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Migratory vertebrates shift migration timing and distributions in a warming Arctic

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Research Article

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Migratory vertebrates shift migration timing and distributions in a warming Arctic

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Abstract: Climate warming in the Arctic has led to warmer and earlier springs, and as a result, many food resources for migratory animals become available earlier in the season, as well as become distributed further northwards. To optimally profit from these resources, migratory animals are expected to arrive earlier in the Arctic, as well as shift their own spatial distributions northwards. Here, we review literature to assess whether Arctic migratory birds and mammals already show shifts in migration timing or distribution in response to the warming climate. Distribution shifts were most prominent in marine mammals, as expected from observed northward shifts of their resources. At least for many bird species, the ability to shift distributions is likely constrained by available habitat further north. Shifts in timing have been shown in many species of terrestrial birds and ungulates, as well as for polar bears. Within species, we found strong variation in shifts in timing and distributions between populations. Our review thus shows that many migratory animals display shifts in migration timing and spatial distribution in reaction to a warming Arctic. Importantly, we identify large knowledge gaps especially concerning distribution shifts and timing of autumn migration, especially for marine mammals. Our understanding of how migratory animals respond to climate change appears to be mostly limited by the lack of long-term monitoring studies.

Keywords: birds; mammals; marine mammals; phenological mismatch; range shift; migration phenology

1 Introduction

The Arctic region is characterised by strong seasonality. During winter, the Arctic forms an inhospitable environment for most animals, with low temperatures, extensive snow and ice cover and long phases of darkness. The summer season is relatively short with long light phases and temperatures above freezing, associated with strong changes in environmental conditions, including melt of snow and break-up of sea ice. In both terrestrial and marine ecosystems, the Arctic summer is also a period of peak productivity, creating a short period of high resource abundance for many species. These strong seasonal changes in environmental conditions explain why many vertebrates occurring in the Arctic have a migratory lifestyle [1, Figure 1]. This allows them to profit from high resource abundance in the Arctic summer, while escaping harsh climatic conditions during winter.

The Arctic climate is changing disproportionately fast [2], with temperature increases three times as fast as the rest of the globe [3], especially accelerating in recent decades [4]. Increases in temperature throughout the year coincide with loss of Arctic sea ice, shorter seasonal duration of snow cover [5], and overall increased ‘greening’ of tundra regions [but with strong variation between sites, 6]. Such changes are predicted to further accelerate in the near future [7]. The warming climate has strong impacts on the availability of resources for Arctic migratory animals. Earlier disappearance of ice and snow in the season can result in shifts in timing and distribution of the main food resources for migrants, including vegetation [8,9] and arthropods on land [10–12], and phytoplankton abundance at sea [13,14]. If migratory animals do not change the timing of their migration and reproduction or their summer distribution in response, phenological mismatches with their food resources may occur, potentially resulting in reduced fitness [15,16] which might affect population dynamics.

To adjust to changes in the timing of resource availability in the Arctic, migratory animals could advance their timing of arrival on the breeding grounds. Given the limited leeway to increase the speed of migration once underway [17,18] for birds which have relatively high travel speeds, this likely also necessitates advancements in migratory fuel deposition and departure from the wintering grounds [19]. Besides changes in spring migration in response to earlier resource availability, longer Arctic summer seasons associated with later freeze-up and snowfall [5] could also drive delays in the timing of autumn migration [20].

In addition to shifts in the timing of migration, animals may respond to a warming Arctic by shifting their summer

distribution northward to locations with later phenology. Animals making this northward shift may then experience the same timing of resource availability in spring without advancing migration timing (Figure 2), although it could also result in later arrival given longer migration distances. However, distributional shifts might be limited by topography or by increased travel costs for some Arctic animals. First, many terrestrial animals in the Arctic already find themselves at the most northern edge of the continent, resulting in shrinking habitat range or “polar squeeze” (Figure 2). Second, suitable habitats may not be present further north. For example, marine mammals are largely reliant on sea ice for feeding (and reproducing in case of pinnipeds), and may find themselves without any available habitat with the predicted disappearance of sea ice in summer [21]. Changes in timing of migration and reproduction [22,23], and to a limited extent shifts in breeding distribution [24,25], have already been observed in Arctic migratory animals. Those species which have been unable to shift timing of reproduction sufficiently, often suffer from reductions in reproductive success and survival [15,16]. As Arctic migratory animals are an essential part of local Arctic ecosystems [26,27], as well as provide important resources for local Indigenous Peoples [28,29], any changes in the migration timing and distribution of migratory animals will have far-reaching consequences.

Here we review literature on Arctic migratory animals for evidence of shifts in timing of migration and shifts in distribution. We focus on groups of endothermic migratory vertebrates that perform seasonal migrations to, or within, the Arctic, including terrestrial and marine birds, ungulates, cetaceans, pinnipeds and polar bears (Figure 1). These animals differ strongly in their habitats (marine, coastal and terrestrial habitats) as well as in their diet (plankton, benthic invertebrates, fish, pinnipeds, plants, arthropods, rodents). We expect to find variation in both shifts in timing and distribution across taxonomic groups of Arctic migratory animals. Concerning migration timing, we predict that long-distance migrants (most birds and cetaceans, with one-way journeys on average exceeding 2000 kilometres) will show smaller shifts in migration timing in comparison to short-distance migrants (including some cetaceans, all ungulates, pinnipeds and polar bear), as long-distance migrants cannot predict conditions in the Arctic from their distant wintering grounds [30,31]. Concerning shifts in distribution, we expect terrestrial animals (including land-breeding marine birds), to be more constrained in making large shifts [32] compared to marine animals. For terrestrial animals, suitable alternative habitat further northward may not be available due to lagging changes in suitable vegetation communities, or



Figure 1: Examples of warm-blooded vertebrates migrating to the Arctic, showing (top left), reindeer (*Rangifer tarandus*) crossing a frozen river on the way to their calving grounds, (top right), red knots (*Calidris canutus*) on a spring staging site in northern Norway, (bottom left), walrus (*Odobenus rosmarus*) resting on sea ice with their young, and (bottom right), a minke whale (*Balaenoptera acutorostrata*) in a fjord in Svalbard. Photographs by Paul Asman & Jill Lenoble (top left), GRID Arendal (top right), Alaska Region US Fish & Wildlife (bottom left), and Guillaume Baviere (bottom right).

