Commentary

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Understanding the dynamics of Arctic animal migrations in a changing world

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Abstract: This is submitted as an introduction to the special collection on, "Arctic Migrations in a Changing World".

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Each summer, the Arctic is transformed by migration (Fig. 1). Millions of animals travel north on foot, by sea and by air for a season of sunlight, ample food, and reduced predation risk, often to breed and raise young. Animals that live and breed in the Arctic are uniquely adapted to do so [1, 2], and many species undertake energetically demanding journeys to benefit from seasonal resources in Arctic habitats (Fig. 2) [3]. Arctic migrations range in length from the "micro-migrations" of lemmings [Berteaux and Lai, this issue] to the global treks of Arctic terns [4]. Migration connects the Arctic to the rest of the world through the long-distance migrations of species that spend substantial portions of their annual life cycle in temperate or tropical regions, travel from freshwater to estuarine and marine habitats, and roam between linked Arctic and boreal landscapes [5, 6] [Carey et al.; Joly et al., both this issue]. In addition to playing a defining role in Arctic ecosystems, migratory species are embedded within the economy and culture of local and Indigenous communities in the Arctic [6].

The Arctic climate is characterized by the world's largest variability and trends in air temperature, a natural

phenomenon known as Arctic amplification [7]. Migrations represent key behavioral adaptations that allow animals to persist in such conditions [2]. Changing ice conditions in the region over seasonal and evolutionary timescales have led mobile species, including humans, to evolve long-distance dispersal [8] and seasonal migration routes [5, 9]. The region's extreme and variable climate also help explain the relatively low historical human disturbance in the Arctic, and the maintenance of the world's longest remaining terrestrial migrations, those of barren-ground caribou [10] [Joly et al., this issue]. However, due to Arctic amplification, anthropogenic warming in the region over the past 50 years is now three times the global average [11]. Arctic warming is predicted to continue even with aggressive global emissions reductions [12], and global efforts to mitigate warming by reducing the rate of anthropogenic greenhouse gas emissions have not yet even initiated its decline [13]. The region is thus experiencing rapid and profound ecological change [14]. Arctic fauna will be exposed to the impacts of a variety of warming-induced changes, including continued permafrost thaw and ice loss, with at least one virtually ice-free summer likely before 2050 [12], continued advancement of spring phenology [15], and new human infrastructure and disturbances [6]. Many Arctic animal species are considered particularly vulnerable due to the speed of warming, their dependence on ice and snow, and limited prior exposure to competitor and predator species, disease agents, and environmental contaminants that are expanding into the region [2, 6, 16]. Long-distance Arctic migrants are further affected by conditions in other regions in which they live or travel throughout the year, including harvesting, habitat loss, conservation efforts, shipping traffic, pesticide use, and coastal development [6].

Because adaptive evolutionary change via natural selection will be limited by the rapid speed of these environmental changes relative to the generation time of many Arctic vertebrates, a first and primary response is expected to arise through phenotypic plasticity, including changes in the phenology and range of individuals within their lifetimes [1, 2]. Migration, in its simplest form, is a means to track changes in seasonal food and resource availability,

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Figure 1. Animal occurrences within the Arctic Circle (above 66.5°N) from the Global Biodiversity Information Facility (GBIF) in winter (January–December) and summer (May–July) [46, 47]. Maps show animal density using a logarithmic scale, calculated as the number of occurrences within ~50-km-wide hexagonal grid cells (~2,600 km²) in winter (A) and summer (B), calculated using ‘dgggridR’ v3.0 in R v4.0.2 [48]. Graph (C) shows the proportional source for and number of species and occurrences in each season. The larger number of summer occurrences reflects the seasonal influx of animals and species, as well as a greater number of human observers. These illustrations also reflect geographic gaps and a negligible number of sensor-based measurements (included in “Other”) in contributions to GBIF. Individual tracking [35] and other remote observation methods [37–40] can help correct for the lack of human observers.

and the ability to migrate serves as a means for migratory animals to escape unfavorable environmental conditions, suggesting that migratory individuals might be well-suited to make such adjustments and thus relatively resilient to climate change [Joly et al., this issue]. However, migratory species vary in their lability in response to climate change [17], and Arctic animals can be sensitive to changing vegetation phenology [18], the introduction of new species expanding their range [19], habitat loss, and the impact of stressors prior to northward migration and breeding [6]. Further, with increasing temperatures and ice loss, some Arctic species could reach the limits of their plasticity and ability to adapt [20, 21].

