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Opinion

Animal migration to northern latitudes: environmental changes and increasing threats

Vojtěch Kubelka,[1,2,3,4,*] Brett K. Sandercock,[5] Tamás Székely,[3,6] and Robert P. Freckleton[1,*]

Every year, many wild animals undertake long-distance migration to breed in the north, taking advantage of seasonally high pulses in food supply, fewer parasites, and lower predation pressure in comparison with equatorial latitudes. Growing evidence suggests that climate-change-induced phenological mismatches have reduced food availability. Furthermore, novel pathogens and parasites are spreading northwards, and nest or offspring predation has increased at many Arctic and northern temperate locations. Altered trophic interactions have decreased the reproductive success and survival of migratory animals. Reduced advantages for long-distance migration have potentially serious consequences for community structure and ecosystem function. Changes in the benefits of migration need to be integrated into projections of population and ecosystem dynamics and targeted by innovative conservation actions.

Highlights

Population declines have been greater among migratory species because of their vulnerability to climate change and human pressure. Growing concerns for migratory animals necessitate new assessments of the outcome of environmental changes for species that rely on long-distance migration to the north.

A growing body of evidence suggests that northern temperate and Arctic animals are currently experiencing lower food supply and availability, higher pathogen and parasite pressure, as well as increased predation rates, compared with previous decades.

We hypothesise that the natural advantages of migration to northern latitudes are being eroded. Understanding the underlying mechanisms of ecological impacts will allow better forecasting and mitigation, as well as insights into consequences for population dynamics of migratory animals.

The northward migration

Each year numerous wild animals migrate to Arctic or North temperate **breeding grounds** (see Glossary). Migratory taxa include mammals, insects and, notably, many birds [1,2] (Figure 1 and Figure S1 in the supplemental information online), but the evolution and ecological implications of migratory behaviour are still not fully understood [1,3,4]. For such extensive, costly and dangerous behaviour to evolve, the benefits must be considerable [5,6]. Breeding at higher latitudes is assumed to have several advantages that outweigh the physiological costs and mortality risk connected with **migration**. Major benefits include (i) seasonal pulses of food supplies and long days for foraging [1,7], (ii) low prevalence of pathogens and parasites [8,9], and (iii) reduced predation pressure in comparison with southern areas [10,11].

Currently, many populations of terrestrial animals undertaking **long-distance migration** are threatened, declining in numbers, and performing worse than their resident counterparts [12–15]. Changes along **migratory routes**, especially habitat loss or deterioration, or disturbance and persecution on nonbreeding areas, **stopover and staging sites** have already received considerable attention and are now well-recognised drivers of population declines through reductions in adult survival [12,16,17]. But here, we suggest that the recent declines are also driven, in part, by deterioration in the ecological quality of northern temperate and Arctic breeding grounds. Breeding grounds have received less attention because they are often remote or inaccessible areas with less anthropogenic activity. Here, we highlight recently documented impacts on ecological outcomes following long-distance migration in a range of terrestrial animals (Figures 2 and 3 and Table 1).

In forecasting the impacts of future threats, the spatial and temporal extents of possible changes are critical factors (Figure 3). For example, disturbances such as storms or temporary mismatch with food resources may be individually relatively brief **acute stressors (pulses)** leading to short impacts and fast recovery (Figure 3A). By contrast, long-term **chronic stressors (presses)**,

[1]School of Biosciences, University of Sheffield, Alfred Denny Building, Western Bank, Sheffield S10 2TN, UK
[2]Department of Zoology and Centre for Polar Ecology, Faculty of Science, University of South Bohemia, Branišovská 1760, České Budějovice, 370 05, Czech Republic
[3]Department of Evolutionary Zoology and Human Biology, Faculty of Science, University of Debrecen, Egyetem tér 1, Debrecen, Hungary
[4]Department of Biodiversity Research, Global Change Research Institute, Czech Academy of Sciences, Bělidla 986/4a, Brno, 603 00, Czech Republic
[5]Department of Terrestrial Ecology, Norwegian Institute for Nature Research, Høgskoleringen 9, Trondheim, 7485, Norway
[6]Milner Centre for Evolution, University of Bath, Claverton Down, Bath BA2 7AY, UK

