and with less or drier snow (Weladji and Holand 2006). Migration distances in Finnmark, Norway, range from 100 to 350 km one way from summer to winter pastures (Kelman and Næss 2019; Weladji and Holand 2006). The owners earmark their individuals, but individuals from different owners typically mix and move together and are looked after by cooperative herding units (Næss 2012).

2.3.4 Marine Migrants: Travelling to the Arctic to Feed

Despite the mainly terrestrial focus of this chapter, many marine species also use Arctic and sub-Arctic waters for parts of the year or migrate within the Arctic. A notable feature is that instead of migrating to the Arctic to *breed* which is typical for birds (Drent et al. 2006), many marine species migrate to the Arctic to *feed*. They then use the highly but only seasonally productive northern seas for growth and storage and for preparation for breeding elsewhere. For instance, several species of large whales feed in high-latitude systems during the northern summer and move south to low latitudes, often tropical locations, for breeding and calving (Table 1). The eastern pacific population of grey whale (*Eschrichtius robustus*), which migrates south and north along the western North American coast, is one such example (Guazzo et al. 2019; Rice and Wolman 1971; Swartz et al. 2006). Its core feeding grounds are in the Bering and Chukchi seas where it primarily feeds on benthic prey, in particular tube-dwelling amphipods (Rice and Wolman 1971). The grey whales are observed on their southward migration from November onwards, with near-term pregnant females migrating first (Rice and Wolman 1971). The lagoons in Baja California, Mexico, are key calving and nursing areas. The return migration to the Arctic takes place in spring, with arrival to the feeding grounds from May onwards (Swartz et al. 2006). Humpback whales (*Megaptera novaeangliae*) follow a similar scheme (Darling and McSweeney 1985), but with major calving and breeding areas near oceanic islands, such as Hawaii for the Pacific population (Calambokidis et al. 2001) and Capp Verde and Caribbean islands for the North Atlantic population (Stevick et al. 2016). For humpback whales, genetic evidence suggests that the North Pacific, North Atlantic, and Southern Hemisphere populations are different and could be regarded sub-species (Jackson et al. 2014). The humpback and the grey whale illustrate how several large baleen whales rely on Arctic feeding grounds and combine that with capital breeding, long distance migrations, and none or limited feeding during the period away from the Arctic. Lower predation risk from killer whales at low latitudes have been proposed as one potential ultimate driver of these breeding migrations into biologically unproductive waters (Corkeron and Connor 1999). As for most migratory species, understanding the complex set of cues and navigational aids used by the individuals is challenging, with whales being no exception (Burnham 2020).

Several fish populations in the North Atlantic are also examples of the travelling to feed strategy. They migrate northward into foraging areas during summer and return south to the spawning grounds. Some of the most northern feeding grounds are within the Arctic, and several species are feeding in sub-Arctic seas. Atlantic cod (*Gadus morhua*) and herring (*Clupea harengus*) are two examples of large populations with such seasonal migrations. The migratory Northeast Arctic cod feeds in the Barents Sea, including the waters around Svalbard, and migrate south to Lofoten and other areas along the Norwegian coast to spawn (Jørgensen et al. 2008; Ottersen et al. 2014). The Norwegian spring-spawning herring has a more oceanic feeding migration into the Norwegian Sea (Claireaux et al. 2020; Varpe et al. 2005) and typically reach sub-Arctic waters towards the end of the summer. The extent that planktivourus fish, such as herring but also capelin (*Mallotus villosus*) and Atlantic mackerel (*Scomber scombrus*), move north during a given year is dependent on population size, as captured by the concept of density dependent migratory waves (Fauchald et al. 2006). After its seasonal feeding migration, the herring returns to the coast of Norway for wintering followed by spawning in March and April. For herring as well as cod, this annual routine has evolved in close connection with a seasonal food source (Varpe and Fiksen 2010) and with the ocean currents. Larvae of both species drift northward and into the Barents Sea where the individuals grow and develop for several years until maturation (Ottersen et al. 2014; Skagseth et al. 2015).