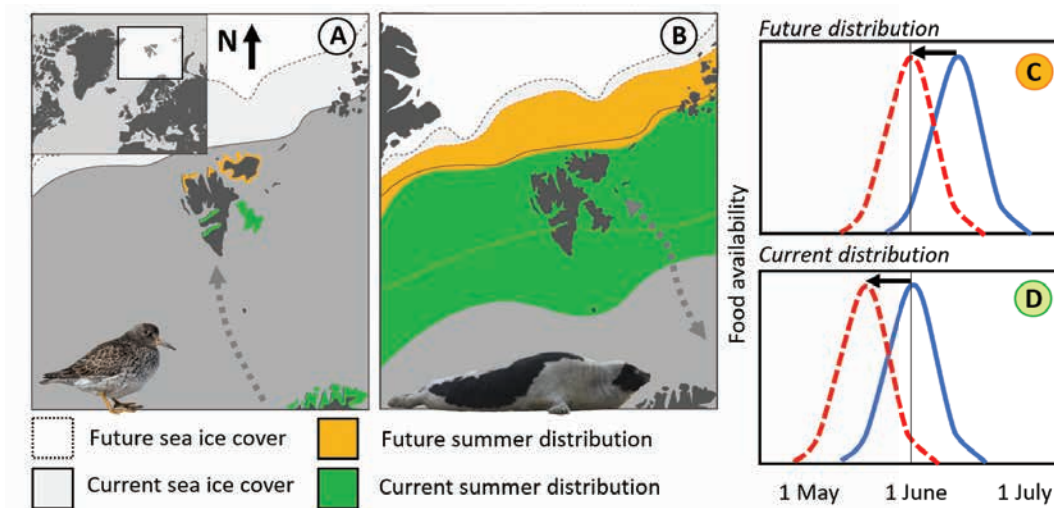


Figure 2: (A-B) Maps showing examples of current (green) and hypothetical future summer distributions (orange) of purple sandpipers *Calidris maritima* (A) and harp seals *Pagophilus groenlandicus* (B) around Svalbard. While harp seals can shift their distribution northward with retreating sea ice, purple sandpipers are constrained by available land mass of Svalbard to shift their distributions far north. Median sea ice cover (during summer months 1981 - 2010) is shown as light grey area in the north, outlined by a solid black line, and hypothetical change in future ice cover is depicted by the white area outlined by dashed black line. Grey dashed arrows show migration directions of the sandpipers and seals. Distributions and migration directions are based on [73,195,231]. (C-D) With a warming climate, timing of food availability (blue lines) is expected to advance (red dashed lines), both in current distributions (D) as well as hypothetical future distribution ranges (C). To maintain a synchrony with these peaks in food availability, animals are expected to advance their own timing of migration, but may also be able to maintain a synchrony by shifting their distribution northward (towards distribution C) where the food becomes available later in the season.

as it is limited by topographical barriers in the landscape such as the northern edge of the continent (Figure 2). In comparison, animals in marine environments that can freely navigate the oceans and enter the Arctic basin, may show stronger shifts in their distribution [32], for example by following the edge of pack ice, or the distribution shifts of their main prey [33,34].

In this review, we first introduce the focal taxonomic groups of endothermic vertebrates and their migrations. Thereafter we introduce the resources on which animals depend and discuss how the phenology and abundance of these resources are expected to change in a warming climate. Finally, following a systematic literature search, we review scientific literature on evidence for shifts in timing of migration and shifts in distribution of focal taxonomic groups, and quantify whether shifts in timing differ between taxonomic groups.

2 Migrations of Arctic, warm-blooded vertebrates

2.1 Bird migration

The most abundant birds with Arctic distributions are seabirds, shorebirds, and waterfowl, with other less represented species groups including passerines, grouse and birds of prey [1]. Most of these species are migratory [35] and spend the winter in more southern regions. The extent of these migrations varies enormously, with some seabird species wintering in Arctic waters [36,37], most waterfowl, passerines, and birds of prey wintering in temperate regions [38–40], and many shorebird and seabird species wintering in areas that range from temperate and tropical regions [41–43] down to Antarctic waters [44,45]. Differences in wintering areas, and therefore migration distance, likely relate strongly to availability of suitable wintering habitat with available resources. Fish-eating seabirds may be able to winter in Arctic waters as long as fish are available and accessible [46,47], while shorebirds, depending on benthic invertebrates, travel to temperate and tropical intertidal flats that do not freeze in winter [42]. Given long migration distances, many bird species require stopover sites to gain energy stores between leaps of migration [48]. During spring migration, at least some species of waterfowl appear to track peaks in food quality and availability [49–51] and the onset of ice break-up and snowmelt at staging sites [52,53]. This, however, does not appear to be the case for all species of waterfowl [51] nor for

shorebirds [54]. Birds of prey also track snowmelt during northward migration, possibly as areas with melting snow contain high availability of rodent prey [38]. All Arctic migratory birds reproduce during the Arctic summer, and many species (including waterfowl, shorebirds and marine birds) appear to attempt to synchronize their reproduction with prey availability for their offspring.

2.2 Ungulate migration

The Arctic is inhabited by a limited set of ungulate species, including reindeer (*Rangifer tarandus*), moose (*Alces alces*), muskox (*Ovibos moschatus*), Dall's sheep (*Ovis dalli*) and snow sheep (*Ovis nivicola*). Movements of the three latter species are limited to short-distances (up to 100 km), which can be seasonal but often follow nomadic patterns [55] in search for suitable foraging grounds. On the other hand, moose [56,57] and reindeer are considered partial migrants, and especially some populations of reindeer make large migratory movements up to 1300 km [58] from taiga wintering areas to calving grounds at coastal Arctic tundra zones. Other populations of reindeer migrate shorter distances [59] or are resident [60]. By migrating, ungulates can winter in areas with more suitable conditions for both adults and their offspring [56], travel northwards in spring along a wave of vegetation green-up [61], and match calving with local peaks in food quality [15,62]. Studies on the migrations of moose are largely limited to their southern ranges, and in this review we therefore focus on reindeer.

2.3 Cetacean migration

Cetaceans occurring in the Arctic are mostly represented by baleen whales (Mysticeti), including rorquals (Balainopteridae) and grey whales (*Eschrichtius robustus*), and fewer toothed whales (Odontoceti), including belugas (*Delphinapterus leucas*), narwhals (*Monodon monoceros*), sperm whales (*Physeter macrocephalus*) and northern beaked whales (*Hyperoodon ampullatus*). With the exception of the pagophilic (i.e. sea-ice loving) beluga, narwhal and bowhead whale (*Balaena mysticetus*), which make seasonal migrations within the Arctic, cetaceans are seasonal visitors to the Arctic. In contrast to birds and ungulates that migrate to the Arctic for reproduction, migratory whales use the high latitude summer grounds exclusively for feeding, while reproduction occurs in low latitude winter grounds, where food availability is generally scarce or non-existent [63]. The mechanism driving this migra-

tory pattern remains largely unknown. It has been suggested that whales migrate to reduce predation pressure on calves [64,65], or that the higher temperatures of low latitude waters bring thermoregulation benefits for calves (and/or adults) [66,67]. However, recent new evidence suggests that deferred skin moult could be the main driver of long-distance cetacean migration [67]. In colder waters, cetaceans reduce blood flow to their skin to conserve body heat. It appears that cetaceans migrate to warmer waters at lower latitudes to reduce heat loss during moult, a period during which they enlarge blood flow through the skin. Similarly, the pagophilic species that remain in the Arctic year-round, make seasonal migrations towards warmer waters in estuaries and shallows to moult [68–70].