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*Correspondence:
kubelkav@gmail.com (V. Kubelka) and
r.freckleton@sheffield.ac.uk
(R.P. Freckleton).

such as changes in ambient CO_2 and temperature, are slower directional changes occurring over periods of decades [18] (Figure 3B). Acute and chronic stressors create a continuum: for instance, repeated pulses due to increasing frequency of storms or predation pressure can also act as presses. Moreover, once chronic stressors exceed a threshold, the state of an entire system can change, leading to population extinction or regime shift (Figure 3B). Similarly, characterizing the spatial extent of impacts is important (Figure 3C), because the scale over which changes occur determines not just the extent of impacts but also the feasibility of conservation efforts.

Here, we review and discuss factors that appear to be driving reduced profitability of northward breeding grounds for different groups of migrating animals (Figures 2 and 3, Table 1). We argue that various ongoing environmental changes are resulting in large-scale chronic stressors degrading habitats, emphasising needs for targeted conservation actions.

Evidence for reduced benefits of animal migration

Food supply

Recent climate change has affected food supplies and their seasonal availability in northern latitudes [19,20]. To successfully exploit short-term peaks of food abundance, reproduction of higher trophic levels needs to be synchronised with relevant periods of plant phenology or insect emergence [21]. However, mismatches are well recognised, and have been documented for various taxa [19,22]. The phenomenon is termed **trophic/phenological mismatch** and can occur at various scales (Figure 2 and Table 1).

Phenological mismatch alone may not necessarily lead to detrimental fitness consequences. If minimum food requirements are still met, young can grow and survive, even if food abundance is not at its peak [23,24]. Global warming usually advances the plant-growing season and the peak of arthropod abundance (Table 1), but the number of days with an adequate food supply may be unchanged [7,25]. Local and temporary mismatches represent acute stressors, whereas continuous imbalance between reproduction timing and food availability may result in long-term and large-scale chronic stressors affecting the entire ecosystem (Figure 3).

The number and intensity of summer storms is increasing [26]. Arthropod availability for insectivorous migrants is reduced during inclement weather events [21,25], and may reduce the availability of food during critical windows during the offspring-rearing period, increasing the probabilities of abandonment and mortality of young [21]. By contrast, for herbivorous migrants such as caribou and geese, climate warming may increase available plant biomass during the brood-rearing period in summer [17,27]. However, it is possible that increasing plant biomass may not be sufficient to negate the consequences of phenological mismatch [27]. Predatory long-distance migrants, such as skuas (*Stercorarius* spp.) can be negatively affected by long-term chronic stressors at breeding grounds due to ongoing shortages in the abundance of prey species, as well as increased competition with other predators [28].

Pathogens and parasites

The prevalence of disease agents was historically low in boreal and Arctic regions, because the pathogens are typically unable to complete their life cycle in harsh environments, as well as because of a limited number of suitable vectors [8,9]. There is now evidence that a variety of pathogens, parasites and their vectors have shown poleward shifts in their distributions. Emerging diseases are consistent with earlier projections based on impacts of global warming [29,30] and novel pathogens represent an increasing threat for wildlife at high latitudes [31–33] (Figures 2 and 3 and Table 1). Examples include acute stressors, such as avian cholera outbreaks in the Canadian Arctic leading to mortality of common eiders (*Somateria mollissima*) [34] or an extensive and rapid mass mortality event at calving grounds of saiga antelopes (*Saiga tatarica*) in Central Kazakhstan caused by haemorrhagic septicaemia following unusually high temperatures and humidity in the region [35,36]. New pathogens and parasites invading northern latitudes including helminths of mammals and birds represent chronic stressors for migrating animals (Figures 2 and 3 and Table 1). Migratory birds or bats are also important because they transport non-native pathogens. For example, the *Plasmodium* causing avian malaria is now able to complete the transmission cycle in the Arctic [37].