Marine species also display long seasonal migrations within the Arctic. Seals, whales, the polar bear (*Ursus maritimus*), and the Arctic char (*Salvelinus alpinus*), all have distinct movement patterns through the year. Ringed seals (*Phoca hispida*) breed in fjords and in relation to fjord ice during spring, but some individuals have offshore migrations during their non-breeding and post-molting period (Freitas et al. 2008). Similarly, some polar bears tend to be more local year round, whereas others are oceanic and operate in the open ocean sea ice ecosystems (Mauritzen et al. 2001). Pregnant polar bears will return to land during autumn and to suitable denning areas. Beluga whales (*Delphinapterus leucas*) offer another example. In the waters near Alaska and Russia, these whales perform foraging migrations into the seasonally sea-ice covered Eastern Chukchi Sea and Eastern Beaufort Sea (Hauser et al. 2017), and prior to freeze up in the late autumn, they return to wintering areas in the Bering Sea. Offspring are thought to learn these migrations from their mothers (Hauser et al. 2017), a phenomenon also highlighted for other Beluga whale populations (Colbeck et al. 2013).

The anadromous Arctic char also illustrates seasonal migrations within the Arctic. Arctic char has a circumpolar distribution in Arctic and sub-Arctic coastal waters and can be found both as landlocked populations spending all their life in the lake or as anadromous populations that spend part of the summer in the ocean (Klemetsen et al. 2003). In some lakes, some individuals are anadromous, whereas others stay in the lake all year round, with permanent residents typically reaching much smaller body size. For high-latitude populations, the melt-up of the river connecting lake and sea usually determines the timing of the migration to the sea, which can be highly synchronous (Gulseth and Nilssen 2000). The high productivity of the ocean and the good marine feeding conditions is the central benefit of this migration, but the time at sea comes with higher risk as well as energetic costs related to osmoregulation in salt water (Klemetsen et al. 2003; Nilssen et al. 1997). During the winter, all individuals are in the lake. Feeding within the lake also displays pronounced seasonality, partly driven by the seasonal light conditions (Svenning et al. 2007).

Finally, a variety of zooplankton species in northern waters have evolved prominent seasonal vertical migrations in the water column (Bandara et al. 2021). These migrations form key parts of annual routines, such as for herbivorous species that feed in surface waters and migrate to deeper diapause habitats (Conover 1988; Varpe 2012), and result in seasonal patterns of food availability for higher trophic levels (Varpe and Fiksen 2010).

3 Migratory Animals and Their Role as Long-Distance Dispersers of Infectious Agents

Migratory animals are commonly assumed to act as long-distance dispersers of infectious agents (Altizer et al. 2011; McKay and Hoye 2016; Westerdahl et al. 2014). As many of the infectious agents of wildlife have the potential to also infect humans and livestock, understanding the role of migratory animals in the spread of zoonotic agents has important implications for human health and economy. Still, and as argued in a recent review, much remains to be investigated to integrate migrations within disease ecology (McKay and Hoye 2016).

Migrants travel astonishing distances, establish unique geographic links between otherwise separated communities and thus encounter a greater diversity of infectious agents than resident species (Gutiérrez et al. 2019). For instance, migratory birds harboured a higher diversity of intestinal (Koprivnikar and Leung 2015; Leung and Koprivnikar 2016) or blood parasites (Emmenegger et al. 2018) and migratory ungulates generally had a higher parasite diversity than resident or nomadic species (Teitelbaum et al. 2018).

Furthermore, many migrants aggregate during migration—either for the migratory movement itself or on intermittent stopover sites where they refuel for the next migratory bout. Individuals are then in close contact, which constitutes an ideal transmission scenario. Prominent examples for aggregations on highly profitable stopover sites are the Yellow sea or Hudson Bay, where millions of shorebirds gather during a short time period in spring (Krauss et al. 2010). The high densities of multiple species on these sites facilitate the transmission of infectious agents such that, e.g., the prevalence of avian influenza in Delaware Bay is higher than anywhere in the world (Krauss et al. 2010).