2.4 Pinniped migration

Several pinniped species are year-round residents in the Arctic regions, like harp seal (*Pagophilus groenlandicus*), ringed seal (*Pusa hispida*), hooded seal (*Cystophora cristata*), bearded seal (*Erignathus barbatus*), spotted seal (*Phoca largha*), ribbon seal (*Histiophoca fasciata*) and walrus (*Odobenus rosmarus*). In addition, the distributions of other species like harbour seals (*Phoca vitulina*) and grey seals (*Halichoerus grypus*), Steller sea lion (*Eumetopias jubatus*) and northern fur seal (*Callorhinus ursinus*) extend into the polar regions. While pinnipeds feed at sea, they require land or ice to reproduce, moult and periodically rest, which severely constrains their at-sea distribution. To avoid land predators, most Arctic pinnipeds spend the breeding and moulting season on land-fast ice or free-floating pack ice in late winter and spring [71], after which they disperse. While some individuals move long distances away from the ice (e.g. harp seals and walrus), most pinniped species remain associated with outer edges of the pack ice, where they feed on fish and invertebrates [72], while using the pack ice as resting platforms. Resident Arctic pinnipeds feed on prey that is present and accessible in the Arctic regions year-round, which provides no strong incentive to leave the Arctic region altogether, as opposed to most birds and cetaceans. However, pinnipeds do show seasonal long-distance movements [73], but this seasonal migratory pattern mostly involves movement between foraging areas, breeding and moulting locations, largely driven by the extent of the pack ice [74].

2.5 Polar bear migration

Polar bears (*Ursus maritimus*) depend on sea ice platforms to hunt fatty, energy-dense pinniped prey [75], primarily ringed seals and bearded seals [76]. The bears consume around two-thirds of their annual food intake from February up to mid-April, when seals give birth on the sea ice [75,77]. When sea ice melts and becomes fractured in spring, the polar bears' mobility and seal hunting technique become inefficient [78], and bears either move with the receding pack ice, or migrate towards terrestrial habitats [75]. The summer is typically a period of fasting for polar bears during which they rely on endogenous energy reserves [79]. Most polar bears move back onto the pack ice after autumn, when pack ice extent increases, while pregnant female bears will enter terrestrial maternity dens along the coast where they give birth to their young [80].

3 Changing resources under climate warming

Temperatures in the Arctic are increasing year-round, with temperatures above freezing occurring earlier in spring [81], associated with earlier timing of snow melt, active layer melt and ice break-up [5]. These climatic changes can result in earlier availability of resources for migrants (although the relative importance of climatic factors may differ at regional scales, e.g. [82]). In addition, higher summer temperatures may lengthen the period of resource availability, and climatic changes may also cause a northward shift in the spatial distribution of resources, as well as of suitable habitats for migrants. We discuss these aspects in detail in the following sections.

3.1 Earlier resource availability

Lower trophic levels, including the food resources for many migratory animals (Figure 3), are known to rapidly adjust their phenology to a warming climate [83]. In terrestrial habitats, earlier snowmelt and increasing temperatures have led to an advancement in the growing season of many plants [84], and thereby an advancement in the moment of peak quality and availability of forage plants for herbivorous birds and ungulates [8,9,85]. Arthropods, which form the main prey for Arctic-breeding shorebirds and passerines [86], respond to earlier dates of snow and active layer melt and increasing temperatures by earlier emergence [10,22,87] and changes in their abundance

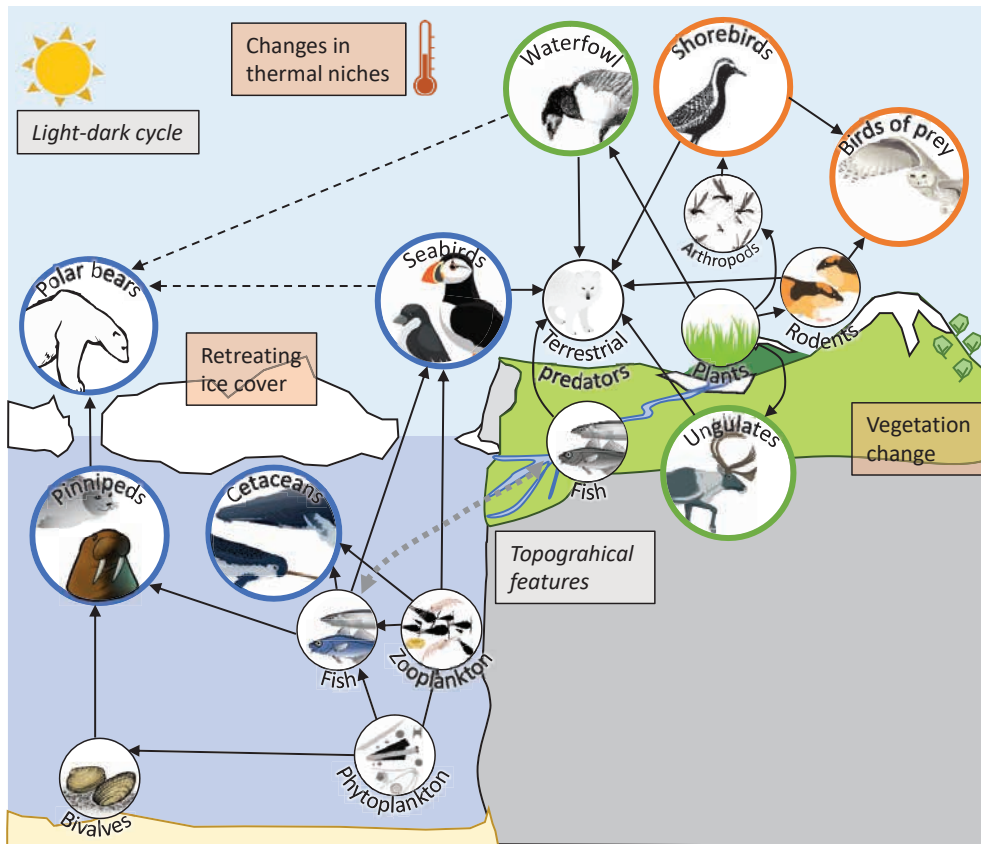


Figure 3: Simplified food webs in marine Arctic habitats (left) and terrestrial habitats (right), with the focal groups of marine migrants (blue), terrestrial herbivore migrants (green) and terrestrial carnivores (orange) displayed in circles. Resources, as well as predators which do not display typical migratory behaviour, are displayed in black, smaller circles. Several marine fish species make semelparous migrations to streams and rivers to spawn (as indicated by the grey dashed arrow), and are thus available as resource to both marine and terrestrial animals. In marine habitats, migratory seabirds, cetaceans and pinnipeds are expected to adjust timing of migration and / or distribution with availability of zooplankton, benthic organisms such as bivalves, and fish, which in turn rely on phytoplankton (including ice algae). Polar bears rely on the presence of pack ice to prey on pinnipeds during winter months, but with a warming climate spend more time in terrestrial habitats where they have started to prey on bird's eggs. In terrestrial habitats, herbivores feed on forage plants and time arrival with peaks in nutritional quality of plants. Shorebirds time migration in synchrony with availability of arthropods, and birds of prey rely on availability of rodents for successful reproduction. In turn, terrestrial predators such as Arctic foxes prey on bird's nests, especially in years when cyclic rodent populations are depressed. Besides shifts in phenology of resources, climate warming may also impact habitat suitability via changes in thermal niches, retreating pack ice and vegetation community change (shown in orange boxes). Other aspects such as light-dark cycles and topographical features (such as cliffs which seabirds require for nesting, shown in grey boxes) will not change, potentially constraining distribution shifts of animals.