Predation

In general, predation pressure appears to be increasing for Arctic and northern temperate wildlife (Figure 2 and Table 1). The impacts range from acute to chronic stressors, both at various spatial scales (Figure 3), creating novel predator–prey interactions [38]. Historically, predation pressure has been thought to decline from the tropics towards the poles [10,11,39]. However, climatically induced rapid alterations in boreal and the Arctic ecosystems, including changes in predator numbers and predator guild composition, have been predicted to induce increased predation

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Figure 1. Examples of migratory terrestrial animals with recently reduced long-distance migration benefits. Clockwise from top left: Arctic tern *Sterna paradisaea*; chicks and eggs of American golden plover *Pluvialis dominica*; semipalmated plover *Charadrius semipalmatus* in distraction display; Arctic skua *Stercorarius parasiticus* incubating a clutch; saiga antelope *Saiga tatarica* family (photo by Navinder Singh); monarch butterfly *Danaus plexippus*; resting caribou *Rangifer tarandus* (photo by Robert McCaw); flying common green darner *Anax junius* (photo by Peter Chen, Wikimedia Commons); and hunting eastern red bat *Lasiurus borealis* (centre, photo by Michael Durham). All other photos by Vojtěch Kubelka. See also Figure S1 in the supplemental information online. Note that the pool of long-distance terrestrial migrants travelling more than 1000 km to northern temperate and Arctic breeding grounds includes numerous birds (800+ long-distance migrants, mostly insectivorous or herbivorous and some predatory species), some well-studied species of insects (~12+ species, dragonflies, butterflies, and moths) and a few species of mammals (~5+ species, bats, caribou, and saiga antelope).