Moreover, the metabolically costly migrations usually involve physiological and morphological adjustments that might be made at the expense of immune function (Buehler et al. 2010). If migrants suppress their immune system, latent infections may be reactivated and passed on to vectors or new hosts (Becker et al. 2020). This mechanism has been suggested for migrating birds that carry ixodid ticks which are vectors of *Borrelia burgdorferi* sensu *lato* (Gylfe et al. 2000), a bacteria that can cause Lyme disease in humans.

Despite the long distances that migratory animals travel, the diversity of infectious agents they encounter and the dense aggregations they form, migrations can also provide effective mechanism for hampering the transmission of infectious agents, through migratory escape, migratory culling, and migratory separation (Fig. 2) (Hall et al. 2014; McElroy and de Buron 2014; Satterfield et al. 2015; Shaw and Binning 2016).

Migratory Escape For infectious agents that are transmitted via the environment or via local vectors, migration may lead animals away from pathogen- or vector-rich places. If conditions during the absence of migratory hosts become unfavourable for the persistence of pathogens or vectors, migrants will then return to an almost pathogen-free environment.

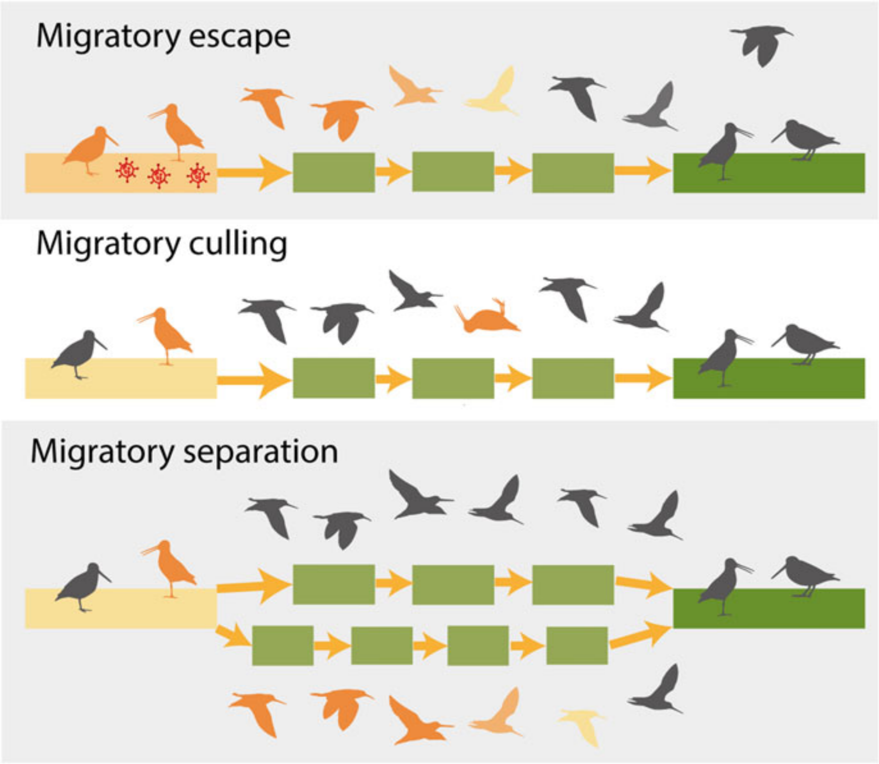

Fig. 2 Migration from a non-breeding area (left) to a breeding area (right) via several intermittent stopover sites can effectively interrupt the transmission-cycle of infectious agents through migratory escape, culling, or separation. In migratory escape, animals leave areas with high infection pressure, clear infections on the way, as indicated by color change from infected (red) to uninfected (grey), and reach a relatively pathogen-free breeding location. Similarly, for migratory culling, infected individuals die at a higher rate such that mostly uninfected individuals reach the breeding area. Finally, under migratory separation, infected individuals migrate along a different route or at different times than uninfected individuals, and this separation of infected from uninfected individuals hampers the spread of parasites in the population

Migratory culling If infectious agents are relatively virulent and/or hosts relatively susceptible, infected individuals may die at a higher rate than uninfected individuals. Consequently, infected individuals are "weeded" out from the population, and the risk of transmission to uninfected individuals decreases overall.