The transformation of the Arctic raises countless questions about how migratory animals will respond. For example: What are the limits of behavioral responses,

such as range shifts, in responding to changing conditions? How will the breeding success of Arctic migrants be impacted by changes in other regions within their ranges? What species will migrate to and within the Arctic by the end of the century, and what cascading ecological and evolutionary ripple effects will result from new and extirpated migrations? Given the increasing impacts of climate change and human development in the Arctic, the goal of this special issue is to summarize our understanding of Arctic migrations, learn how migratory Arctic species are coping or adjusting under current conditions, and identify information gaps as well as opportunities to improve research and conservation efforts. Our hope for this issue is to offer context and paths forward for understanding Arctic migrations and their role in unfolding regional and global changes.

Figure 2. Photographs of terrestrial migrants featured in this special issue in the seasonal environments that they inhabit and that motivate seasonal migrations, from the lush landscape and midnight sun of summer to the snow and ice of winter. Photos at top from left to right show the seasonal camouflage of the Arctic fox (*Vulpes lagopus*) in summer, during the changing season, and in winter. Arctic foxes exhibit morphological changes and a variety of migratory behaviors, adaptations to Arctic conditions (Berteaux and Lai, this issue). Photos at bottom from left to right show caribou (*Rangifer tarandus*) during fall and spring migration, respectively, and a polar bear (*Ursus maritimus*) walking on sea ice. Caribou make the longest terrestrial migrations in the world [10] and can adjust whether and along which route to migrate in response to local conditions if allowed free passage, but complex impacts of climate change and human development in the region make the future of these migrations hard to predict (Joly et al., this issue). While polar bears have shifted their range and migration timing in response to reduced pack ice, like other ice-obligate migratory species, they are vulnerable to continued Arctic warming (Lameris et al., this issue). Changes in water phase between liquid (water) and solid (snow and ice) define the ability for animals to move in the Arctic (Berteaux and Lai; Carey et al., both this issue). Photo credits, in order of description above: Charlotte Dupont (flickr, licensed with CC BY-NC-ND 2.0), Dominique Berteaux (author in issue), Steve Sayles (flickr, licensed with CC BY-NC-ND 2.0), Kyle Joly (both caribou pictures, author in this issue) and Mario Hoppmann (flickr, licensed with CC BY 2.0).

The nine articles in this issue can be broken out into two broad research approaches: reports and analysis of new migration and occurrence data, and synthesis assessments. The first set of articles uncover previously undocumented components of migratory routes [Baak et al., A; Baak et al., B; Gutowsky et al.; Hagelin et al., all this issue] and evidence of potential species range expansions [McNicholl et al., this issue], together documenting new or noteworthy occurrence data for twelve species. The second set provides cross-species assessments of migratory behavior in fish [Carey et al., this issue], terrestrial mammals [Berteaux and Lai, this issue], and vertebrates [Lameris et al., this issue] and a cross-population assessment of caribou and reindeer [Joly et al., this issue]. Taken together, this issue enables discovery and comparison of migration strategies and possible adaptive and plastic behaviors across avian, freshwater, marine, and terres-

trial species, and indicates common threads of guidance for future work.