[10]. The annual cycles of Arctic rodents, the main prey of Arctic raptors and skuas [88], seem to be little impacted by a warming climate [89] (but see reports on irregularity of these cycles [90]). At the same time, the accessibility of rodents as prey for birds is potentially dependent on snow cover, with high concentrations of accessible rodents around the time of snow melt [38]. Despite increasing temperatures, increasing precipitation in winter (another aspect of climate change in the Arctic, 91) may also result in abundant snow and late melt thereof, which has the potential to largely disrupt reproduction of all terrestrial animals [92].

In marine environments, ice algae and phytoplankton form the most important primary producers and are the basis of the Arctic marine food web [93]. Ice algae grow under thinning ice edges, and their phenology is regulated by light [94]. While a warming climate would result in a more permeable ice layer and earlier ice algal blooms may be expected, short day-length at high latitudes limit phenological advancements of ice algae [94,95]. The other main primary producer, phytoplankton, blooms later in the season at ice edges, regulated by light and nutrient upwelling [95]. Earlier ice disappearance has caused an advancement in timing of phytoplankton blooms [96]

and a decreasing time-lag between ice algae and phytoplankton blooms [95], which together form the main food resource for many species of bivalves and zooplankton [97]. Zooplankton may suffer from reductions in survival (measured as lower available zooplankton biomass) when they are not able to adjust their phenology in response to advanced phytoplankton blooms [97–99], as well as possibly due to the segregation of ice algae and phytoplankton blooms. Nevertheless, other studies found stable zooplankton biomass following earlier phytoplankton blooms [100]. Zooplankton is the main food resource for fish species, and both zooplankton and fish are eaten by most baleen whales, pinnipeds and seabirds [101,102]. Both timing and abundance of zooplankton may affect the abundance and availability of fish species as prey for higher trophic levels. For seabirds and whales, important prey fish species may occur earlier in the season, or decrease in abundance due to phenological mismatches with algal and plankton blooms.

3.2 Longer period of resource availability

While a warming climate will advance the timing when resources become available, it can also impact the abundance of resources [10], as well as result in a longer period of availability of resources. Although their nutritional value declines over the season, forage plants are available for herbivorous birds until covered by first snowfall in autumn, which is occurring later in the season in recent years [5]. This is also beneficial for many ungulates, which, despite their ability to find forage plants under shallow layers of snow, cannot deal with deeper layers of snow [103] or ice crust formation [104]. Terrestrial arthropods may remain active as long as temperatures are above freezing, but their availability to predators could be limited due to a restricted number of generations emerging in one season [105] but see [106], and Arctic shorebirds are thus unlikely to profit from a longer breeding season through re-nesting [107]. With increasing temperatures, warming Arctic waters may facilitate longer resource availability, by driving the emergence of a second phytoplankton bloom [100,108] and a second generation of copepods [109] during autumn.

3.3 Northward shifts in suitable habitats and resources

A change in climate is expected to change the habitat suitability for migratory animals as well as for their resources, and both may show northward shifts of their distribution in response (Figure 2). First of all, many organisms thrive within a specific ‘thermal niche’ or ‘thermal preference’, and experience fitness reductions outside this niche [110,111]. With a warming climate, the location of this thermal niche and therefore the suitability of habitats is predicted to shift northwards [34,112]. This may lead to distribution shifts for endothermic vertebrates, as well as for their food resources, often ectothermic animals or vegetation. Although at high latitudes most endothermic animals live at temperatures well below their thermal maximum and thus have leeway under increasing temperatures [113,114], habitat suitability of ectothermic organisms is more sensitive to changing temperatures [110], and these potentially make larger distribution shifts [115]. At the same time, vegetation communities and thereby distribution of specific plant species appear to change at relatively slow rates [6,116]. Such shifts in the distribution of resources will also change habitat suitability for migrants. For example, in marine environments, many fish species are showing northward distribution shifts, changing local community composition of potential prey species for marine predators [117]. At the same time, some fish species from lower latitudes may be unable to find refuge away from predators during the continuous light of polar summer, which may constrain their abundance under certain climate change scenarios [118].

Some factors of habitat suitability are closely linked to climatic conditions, including the thermal niche and resource distribution as explained above, as well as specific environmental aspects of habitats, such as cover of sea ice as resting platforms for pinnipeds and hunting platforms for polar bears. While climate warming will directly change these aspects of habitat suitability, other aspects are geographically fixed, for example topographical features (e.g. cliffs making up suitable nesting habitat for seabirds) and the duration of the light-dark cycle (which is fixed by latitude and date). Advances in the timing of resource availability and rapid-changing aspects of habitat suitability as a result of climate warming may drive northward distribution shifts of animals, but slow-changing or fixed aspects of habitat suitability may at the same time form constraints for distribution shifts [118,119]. Moreover, such differences in the rate of northward shifts could cause reductions in suitable habitat altogether.

4 Shifts in migration timing and distributions

4.1 Methods to quantify differences in responses between taxonomic groups

To review whether vertebrates display shifts in migration timing and distributions in response to a warming climate, we searched for relevant papers using the Web of Science database. We used the search term Arctic AND (range shift OR migration timing) AND (bird OR avian OR ungulate OR herbivore OR cetacean OR whale OR beluga OR narwal OR pinniped OR seal OR walrus OR polar bear). This query resulted in 486 papers, from which we only included papers that (1) dealt with Arctic migratory species, (2) reporting on changes in either timing of spring or autumn migration, timing of reproduction or changes in distribution, (3) either as trends over time (as measured over a period of at least 5 years) or (4) in relation to climatic and environmental conditions in the Arctic (as measured over a period of at least 3 years). To determine which species are considered ‘Arctic species’, we used species lists as provided by the Arctic Biodiversity Assessment [35], with the exception that we only included bird species for which the majority or complete population breeds in the Arctic. We excluded papers that did not report species-specific results. Eventually this selection resulted in 32 papers. In addition to these papers, we added 35 relevant papers (matching the criteria mentioned above) that we found within reference lists of the 32 selected papers, as well as relevant papers found within the reference lists of two review studies on marine mammals [74,120].