Migratory Separation Perhaps a less severe form of migratory culling, for migratory separation, migratory hosts are also affected by parasites but sublethally and lead to infected individuals taking other migration routes, using different stopover sites or migrating at other times than uninfected individuals. For instance, many infections and diseases reduce their hosts' appetite, induce fatigue, or shift daily activity rhythms towards more resting. Pathogens can also change their hosts' gut surface area or passage time, effectively reducing the uptake of nutrients and energy, which, in turn, prolongs fueling and delays migratory departures, e.g. in Bewicks' swans (*Cygnus columbianus bewickii*) infected with Avian influenza (van Gils et al. 2007).

Pathogens can also increase their hosts' daily energy expenditure, as they evoke immune responses and/or increase metabolic rates. Both immune responses and higher metabolic rates require nutrients and energy, which cannot be devoted to other processes such as migration. Indeed, higher resting metabolic rates have been shown for birds with parasites, e.g. blood-sucking ectoparasites in tree swallows (Sun et al. 2020), but these effects are not consistent across species or life-history stages (Hahn et al. 2018; Robar et al. 2011). Similarly, ectoparasites such as feather mites or sea lice may invoke structural changes that alter aerodynamics or hydrodynamics and increase costs for locomotion, e.g. through more energy required for a distance flown or swum, and/or lower flight or swim speed (Binning et al. 2013, 2017).

Any of these changes may result in infected individuals not replenishing resources at their typical rate or using them up faster. Consequently, infected individuals may require more frequent fueling during migration or more time to complete migration, and although this temporal or spatial separation usually lasts over a relatively short period only, this might be sufficient for separating infected and uninfected individuals and interrupting the transmission cycle and ultimately lower prevalence (Altizer et al. 2011; Bauer et al. 2016; Hall et al. 2014).

4 Outlook

4.1 Changing Migrations and Threats to Migrants

Our era has been coined the Anthropocene as human impacts on nature are substantial, and as a consequence, biodiversity is lost at an unprecedented rate (IPBES 2019). Many migratory populations have declined as a result of changing landscapes and habitat alterations, new obstacles with rapid expansions of human structures and activities, and climate change effects such as altered phenology and abundance of both food and predators along their migration routes (e.g. Wilcove and Wikelski 2008).

Climate Change Over the past decades, global average temperatures have risen with 0.2 °C per decade and are projected to continue to rise (IPCC 2013). However, climate change is highly uneven across regions and times of the year with, e.g. temperatures increasing more rapidly in the Arctic (IPCC 2013) and extreme events occurring more frequently, which will have a broad range of effects in nature and societies (Hansen et al. 2014; Langbehn and Varpe 2017; Schmidt et al. 2019; Vincent et al. 2011; Wassmann et al. 2011). One consequence is a rapidly changing phenology in the Arctic with concomitant consequences for the optimal time window for many life-history processes of Arctic migrants (Fjelldal et al. 2020; Lameris et al. 2018). For instance, in migratory birds, reproductive success often depends on arriving early enough to the Arctic to synchronize breeding (or feeding) with the spring onset (Doiron et al. 2015; Lameris et al. 2018). If migrants cannot respond to an advancing spring, the periods of high demand will not match those of high productivity with negative effects on individual fitness and eventually on population trends (Cohen et al. 2018; Samplonius et al. 2021). For instance, red knots that breed in the Russian Arctic produce smaller offspring during years when spring starts early (van Gils et al. 2016), likely as a result of parents arriving (and starting to breed) too late. Consequently, their chicks miss the peak of insect abundance and grow slower or to a smaller adult size. When those smaller individuals migrate to non-breeding grounds in West Africa, they face the problem that their short bills cannot reach their preferred food, which is deeply buried clams. Although the size differences may seem small, they culminate in lower survival and shorter life expectancy for smaller compared to larger individuals (van Gils et al. 2016).