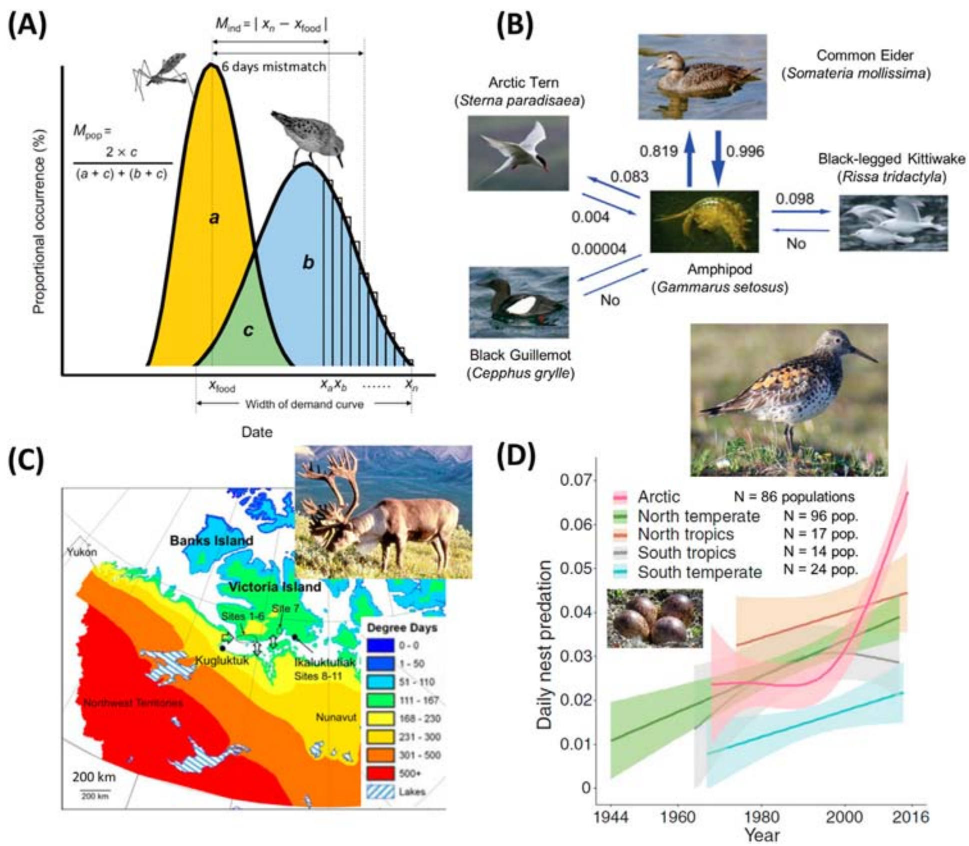

Figure 2. Novel emerging threats for migratory animals at northern latitudes. Selected examples from Table 1. (A) Food supply and trophic mismatch. Mean values (+6 days on average from a range -20 to +22 days range) of individual-nest-level mismatch between food (insect) abundance peak and chick food demand peak for six shorebird species across the North American Arctic. Modified from [24]. (B) Novel host–parasite interactions. Circulation and transmission rates of the acanthocephalan *Polymorphus phippsi* and the main host, common eider *Somateria mollissima*. The host–parasite network has recently expanded and the parasite has colonised new avian host species of seabirds, starting with low infection rates. Modified from [33]. (C) Geographic expansion of parasites. Continuous degree-day surface map showing accumulation of degree-days for the development of protostrongylid lungworm *Umingmakstrongylus pallikuukensis* from first larvae (L1) to infective third (L3) stage. From 2000 to 2006, development from L1 to L3 (167 degree-days accumulated) could occur in a single summer on Southwestern Victoria Island whereas previously conditions were unsuitable. Protostrongylids parasitize caribou *Rangifer tarandus* (depicted, photo by Dean Biggins, Wikimedia Commons). Modified from [75]. (D) Temporal increase in nest predation. Nest predation rates for 237 populations of 111 shorebird species worldwide, divided according to five latitudinal areas. Generalized additive model fits with 95% confidence intervals. Adult and eggs of great knot *Calidris tenuirostris* are depicted (photos by Vojtěch Kubelka). Modified from [45].

pressure on breeding birds [21,40,41] and such changes have been recently detected (Figure 2 and Table 1).

In some Arctic regions, climate-change-induced damping of the population cycles and abundance of lemmings and voles [42–44] may have influenced the behaviour of predators that consume nests and chicks of birds as alternative prey [21,45]. For example, loss of lemming cycles may be a factor limiting breeding productivity and population size of brant geese *Branta bernicla* [46]. Elevated nest predation rates have also been reported in temperate Europe [45,47], together with changes in cyclicity and lower abundances of voles [48,49], and similar ecological mechanisms may occur in both northern temperate and Arctic regions [50].

Glossary

Acute stressors (pulses): abrupt changes in ecological parameters; for example, food/prey abundance or pathogens pressure, following (mis)match in the given year or disease outbreak. This stressing event is changing the environment temporally, returning (pulsing) back to original state.

Breeding grounds: specific locations within the species breeding distribution range used for reproduction. For long-distance migrants, breeding grounds are often separated from nonbreeding areas which include migration routes with stopover sites, staging sites and wintering grounds.

Chronic stressors (presses): gradual and directional changes in ecological parameters, persisting stress impacting ecosystems at a longer temporal scale, not returning to the original state, such as increased predation pressure over the years, loss of alternative prey and food web alterations or loss of permafrost/sea ice.

Ecological traps and degraded environments: ecological traps emerge when organisms make settlement decisions in a given location based on cues that were correlated formerly with habitat quality in a situation when better habitat alternatives are available nearby. The use of unreliable cues can lead to reduced reproductive output. By contrast to ecological traps, if there are no suitable alternatives in the surrounding area, then the entire landscape represents a degraded environment, with negative consequences for the population dynamics of species settling in the area.

Long-distance migration: migration when animals of the given species migrate regularly over 1000 km between breeding and wintering grounds.

Migration: seasonal movements of individual animals or whole populations between breeding and wintering grounds.

Migratory routes: geographic routes along which animals migrate; for birds they are usually referred to as flyways.

Stopover and staging sites: important locations along migratory routes used by migrating animals for resting and energy refuelling, migrating animals can be found in high concentrations at those places.

Trophic/phenological mismatch: different rates of change of the seasonal timing of key phases in life cycles of interacting species, resulting in trophic asynchrony where the peak requirements of a predator species are offset from peaks in the abundance and availability of the prey.