This issue also highlights the application of a range of research methods (Fig. 3). Studies document avian migration tracking using Global Positioning System (GPS) loggers [Baak et al., B; Hagelin et al., both this issue], light-level geolocation (global location sensors, GLS) [Baak et al., A, Baak et al., B; Hagelin et al., all this issue], and satellite telemetry [Gutowsky et al., this issue]. Hagelin et al. [this issue] further share a new analytical method for identifying key stopover regions that accounts for the high uncertainty in locations estimated through solar geolocation, as well as recommendations for animal capture and device attachment. McNicholl et al. [this issue] identify and confirm novel species occurrences reported through a government monitoring program, a community observation network, and local media reports. Finally, the review

Figure 3. Photographs of migratory avian (top) and aquatic (bottom) species featured or discussed in this issue. Many avian, fish, pinniped and cetacean species migrate in and out of the Arctic each year in response to seasonal changes in habitat and resources (Lameris et al., this issue). Photos from top to bottom, left to right, show an olive-sided flycatcher (*Contopus cooperi*) wearing an archival light-level geolocator (GLS logger) (Hagelin et al., this issue), Sabine's gull (*Xema sabini*; Gutowsky et al., this issue), glaucous gulls (*Larus hyperboreus*) with GLS loggers attached to leg bands (Baak et al., this issue, B), herring gulls (*Larus argentatus*; Baak et al., this issue, A), pink salmon (*Oncorhynchus gorbuscha*; McNicholl et al., this issue), a ribbon seal equipped with a satellite transmitter (*Histriophoca fasciata*) and Dolly Varden (*Salvelinus malma*; Carey et al., this issue). Tracking technology can provide key information about animal behavior and distribution, and is used by several papers in this issue to add to our knowledge of the annual distribution and migration routes of Arctic-breeding birds. Community engagement complements technological innovation, for example by documenting rare species occurrences in the Arctic (McNicholl et al., this issue). These data record the profound change occurring in the Arctic and should be archived in repositories to become discoverable for future use and collaboration. Photo credits, in order of description above: Julie Hagelin (author in issue), Mark Mallory (author in issue), Sarah Poole (from work reported in issue), Corine Bliet (flickr, licensed with CC BY-NC 2.0), Nicole Beaulac (flickr, CC BY-NC-ND 2.0), Michelle Barbieri (flickr, licensed with CC BY-NC-ND 2.0) and Randy Brown (author in issue).

by Lameris et al. [this issue] originated in essays for a Masters' course, allowing this comprehensive assessment to cover a tremendous volume of literature and providing students with an experience in collaborative writing. Here we will summarize the novel results of the articles contributed to this special collection, focusing on three main themes: (1) identifying life cycle components of Arctic migrants, (2) population variability and individual plasticity as possible means for these species to respond to environmental change, and (3) impacts of changing species interactions. We conclude by highlighting information needed to direct conservation and management decisions and finally address ways in which to move the field of Arctic migration ecology forward.

Identifying previously unknown life cycle components. For long-distance migrants, the impacts of climate change on animal ecology are easy to miss when we lack basic information about species' distribution, resource use, and challenges throughout their annual cycle [22]. Animal-borne sensors and communications systems allow tracking the migrations of individual animals by logging and/or transmitting data using a variety of technologies that allow researchers to optimize sensor capac-

ity and size for a given species and purpose [23]. Field and analytical methods using animal-borne sensors allow researchers to uncover the distribution, migratory connectivity, and habitat use of migratory species, and can provide insight into fine-scale movements and impacts of climate change throughout the annual cycle [Berteaux and Lai, this issue]. Several papers in this issue report the use of these methods to document stopover locations, migratory routes, and non-breeding areas of long-distance avian migrants. Baak et al. [this issue, A] provide detailed accounts of the movement of Arctic-breeding herring gulls (*Larus smithsonianus*), demonstrating marked differences between individuals in migration routes and the location, duration, and use of stopovers, and confirm the Great Lakes as an overwintering site for some individuals from this population. Hagelin et al. [this issue] provide the first report of the annual life cycle for the olive-sided flycatcher (*Contopus cooperi*), a passerine landbird experiencing widespread population declines, and quantify the intensity of habitat use to define and identify critical stopover sites from geolocation data. GPS and GLS tags deployed on glaucous gulls (*Larus hyperboreus*) provide the first evidence of migration timing and habitat use