A warming Arctic is impacting the breeding environment of birds and may reduce the areas climatically suitable for breeding. Arctic organisms have few opportunities to shift their distributions further north (Lehikoinen and Virkkala 2016; Maclean et al. 2008) and therefore suffer from contracted breeding ranges. Also, for those able to shift their distributions to higher elevation or to other areas, such shifts may interact with migration routes and potentially lead to restructuring of entire flyways (Wauchope et al. 2017).

In the Arctic marine environment, the reduced spatial extent and thickness of sea ice and its shorter seasonal occurrence are among the most pronounced climate-induced changes (Stroeve et al. 2012). Consequently, more light enters the water column, impacting both pelagic and benthic organisms through possibilities for increased photosynthesis and primary production and through improved conditions for visually searching predators (Clark et al. 2013; Varpe et al. 2015). Fish, for instance, often rely on their vision when hunting, and sea ice loss leads to large areas becoming more profitable for detecting prey. Northward shifts in their distributions may result, particularly likely for seasonal migrants that can make use of the abundant light during summer, but leave the Arctic during the dark winter (Langbehn and Varpe 2017). Sea ice is also a physical hindrance for fish filling their swim bladder by gulping air at the surface (physostomous fish) such as herring (Kaartvedt and Titelman 2018). This constraint has similarities to how marine mammals are prevented from breathing during under-ice excursions (Brierley et al. 2002) or risk entrapment in the sea ice landscape (Ferguson et al. 2010; Stafford 2019).

Human Structures, Overexploitation, Habitat Loss, and Alterations Collisions with man-made structures such as power lines, wind turbines, and buildings kill large numbers of birds and bats annually, but estimates of the resulting fatalities and their ecological significance vary (Cryan et al. 2014; Lambertucci et al. 2015). For instance, mortality from wind turbines appears to represent a substantial population-level threat in bat populations in North America (Frick et al. 2017), but further research is urgently needed.

Similarly, fences, roads, pipelines, and other structures can hinder ungulates during their migrations, and there is concern regarding loss of migration routes and an inability to secure the management measures that could conserve them (Berger 2004). This is also the case for reindeer in the Arctic (Kuemmerle et al. 2014; Taillon et al. 2012). Landscapes used for reindeer husbandry are becoming increasingly fragmented, for instance, through fencing practices (including at national borders), sometimes preventing traditional movement patterns and seasonal migrations by Saami and their reindeer (Kelman and Næss 2019).

Human structures and activities that may prevent or modify migrations are not unique to terrestrial environments. Marine mammals use sounds to communicate and navigate and are likely sensitive to artificial noise (Duarte et al. 2021). There are therefore concerns related to the interaction between marine mammals and the increasing industrial activities, including shipping, in the Arctic (Halliday et al. 2017).

Other species have seen new and increased challenges related to parasites and infections along their migration routes. Atlantic salmon (*Salmo salar*) is one example. Born in rivers and spending much of their life in the ocean, they pass coastal regions twice before reproducing (Klemetsen et al. 2003). In some countries, such as Norway, salmon farms are abundant in fjords and coastal environments, and wild salmon suffer from exposure to salmon lice and other parasites and infectious agents as they proliferate among farmed fish and spread back to the wild (Forseth et al. 2017). With warming waters and less sea ice, aquaculture may be extended to even more northern communities and expand the areas of potential parasite and pathogen transmission.

4.2 What Do These Changes Mean for Migrants as Dispersers of Parasites and Pathogens?

Overall, much remains to be understood about the role of migratory animals in the spread of infectious agents. Only a handful of infectious agents and diseases have been investigated in detail, and these usually include those with zoonotic potential or severe economic implications such as avian influenza or brucellosis.