For every paper, we recorded (1) the study species and taxonomic group (bird, ungulate, cetacean, pinniped, polar bear), (2) the region where the study was conducted, and (3) whether evidence was reported for shifts in timing of spring migration, reproduction and autumn migration and shifts in summering distribution. For shifts in timing, we considered evidence to be significant shifts in timing over years (considering study periods of at least 5 years) or with changing climatic variables. For shifts in distribution, we considered evidence to include both increases in the number of sightings (but only when evident that this was unrelated to population increase) as well as latitudinal change in observations [121]. We noted the rate of change in timing of spring and autumn migration (in days per year) when this was reported in studies.

In order to quantify how taxonomic groups differed in responses to changing climatic conditions, we compared the relative number of species per taxonomic group for

which shifts in migration and distribution were recorded. We quantified whether shifts in migration timing differed between taxonomic groups by comparing slopes of reported shifts in spring and autumn migration. In addition, comparing the number of species and study regions for which we found relevant studies allowed us to quantify how knowledge gaps differed between groups and regions.

4.2 Shifts in migration timing

4.2.1 Terrestrial and marine birds

Most of the time series available on migration timing of terrestrial birds show no clear advancements in the timing of migration departure from wintering areas [16,22,122–124]. However, in the last decades, some species of waterfowl and one shorebird have shown profound shifts in timing of departure [123,125–128], but these shifts appear mostly linked to changes in suitable stopover sites along their migratory route. At the same time, many terrestrial bird species have advanced timing of arrival in the Arctic, with studies showing species to adjust migration timing to annual variation in climatic conditions in the Arctic [16,22,129–131] and some studies also showing clear trends of advanced arrival over time [22,132–134]. While one study shows stronger shifts in advancement of arrival in short-distance migrants compared to long-distance migrants [133], other studies find no clear differences between short- and long-distance migrants [129]. Along with advancements in migration timing, some terrestrial bird species show advancements in the timing of reproduction [22,135–139], but this is not found for all species [11,140,141], and advancements in reproduction timing can lag behind advancements in arrival [16]. Trends in autumn migration are mixed, with some species showing delayed arrival in wintering grounds, associated with higher temperatures at northern summering and staging sites [126,142]. Several other species show earlier arrivals of adult birds [142,143], possibly explained by disrupted breeding seasons.

In contrast to many terrestrial bird species, less is known about changes in timing of migration in Arctic seabirds. For species for which data are available, advancements in migration timing are relatively small, with the exception of Arctic-breeding guillemots (*Uria* spp.) which have advanced arrival in breeding colonies all over the Arctic [144]. A large meta-analysis, that included many Arctic breeding seabirds, showed that seabirds in general have not adjusted their timing of reproduction in response

to higher sea-surface temperature [145]. In the Arctic, advancements in reproduction phenology over time have been found for surface-feeding species (gulls and tubenoses) in the Pacific ocean but not in the Atlantic ocean, while pursuit-diving species (alcids) showed no trends in either ocean [146]. While this may be the general pattern, some pursuit-diving and benthic-feeding species do show advancements in reproduction timing in response to local earlier ice break-up [147–149] and increases in air temperature [150]. We did not find studies reporting trends in timing of autumn migration in sea birds.

4.2.2 Ungulates

A variety of trends on reindeer migration timing emerge from the literature. A delay in spring migration over time was found for reindeer populations on Newfoundland up to the year 2000 [59], earlier spring departures but not earlier arrivals were shown for populations in Northern Quebec between 2000 and 2011 [151] and no trends in departure dates but earlier arrival were found for populations in north-western Canada and Alaska between 2000 and 2017 [23]. It is suggested that reindeer adjust departure dates and travel speed to local as well as large-scale climatic conditions [23], allowing them to pass through areas just prior to snowmelt [62], which facilitates easier passage over partly frozen soil and ice [152]. In addition, by pacing migration speed with local timing of snowmelt, reindeer may be able to optimally time their arrival on the calving grounds to match local dates of snow melt and vegetation green-up [23,62]. As a result, calving date has advanced in several populations of reindeer in response to a warming climate [153]. However, large variation exists in the extent to which reindeer appear to be able to keep up their timing of reproduction with the local climate. Domestic reindeer in Northern Finland have been able to advance timing of calving with earlier springs [154], which has benefitted reproductive success [155]. On the other hand, reindeer populations in Svalbard and Western Greenland do not seem to advance calving dates with earlier springs [15,156], and a mismatch with phenology of local forage plants has resulted in a reduction in reproductive success in Western Greenland [15,85,157,158]. While longer summer seasons could extend the summer period during which forage plants are available, reindeer have been found to advance autumn migration timing [59,151]. It is possible that such changes are a response to resource depletion, but it is yet unclear whether this is mainly driven by climate change or population dynamics.

4.2.3 Cetaceans

An increasing asynchrony between the arrival of migratory cetacean species and local abundance of prey (due to spatial and temporal shifts) has been predicted [71], but long-term data on the timing of migration of Arctic cetacean species is rare, and the few available studies paint a mixed picture [120]. Spring migration phenology shows either no change (beluga whales) or has been delayed (bowhead and grey whale), which could suggest that these species might not keep up with advancing phenology of their prey in the Arctic. In autumn, delays in departure from northern waters have been found for beluga whales, which appears to be a response to later ice formation [159]. However, further south along the migration route, migrating baleen whales are observed on autumn migration earlier in recent years [160].

4.2.4 Pinnipeds

The seasonal distribution of pinnipeds in the Arctic is heavily influenced by the spatial extent of the sea pack ice, which shows large seasonal and inter-annual variation. Most pinnipeds associate with the ice well before the breeding season, which means that ice regions need to be accessible at the onset of the breeding season and remain stable throughout the breeding period in order to be suitable [74]. Some species (e.g. ringed seals) breed on (more stable) fast-ice, as they have a relatively long nursing period (~ 6 weeks) [161,162]. In contrast, pinnipeds that rely on floating pack ice such as hooded seals generally have a shorter nursing period. Hooded seals breed several weeks later than harp seals, during the start of the seasonal ice break-up. To combat the effect of drift, their lactation period is extremely short (~ 4 days). Due to the strong association with sea pack ice, Arctic pinnipeds will be highly influenced by climatic changes in temperature. However, currently, little information is available about changes in phenology of pinnipeds in response to increasing temperatures and changes in ice cover [163]. We found only one study reporting on shifts in timing in pinnipeds, showing a long-term advancement in the arrival of walrus in their summering range, as observed by local Inuit hunters in the Canadian Arctic [29].

4.2.5 Polar bears

Although pinnipeds, the main prey of polar bears, have not been reported to display major shifts in phenology,

climate warming is strongly reducing the seasonal availability of pack ice [164,165], used by pinnipeds and polar bears as haul-out sites and foraging habitat, respectively. Polar bears time their migration towards terrestrial habitats with the break-up of pack ice in spring [166]. As a result, bears have advanced their arrival in terrestrial habitats with earlier ice break-up [78,165], as well as delayed the time when they travel back to the pack ice in winter, which also impacts their condition when entering maternity dens [167]. By shifting their migration timing, bears have increased the fasting period in terrestrial habitats during which they have no access to their pinniped prey [78]. In addition, due to reduced availability of pack ice, bears often have to travel longer distances on terrestrial habitats and swim larger distances in order to migrate back to the pack ice [75]. Longer fasting periods and higher travelling costs have been shown to cause reductions in population vital rates [75,79,168].