outside the breeding period for these seabirds, indicating use of the same three migration corridors in the fall and winter, moderate consistency in the use of overwintering areas, and two primary overwintering strategies associated with pelagic and coastal habitats, noting that the use of pelagic environments in this species are underreported by other sources of occurrence data [Baak et al., this issue, B]. Finally, tracking of Sabine's gulls (*Xema sabini*) using geolocation documents the full annual journeys of birds from a breeding colony in the Canadian High Arctic and confirmed an overland flight path to Hudson Bay during their northward migration [Gutowsky et al., this issue]. Identifying new life cycle components, such as those reported here, can provide a baseline and "jumping off point" for long-term studies to identify how climatic changes are impacting the distribution of migratory species, the timing of their migrations, possible influences on population size and breeding success in the Arctic, and optimal conservation measures [24].

Documenting variation and plasticity. Among-individual variation and within-individual plasticity will impact whether and how species adapt their migratory behavior to changing conditions in the Arctic. Changes in migration dynamics are widely recognized as one way that migratory species are responding to recent climate change [24, 25], and authors in this collection further demonstrate many species' ability to make phenological and distributional shifts in response to environmental change. In their review, Lameris et al. [this issue] provide a detailed overview of hypothesized and documented responses to advancing spring phenology and longer summer seasons in the Arctic through shifts in distribution and migration timing across migratory vertebrate species. They predict that marine animals will show stronger shifts in distribution shifts, while terrestrial animals will instead shift migration timing, because northward distribution shifts are constrained by a lack of suitable habitat. They find evidence supporting both predictions, but with considerable variation among and within species. In the trans-equatorial migrations of the Sabine's gull (*Xema sabini*), Gutowsky et al. [this issue] report individual plasticity in many aspects of migration, including schedules, routes, and duration of stopovers. However, all tracked birds showed reliance on a shared staging ground, and amongst tagged birds, gulls had high fidelity and similar-duration use of stopover sites within years, suggesting that within a year, individuals are adjusting migration dynamics based on perceived environmental conditions and/or conspecific cueing. In their analysis of migrations of the olive-sided flycatcher (*Contopus cooperi*), Hagelin et al. [this issue] found that birds appeared to adjust their

migration speed to account for longer breeding periods, indicating physiological plasticity. Berteaux and Lai [this issue] find that facultative and partial migration appear to be common in Arctic terrestrial mammals, indicating individual behavioral flexibility in deciding whether and when to migrate. In their review of migration in caribou and reindeer (*Rangifer tarandus*), which occur in multiple biomes from temperate forests to polar deserts, Joly et al. [this issue] exemplify this finding, describing this species' remarkable range in migratory behavior and behavioral plasticity, including the ability to alter distribution. We also see flexible adjustments to environmental cues within the Arctic aquatic environment. Carey et al. [this issue] identify an amphidromous life-history strategy—in which fish migrate between fresh and saltwater for purposes other than spawning—as a successful means to cope with the challenges of living in Arctic waters and predict that salmonid migration phenologies will likely be able to adapt to climate change by responding to local environmental cues. The Dolly Varden (*Salvelinus malma*) in particular exhibits considerable within-population variability in migration behaviors such as partial migration and migration within and between freshwater, estuarine and marine waters, indicating an ability to shift distributions with further Arctic warming and perhaps making them relatively robust to changes in climate. Using monitoring programs and community observation networks, McNicholl et al. [this issue] identified occurrences of six other species of marine fishes outside of their known distributions, concluding that those of pink salmon (*Oncorhynchus gorbuscha*) and broad whitefish (*Coregonus nasus*) are likely experiencing range expansions due to changing environmental conditions. While these articles show evidence of plasticity and variability in the movement behavior of many Arctic migrant species, ultimately, the possibility for species to respond to continued Arctic warming is subject to constraints that pose hard limits to possible shifts in migration timing and distributions. Authors report many examples of such constraints, including human infrastructure [Joly et al., this issue]; presence of suitable marine, coastal, or terrestrial habitat [Lameris et al., this issue]; and, critically, changes to the cryosphere and hydrology [Berteaux and Lai; Carey et al.; Lameris et al., all this issue].