If global and climatic changes alter migration routes, migrants may reach novel breeding, non-breeding, or stopover places and introduce infectious agents into possibly “naïve” communities. Furthermore, a warming and changing Arctic may impact which pathogens can survive year round in the Arctic and hence pose new interactions with seasonal migrants. Increased attention to infectious agents seems both important and fruitful as additions to migration studies that focus on the roles of the changing physical environment or the changing abundance and phenology of food or predators.

4.3 Conservation of Migrants and Migrations

With the multiple threats that migratory species face and their declining populations, conserving migrants and migrations has become an internationally shared objective. However, conserving mobile species is a challenging endeavour as migrants rely on multiple locations to complete their annual or life cycles (Runge et al. 2014). The use of these sites is interdependent such that the conditions on one site will have consequences for the use of others, and therefore, management actions on single sites may be futile if they do not take into account actions elsewhere (Bauer et al. 2018).

For many species, elements of their migrations may also change considerably between years, such as variability in the wintering area of caribou (Le Corre et al. 2020) or in location and size of calving grounds (Taillon et al. 2012). Such dynamics are clearly challenging to account for when most management and conservation measures are built around static approaches such as reserves with constant boundaries. Dynamic approaches are called for (Taillon et al. 2012). Similar challenges exist for managing moving fish populations where seasonal migrations include waters managed by multiple countries, as well as international waters, for which international negotiations are needed to implement sustainable management. For instance, the wintering area of the Norwegian spring-spawning herring has varied considerably during the last century, including areas many hundreds of kilometres apart, such as near Iceland during the 1950s and early 1960s but wintering primarily in near-coast areas of Northern Norway from about 1980 and onwards (Claireaux et al. 2020; Dragesund et al. 1997). Clearly, such dynamics present challenges not only for fisheries management but also for predicting impacts of climate change and other stressors on the population and its large-scale movement.

Management practices may lead to changes in movements and migrations. The presence and extent of goose hunting impact the timing of migrations and how long geese stay on a particular stopover site (Bauer et al. 2018). Furthermore, management may sometimes include the eradication of entire populations, e.g. to halt the spread of the chronic wasting disease from an infected reindeer population (Mysterud et al. 2020). However, we need to be aware that any management measure, but particularly massive culling, may have side- or carryover effects, including increased movement and geographic spread (Mysterud et al. 2020).

Moreover, the multiple sites used by migrants and the movements in between form migratory networks that range from linear networks in which sites are used in a sequential manner to diffuse networks where many sites are used interchangeably. The structure of these networks plays an important role in how vulnerable migrant populations are to the degradation or loss of sites (Betini et al. 2015; Xu et al. 2019).

In addition to the structure of migratory networks, the vulnerability of species depends on the capacity of migrants to adapt to changing conditions. Although some species seem to adapt rapidly through altered migration routes or timing, for many other species, it is largely unknown whether and how fast they can respond. Furthermore, threats differ in their consequences for different demographic rates, and likewise, management actions may influence survival or reproductive success differently.

Thus, efficient conservation needs an international approach that entails the entire migration range, spatial prioritization by identifying and conserving crucial sites and crucial connectivity, and the identification of actions that are most effective.

5 Concluding Remarks

Migrations are unique movements that connect the world, and in this network of species and migration routes, the Arctic stands out as a melting pot where migrants from all over the world meet during the Arctic summer, some to breed, others to just feed. Travelling animals connect ecosystems and serve as spatial vectors, of energy and nutrients and of other organisms that follow, sometimes as active hitchhikers, for parts or the entire route. Understanding drivers and patterns of migrations is essential for understanding the dynamics of diseases and must therefore be considered in veterinary and human medicine and the One Health perspective. Current global changes are particularly pronounced in the Arctic with many ongoing environmental changes impacting migrants in a diversity of ways. Interactions with infectious agents are also likely to change, and the abundance of pathogens may increase, for instance, with episodic outbreaks during particularly warm weather (Hueffer et al. 2020). The spatial configuration of many migrations are also rapidly changing, potentially exposing migrants to new infectious agents and creating new connections between previously separated areas.

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