4.3 Changes in winter and summer distributions

4.3.1 Terrestrial and marine birds

Northward shifts in wintering distribution of Arctic migratory birds, also named ‘short-stopping’, have in the past decades been shown for multiple species of Arctic-breeding waterfowl and shorebirds [126,169–171]. For birds wintering in Europe, this mostly translates to shifts in a north-easterly direction up to 13 km/year (as reported for Bewick’s swans, 126). Changing energetic requirements and prey availability under different scenarios of future climate are also expected to affect the winter distributions of the five most numerous species of seabirds in the North Atlantic, many of which breed in the Arctic [172], but shifts in winter distributions have not yet been shown for these species.

The investigation of shifts in breeding distributions of Arctic species is in its infancy, but theoretical exercises predicting shifts in winter and summer ranges are contributing a basis for forecasting potential changes. Shifts in breeding distribution have been predicted for Arctic-breeding shorebirds [173] as well as for Arctic seabirds [174] given the northward shifts of their prey [175]. In this way, climate change may result in shifts in migration destinations and even flyways, for example the predicted establishment of wintering populations of little auks (*Alle alle*) in the Pacific, which would facilitate trans-Arctic migrations [174]. Likewise, Arctic seabirds may also cease migration completely and become year-round residents of

the Arctic. Nevertheless, so far there is little evidence that shifts in breeding distribution are already taking place. In part, this is because range shifts are typically picked up in long-term monitoring studies with high spatial coverage [176], which are rare in the Arctic. In Finland, an average northward shift of 0.8 km/year has been observed in a suite of Arctic bird species [24]. A long-term local study in Arctic Russia has revealed a strong decline in densities of typical high-Arctic breeding shorebird species, while species typical for southern tundra habitats have increased [177].

4.3.2 Ungulates

Reindeer have often been considered to display strong site fidelity, especially during the calving season in summer [178,179]. This idea of site fidelity is under discussion, as reindeer can shift their wintering ranges following overgrazing of pastures [180], and recently, two reindeer herds have started to adjust their calving grounds to annual variation in forage quality, moving further westwards into Alaska in earlier springs [25,181]. Similarly, moose in Alaska have shifted their summering ranges northwards following shrub encroachment in tundra habitats [182].

4.3.3 Cetaceans

For cetacean species, it is predicted that the ranges of 88% of all cetaceans may be affected due to global warming [183]. In accordance, northward shifts in distribution have been revealed for several migratory baleen whales, including typical southern Arctic species [184,185]. Also short-distance migrants, bowhead whales and beluga whales, are shifting their distributions within the Arctic, likely in response to changes in sea ice cover [186,187]. Killer whales (*Orcinus orca*) typically avoid heavy ice concentrations, and are increasingly occurring in the Arctic following reductions in sea ice cover which has opened up movement corridors [188,189]. The increase of this top predator might in turn influence the distribution of cetaceans and pinnipeds restricted to the Arctic. Sea ice reduction might also provide opportunities for cetacean species to move between the North Pacific and North Atlantic, as is supported by recent reports of grey whales in the Mediterranean Sea [190].

4.3.4 Pinnipeds

Most species of pinnipeds restricted to the Arctic are heavily reliant on sea ice for reproduction, moult and resting. During the winter months the sea ice connects to all landmasses surrounding the Arctic Ocean (i.e. Russia, Alaska, Canada, Greenland). However, as a result of climate change, the Arctic sea ice extent, as well as its thickness and age, have decreased [191], with the largest changes during the summer months. Currently, the summer sea ice only connects to the shallow waters of Greenland and Northern Canada [192], and, somewhere between 2030 and 2050, it is expected that the Arctic will be completely ice-free during summer [21,193]. Since most arctic pinnipeds are reliant on sea ice and generally feed in shallower (and coastal) waters, the distribution of sea ice relative to the coastal waters will likely have a main impact on the distribution of Arctic pinnipeds. Probably in a result to changing sea ice conditions, range shifts in pupping grounds have been shown for harp seals [194,195], as well as in summering distributions of harp seal, bearded seal and ringed seal around Svalbard, which show a northward latitudinal trend [121]. In addition, some species (e.g. walrus) are forced to haul-out on land more often in the absence of sea ice, and this may impose additional safety and energy expenditure costs [196], also considering density-dependent effects as fewer haul-out sites are available [197]. The disappearance of sea ice may also provide opportunities for the more temperate seal species that rely on land to rest, moult and reproduce, and these species, like harbour seals, which show an increase in numbers in the Arctic [121,198].

4.3.5 Polar bears

Following reductions in pack ice and earlier ice break-up, polar bears have been observed to have shifted their winter ranges northward [199–201]. Also, polar bears have shifted their maternity dens more often to terrestrial coastal areas rather than on pack ice, in response to absence of stable old ice [202]. In summer, available habitat on pack ice has contracted for several populations of polar bears [199,201], and the number of polar bears spending the summer in terrestrial habitats is increasing [203]. In some regions polar bears are able to cope with sea ice loss by making use of coastal seasonal ice [200]. However, the increasing distance between wintering habitats on pack ice and ter-

restrial summering habitats makes polar bears vulnerable to climate change [75,202].

4.4 Comparisons between species groups

4.4.1 Available data

Most of the studies that we found were on shifts in the timing of migration, while much fewer studies were available on changes in distribution (Figure 4A). Shifts in timing were more often studied for spring migrations and less often for autumn migrations. While terrestrial and marine birds, with data available for 46 out of 126 species, as well as ungulates and polar bear appeared to be well studied, much less studies were available for cetaceans and pinnipeds. Most studies originated from the American and Canadian Arctic, as well as from the Atlantic Arctic (Greenland and Svalbard) (Figure 4B). Much fewer studies were available for the European and West-Russian Arctic, and we found no studies reporting shifts in migration timing and distribution from the East-Russian Arctic.

4.4.2 Shifts in timing

Advancements in spring migration timing were reported for many terrestrial and marine birds, as well as for polar bear and some populations of reindeer, but less often for cetaceans and pinnipeds (Figure 4A). Although few studies were available, polar bears showed stronger advancements in spring migration timing compared to birds (Figure 4C). Unexpectedly, some cetacean species and populations of reindeer showed a delay in spring migration timing. Shifts in autumn migration timing also showed mixed results, with both delayed and advanced timing in birds and cetaceans, advancements in ungulates and a delay for one sub-population of polar bears (reported in one study, Figure 4C).