Understanding species interactions within and across trophic levels. While not directly measured by many studies of Arctic migrations, the possibility of changes in phenological synchrony among species that lead to negative fitness consequences [18, 22, 26, 27], altered predator-prey relationships [28], and the introduction of parasites, pathogens, competitors and pred-

ators as species migrate north [1, 19] pose challenges to Arctic migrants [2, 16] that are discussed by papers in this issue. As the Arctic spring advances [15], the availability and biomass of food resources for many species will peak sooner and extend over a longer period [Lameris et al., this issue]. For example, earlier melting of snow has been shown to trigger earlier emergence of arthropods, small rodents, phytoplankton blooms, and exposure of lichens, impacting the availability of nutrients and prey for many species of shorebirds, passerines, terrestrial mammals, and the Arctic marine food web [Lameris et al.; Joly et al., both this issue]. An extension of the growing and breeding seasons might be beneficial for some prey species (Joly et al., this issue), and the related changes in snow and ice conditions can provide environmental cues to trigger movements in response to changing resource availability (Berteaux and Lai, this issue). It might also lead to delayed or reduced migration, a decline in food quality, new inter-species competition, disease pressure, or other unforeseen impacts down the line [29, 30] [Joly et al., this issue]. In marine environments in particular, northward distribution shifts [19] are expected to introduce new predator species to the Arctic and change the distribution of food resources, which will affect habitat suitability and the costs and benefits of migration [Carey et al.; Lameris et al., both this issue]. Changes in the synchronicity of predator presence and prey availability will also influence migrations and foraging patterns of aquatic species [31] [Carey et al., this issue]. Changing prey distribution is proposed as a possible explanation for the likely range expansion of pink salmon and broad whitefish found by McNicholl et al. [this issue] and use of a more northerly wintering site by individual glaucous gulls in a year of low sea ice documented by Baak et al. [this issue, B]. Broadly, it is possible that migrant phenology will adjust to match climate change or that long- versus shorter-distance migrants might be impacted differently [Carey et al.; Lameris et al., both this issue]. For long-distance migrants, accelerated warming at high latitudes compared to lower-latitude habitats could make it more difficult to maintain arrival timing matched to suitable breeding conditions [Hagelin et al., this issue]. To understand how climate change will impact phenology in the Arctic, further research is needed to describe, manipulate, and model the distribution and timing of key food resources for these species [Joly et al., this issue].

Future work. While needs for future research and conservation efforts are often specific to species and habitats, the articles in this issue identify several overlapping areas for future study. The availability of a large literature, including this special issue, devoted to migratory Arctic

species can mask our gaps in basic information: overall trends in population size and distribution are unknown for most marine mammal stocks [32]; many avian and terrestrial animal populations [33, 34]; as well as herpetofauna, fish and invertebrate species [6]. In their review of terrestrial mammal migration, Berteaux and Lai [this issue] conclude that we do not yet know whether nearly half of Arctic terrestrial mammal species exhibit migratory behavior. Authors also point to missing behavioral information that is difficult to obtain for many species with current methods, including movements and habitat use of juveniles [Baak et al., B; Carey et al., all this issue], non-breeding individuals [Baak et al., this issue, B], and non-commercial coastal fish species [McNicholl et al., this issue], and raise the possibility of publication bias, i.e., that studies failing to demonstrate climate-induced changes are less likely to be published [Lameris et al., this issue]. This lack of baseline data and context means we cannot with certainty identify whether and how many Arctic species have begun to shift the timing or destinations of their migrations, or the possible impacts of shifts on fitness or ecosystem dynamics. One recurring recommendation is for long-term research and monitoring programs [Baak et al., A; Lameris et al., both this issue] that can offer coordinated and adaptive data collection [33]. Large and long-term datasets can provide uniquely valuable evidence of changes and their relationship to climate [35] and fitness [22]. Ecosystem-based biodiversity monitoring plans developed for the Arctic Council—the leading inter-governmental forum for addressing common issues facing the Arctic—offer an international framework for planning, executing, and applying the results of long-term research and monitoring efforts. Such programs can incorporate the study of migration routes and phenology with measures of reproductive success, habitat, and interactions across scales and trophic levels to identify and predict changes as well as their causes [33].