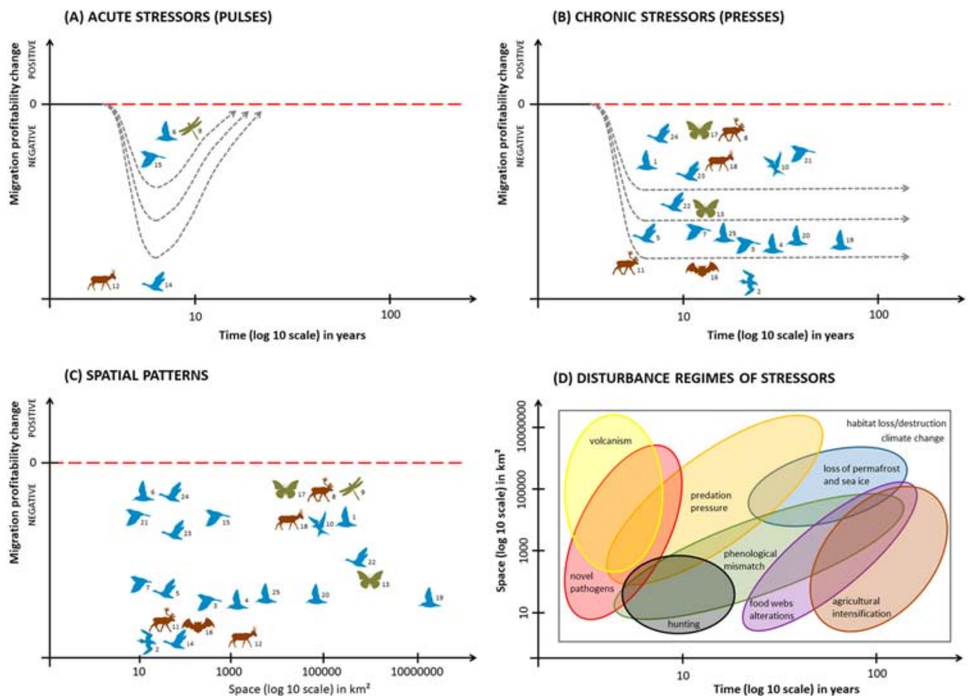

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Figure 3. Temporal and spatial dynamics of changes in profitability of migration for the Arctic and northern temperate long-distance migrants. Visualisations are following the theory of pulse dynamics and disturbance in ecology [18]. Temporal dynamics of migration profitability for acute stressors (A) and chronic stressors (B). Various potential trajectories of stressors (e.g., changing amount or availability of food, pathogens prevalence or predation pressure) are projected. Starting curves for both acute and chronic stressors are similar, because both types of stressors can start changing the given parameters and consequently the migration profitability in a similar way, but acute stressors cease whereas chronic stressors persist over time. (C) Spatial dynamics of acute and chronic stressors. (D) Disturbance regimes of selected acute and chronic stressors in space and time. Note that the discussed migratory benefits (food supply, pathogen prevalence, and predation pressure) can be disrupted at any spatiotemporal scale. Examples from Table 1 are visualised as pictograms, where more negative changes underline more severe population dynamics consequences (A–C). Pictogram colours differentiate taxa (birds, mammals and insect), numbers refer to ordered studies in Table 1. Note that some of the case studies occupy wider space in reality. Similarly, selected stressors presented at spatiotemporal scale may not be limited to the mapped regions only, especially habitat loss/destruction and climate change can affect widely different scales in space and time. (D). See also Figures S2 and S3 in the supplemental information online.

However, interactions of predators with rodents and bird nests as an alternative prey can be highly dynamic and some studies have found only weak relationships between rodent abundance and population trends of other animals [51].

The behaviour of predators may have changed, altering their distributions and increasing their impacts during the breeding season. For example, changing sea ice dynamics (a chronic stressor) have led to stranding of polar bears (*Ursus maritimus*) in coastal areas across the Arctic where they can now prey on breeding colonies of geese, ducks, gulls, and auks [52,53]. The geographic ranges of some generalist predators have also increased northward, including the red fox (*Vulpes vulpes*) [19,21]. Generalist avian predators such gulls and corvids have increased their numbers and spread, supported by human activities [54]. Moreover, sites with increased primary productivity (greening, another chronic stressor for High Arctic wildlife) in a warming Arctic experienced higher predation rates on artificial nests, suggesting an elevated risk of nest predation in tundra ecosystems [55]. Increased predation pressure may not be restricted to migratory species or

Table 1. Studies demonstrating recent disruptions of three historical advantages in northward long-distance migration for terrestrial animals towards the northern temperate and Arctic regions[a].