4.4.3 Shifts in distribution

Despite the low number of studies, it appears that a northward shift in distribution was found for relatively more species of both marine (cetaceans, pinnipeds and polar bear) and terrestrial mammals (ungulates) compared to bird species (Figure 4A).

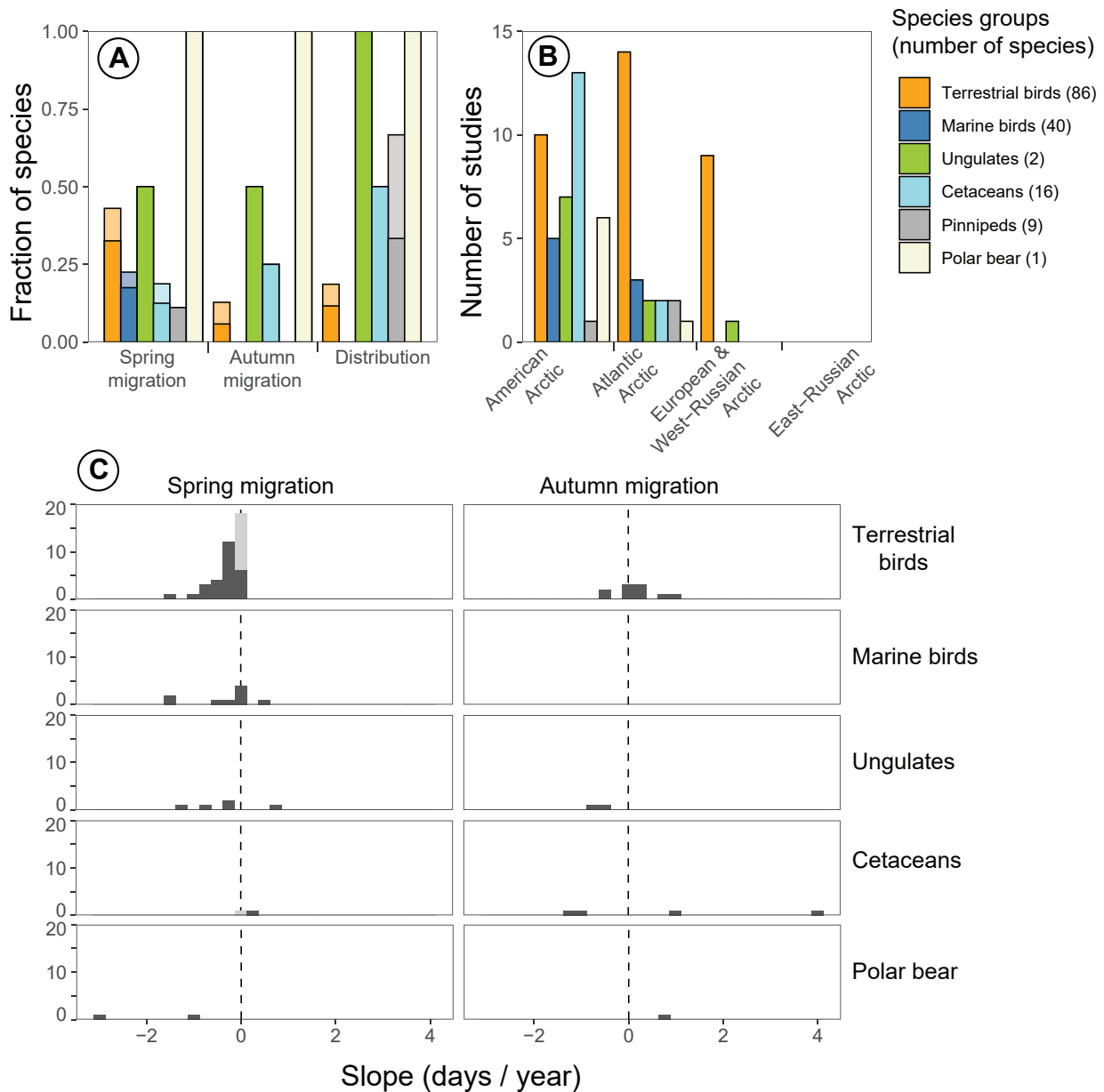


Figure 4: (A) The fraction of species per taxonomic group for which shifts in spring migration timing, autumn migration timing and distribution have been studied (light-coloured bars) and have been observed (dark-coloured bars). The total number of species for each group is noted in brackets in the legend. (B) The number of studies conducted within the four different geographic regions of the Arctic, shown per species group. (C) Histograms of reported trends in migration timing (as the slope in days of change over years), shown in bins of 0.25 as black bars. Grey bars show the number of studies reporting no change in migration timing over years without quantifying the slope. Histograms are shown for spring (left) and autumn migrations (right) and for terrestrial birds, sea birds, ungulates, cetaceans and polar bear. For pinnipeds no trends were reported.

5 Discussion

5.1 Shifts in timing

While many studies highlight the potential for trophic mismatches for Arctic migrants due to their inadequate

advancement of timing of arrival on their summering grounds in a warming climate [15,16,204], our review shows that there are many examples of advancement of migration timing of especially terrestrial Arctic-breeding birds, as well as for polar bears and some populations of ungulates. Advancements are observed both over long time spans (several decades) and in association with

changing environmental conditions, such as increasing temperatures and earlier snowmelt and ice break-up. This suggests that animals adjust their migration timing to locally changing conditions, either as they aim to match reproduction timing with local food abundance, or simply because warmer conditions allow [52,53], or even force, earlier migrations [78]. In comparison to most bird species, polar bears show especially rapid trends in migration timing, matching arrival and departure from pack ice with timing of ice freeze-up and break-up [78]. However, not all species show such flexible changes in timing, as shown by observations of multiple species at a single study site, showing advancements in reproduction timing in some species but not for others [139]. Differential responses in migration timing may also occur within species, which is notable in the differential migration timing for different reindeer populations. Whereas we had expected to find stronger shifts in migration timing for short-distance migrants (ungulates, pinnipeds, polar bear and some cetaceans) compared to long-distance migrants (birds and most cetaceans), we find large variation in both short- and long-distance migrants. Whether or not species and populations advance migration timing therefore likely depends on other factors as well, for example (1) variation in the environmental change that species experience, (2) strategies which animals use for reproduction, as well as (3) potential physiological constraints for making changes in the timing of migration. All these factors may differ between species. First, Arctic regions differ in the rate of climate warming and local response in for example advancement of resource abundance [205], date of snowmelt [135] or sea ice dynamics [159], which can drive differentiation in responses in migration timing. Second, flexibility in migration timing may depend on reproduction strategies, depending on whether animals reproduce in the Arctic or southern wintering grounds [159,160], or whether animals rely more on internal energy reserves or on local resources for successful reproduction [206–208]. Third, Arctic migrants may also be constrained to make advancements in timing by, for example, the time needed for fuel deposition [19,209], little potential to increase travel speed [17], a lack of relevant cues to time their migration [30], or physical barriers during migration, such as earlier ice break-up in rivers [152,210] or available light [119].