Opportunities to improve our understanding of Arctic migrations and apply this knowledge to conserve species include strategies focused on both technology and people. In the case of technology, the use of bio-logging techniques, such as those reported in this issue [Baak et al., A; Baak et al., B; Gutowsky et al.; Hagelin et al., all this issue], provide crucial documentation of the presence, migratory movements and behavior of animals, particularly in Arctic habitats, where in-situ sensor networks and observations through app-based citizen science programs like eBird and iNaturalist are sparse or non-existent over large regions (Fig. 1). Bio-logging sensors can also measure the environments through which animals are moving, serving as a perhaps underutilized source of envi-

ronmental remote sensing data [36]. Bioacoustic networks [37, 38], drones [39], and eDNA [40] offer additional emerging technologies with the potential to remotely monitor species presence in marine and terrestrial Arctic habitats. Human-focused strategies include establishing formal and informal community networks, including citizen science and community-based monitoring programs, which can support research and conservation while also building public trust and interest in these efforts. The biodiversity working group of the Arctic Council reports a need to develop both local and global networks in order to integrate local knowledge and interests and coordinate efforts addressing long-distance migrants [6]. Collaborations with local and Indigenous communities can improve knowledge about distributions and rare occurrences, such as those found by McNicholl et al. [this issue], and better document local activities such as harvesting [32]. Local partnerships can also allow studies to continue when scientists from outside the region are not present, for example to enable monitoring during winter, when less field research takes place [Berteaux and Lai, this issue] (Fig. 1). Such partnerships allowed research projects to continue despite delays and travel restrictions caused by the Covid-19 pandemic [11].

There is promise in research and management strategies that combine technology and partnerships within programs for monitoring, research, and wildlife management. One example is the SEATRACK project, through which researchers from 10 countries are coordinating studies of the non-breeding distribution of seabird species that breed in the North Atlantic, enabling region-wide data collection using shared protocols [41]. Through sensor networks with automated data transmission and active community partnerships, near-real-time communication offers possibilities for dynamic management [42] and identifying signals of tipping points or changes in distribution to allow for faster identification and targeted responses. Through partnerships and networks, we can compile existing historical data and perhaps uncover hidden information from prior years that exists as traditional knowledge; records from government, recreational, and commercial sources; unpublished research on biologists' hard drives [43]; or social media posts. Such efforts can be augmented by technology resources such as shared data platforms [35] and machine learning techniques [44, 45].

The extent and speed of change in the Arctic may require rethinking common goals and assumptions of ecological research and wildlife management. The impact of efforts undertaken by ecologists and wildlife managers will depend on that of global efforts to address the root

causes of anthropogenic climate change and biodiversity loss. Many research studies completed today will not be replicable decades from now due to fundamentally altered or extirpated habitats, ecosystem dynamics, and movement patterns. Goals to preserve discrete animal populations or migration routes may become efforts to minimize extinctions by supporting those that can adapt and persist in the new Arctic. As species begin to enter and migrate to the Arctic, some will become established species that may themselves be the subject of conservation efforts. Given this uncertainty, we have a particular obligation to preserve knowledge of Arctic migrations, such as that presented in this issue, and the data that underlie reported as well as unpublished findings. Animal migration data and data compiled through community-based monitoring and citizen science networks, if archived and made discoverable for future use [35], can serve as a critical reference point for future generations of researchers, residents of the region, and the public, and leave a record of the Arctic as we now know it. The novel findings presented in the research, commentary and review articles included in this special issue offer a broad contribution to the knowledge base on Arctic animal ecology. We hope that ideas presented in this issue will also motivate new contributions to the field to understand the unfolding impacts of climate change on migratory Arctic species and develop novel conservation strategies to protect these charismatic and ecologically important species.

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