Our review suggests that few species of cetaceans and pinnipeds display shifts in migration timing. Admittedly, very few data appear to be available to test for shifts in timing [74,163], and it is therefore a possibility that the low number of observed shifts is caused by the difficulty in observing migration timing in these animals.

Moreover, a publication bias might exist where studies finding no shifts are less often published. In theory, shifts in timing for marine mammals could be constrained by their relatively low travel speed [18], but given the short migration distances of Arctic pinnipeds, this should not form a major constraint for many species. While climate warming changes the trophic interactions between marine mammals and their prey resources, changes in abundance and distribution of resources may have a larger effect on populations than changes in timing. Therefore, as a primary response to a warming climate, marine mammals may be more likely to display shifts in distribution. The same may hold for marine Arctic-breeding birds, for which we find less evidence for shifts in migration timing as compared to terrestrial birds.

5.2 Shifts in distribution

Shifts in distribution over the past decades appear to occur more often in marine mammals, which is in confirmation of our hypothesis. For cetaceans, pinnipeds and polar bears, relatively many species display northward distribution shifts, and it is likely that such shifts are a response to changes in sea ice cover [74] and associated shifts in suitable areas for feeding and reproduction. Most Arctic cetaceans and pinnipeds depend on high food abundance close to the edge of the pack ice, and as a result are expected to shift their ranges with retreating ice cover [186]. Moreover, pinnipeds also rely on sea ice as haul-out platforms for reproduction and moult, and their life-histories are strongly tied to sea ice [195]. The close association with pack ice is also evident for polar bears, for which a large extent of available data shows a combination of northward shifts in winter, matching changes in pack ice, and shifts to terrestrial habitats during summer. With longer stays in terrestrial habitats, an increasing number of bears is preying on eggs of waterfowl and seabirds [203,211], even though this prey is unlikely to compensate for the increasing periods of fasting under declining sea ice [212].

Our review suggests distribution shifts to be less evident for marine and terrestrial bird species. Although this could be explained by the rarity of long-term monitoring programmes with extensive cover, there are also ecological explanations. Marine birds, given observed distribution shifts of their prey [117], would be expected to show shifts in distribution, similar to marine mammals. Instead, observed shifts in diet show that some species of marine birds may cope with shifts in prey species distribution by preying on different resources [213–215]. While

such diet shifts may be a possibility for generalist species, like certain cetacean and pinniped species [216], species with a more specialized diet (e.g. planktivorous marine birds) may not be able to switch prey, and face potentially severe fitness impacts following shifts in prey species distribution, should they not be able to respond adequately by shifting their own distribution [217–219]. In addition, distribution shifts in marine birds are also potentially constrained by available habitat for their breeding colonies at higher latitudes.

For terrestrial bird species, our review suggests relatively few distribution shifts, which is possibly explained by adequate responses in migration timing, as well as no clear evidence for shifts in distribution ranges of prey resources. In addition, several terrestrial bird species have been shown to be rather flexible in choice of habitat within their current range [220] and their choice for prey species [221], which could also reduce the need for distribution shifts. For ungulates, several studies show shifts in calving grounds, presumably to locations with higher food abundance and more suitable habitats. Possibly, terrestrial ungulates possess such adaptive responses to changing conditions, as they continuously need to shift ranges in response to overgrazing events [210].

Remarkably, in the cases where shifts in distributions are observed, these often show sub-Arctic species extending their range into the Arctic, such as common seals, southern cetacean species, and shorebird species of southern tundra regions [74,177,198]. At the same time, shifts in distribution for species within the Arctic are less often observed.

5.3 Implications of inadequate shifts in timing and distribution

Many populations of Arctic migratory endothermic vertebrates appear able to shift their timing of migration and their distributions, yet not all species are making such shifts, nor do we know whether such shifts are in fact adequate responses to changes in distribution and abundance of food. As a result from inadequate responses in either the timing of migration and reproduction, or inadequate shifts in distribution, phenological mismatches between the period of offspring growth and timing of peak food abundance may arise. Such mismatches have been shown for several species of Arctic terrestrial birds [16,204], marine birds [149] and terrestrial ungulates [15], resulting in reductions in reproductive success. In temperate-breeding migratory songbirds, slow adjustments in migration timing have even been linked to population declines [222]

but see [223]. At the same time, not all species which show little change in timing of breeding and reproduction, experience mismatches with reductions in reproductive success (e.g. [11]). While generally, timing of food availability may advance in a warming Arctic, and more rapidly when compared with temperate regions [4,224], the rate of warming and the responses of prey species can strongly differ between regions [205]. Such regional differences could be an important explanation for the absence of shifts in timing and distribution of migratory species, rather than it reflecting suboptimal behaviour. Fitness consequences for Arctic migratory species may also arise from increased competition with sub-Arctic species, extending their ranges into the Arctic. However, northward shifts in distribution by some species originating from outside the Arctic circle may be constrained by the unique light environment at high latitudes [118,119], complicating forecasts of future ranges of birds and mammals in the Arctic. As such, it is difficult to predict whether or not migratory populations will suffer from reproductive consequences in a warming climate, based on whether populations are showing shifts in their migratory behaviour and distributions.

5.4 Future outlook

This review suggests the potential for many Arctic migratory animals to make shifts in the timing of migration and in their distribution in the Arctic, potentially allowing them to adequately respond to changed resource distribution in a warming Arctic. Yet, our review also highlights potential constraints for animals to make such shifts, which could eventually result in inadequate or no shifts, with possible negative effects on fitness. The potential for animal populations to make shifts in distribution and timing likely relies on the potential for making shifts in migration schedules and strategies, either by individual flexibility [127], or by changes in subsequent generations [225]. In the latter case, the ability of populations to shift in response to a warming climate is linked to its reproductive success under current conditions.

Our review also suggests a severe lack of data, limiting our ability to identify shifts in timing and distribution. Data are especially lacking for migration timing in cetaceans and pinnipeds, but also in other taxonomic groups potential shifts in timing and distribution have not been studied. It is striking that shifts in spring migration timing have received much more attention than shifts in autumn migration timing [226], and also there are relatively few studies on shifts in distribution. Our review also suggests strong regional differences in available data, with most

data available for Arctic vertebrates in Alaska, Northern Canada, Greenland, Svalbard and Scandinavia, and fewer data for the European and Russian Arctic. The need for long-term data collection over the entire Arctic region is well recognised [227], as advised in recent reports on population monitoring for marine as well as terrestrial monitoring [228,229]. Given the rate of climatic changes in the Arctic, it is likely that shifts in timing of migration and distribution of migratory animals will become more prominent. Better monitoring of migratory animals will allow an increased understanding of the responses of these animals to global warming, which may help to identify the possible limitations that restrict adaptations of animals to the globally changing conditions, and the potential impacts on their populations. Such data will be essential for the conservation of migratory species in a warming climate, as well as for the persistence of Indigenous and local human communities in the Arctic, which are often culturally and nutritionally dependent on the presence of migratory vertebrates [230].

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