Location, taxa, and study type	Description of current problems	Refs
	Food supply and availability	
(1) Alaskan and Canadian Arctic, six shorebird species (comparative study)	Despite high variability, generally prevailing mismatch between arthropod prey abundance and timing of breeding in shorebirds was connected to the snowmelt time, mismatches were more profound in Eastern locations, associated with steeper population declines of shorebird species there.	[24], Figure 2
(2) Scotland, UK, Arctic skua *Stercorarius parasiticus* (case study)	Breeding population size of Arctic skuas declined by 81% between 1992 and 2015 alongside sharp declines in populations of their prey species black-legged kittiwake *Rissa tridactyla*, common guillemot *Uria aalge*, Atlantic puffin *Fratercula arctica*, Arctic tern *Sterna paradisaea*, linked to human and climate change impacts on food webs.	[28]
(3) The Netherlands, 10 migrating passerines (case study)	Mismatches for insectivorous passerine species and they prey was detected, with negative consequence for populations of migrating forest birds.	[76]
(4) Taimyr, Arctic Russia, red knot *Calidris canutus* (case study)	Reduced body size as a result of potential malnutrition during early life (mismatch with arthropod prey) was found with a negative consequence for survival at winter grounds in Mauritania, Africa.	[77]
(5) Kolguev Island, Kolokolkova Bay, Arctic Russia barnacle goose *Branta leucopsis* (case study)	The barnacle goose can skip stopover sites to advance its arrival to warming Arctic breeding grounds, but needs to refuel before egg-laying, resulting in a phenological mismatch between plants and offspring hatching date, reducing gosling survival.	[27]
(6) Barrow, Alaska, six shorebird species (case study)	Variable phenological mismatch was found but generally not sufficient food supply for families of three shorebird species.	[23]
(7) Svalbard, Norway, snow bunting *Plectrophenax nivalis* (case study)	Changes in ambient temperature and precipitation on breeding grounds influence breeding productivity, suggesting decline in mean nestling body mass from 1998 to 2012.	[78]
(8) Canada, caribou *Rangifer tarandus* (several case studies)	Phenological mismatches between plants and caribou at their summer grounds were suggested and discussed in several populations. From long-term perspective, caribou could benefit from increasing productivity in the Arctic, but altered plant community composition could be dominated by potentially less nutritious species.	[17]
(9) North America, common green darner *Anax junius* (case study)	Dragonflies' migration is triggered by temperature and warming climate is expected to induce earlier spring flights, trigger later autumn flights and potentially shorten migratory distances and change wintering grounds and prey supplies.	[79]
	Pathogens and parasites	
(10) Eurasian Arctic, gulls, terns, auks, shorebirds and ducks (several case studies)	Spreading of helminth parasites and their increased impact on Arctic birds was described with examples of new host species colonisation, where parasites can reach maturity, although new hosts are phylogenetically unrelated to the main host.	[33], Figure 2
(11) Victoria Island, Canada, caribou *Rangifer tarandus* (case study)	Two species of protostrongylid nematodes have emerged for the first time in caribou, milder climates have facilitated spread of both parasites.	[75], Figure 2

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Table 1. (continued)

Location, taxa, and study type	Description of current problems	Refs
(12) Central Kazakhstan, saiga antelope *Saiga tatarica* (case study)	More than 200 000 saiga antelopes died in May 2015 from haemorrhagic septicaemia caused by *Pasteurella multocida* type B, following unusually high temperatures and humidity. The mass mortality event was spread across numerous calving grounds, reducing the regional population size of saigas by 85%.	[35,36]
(13) North America, monarch butterfly *Danaus plexippus* (several case studies)	More northerly hatched butterflies are recently more negatively affected by the parasite protozoan *Ophryocystis elektroscirrha* and fewer of them reach wintering sites in Mexico. Moreover, recently observed climate and human-induced shift of migratory to sedentary behaviour in several populations will likely lead to greater infection prevalence and can contribute to the species observed declines.	[80]
(14) Canadian Arctic, common eider *Somateria mollissima* (case study)	Recent outbreak of avian cholera caused by the bacterium *Pasteurella multocida* was recorded, with mortality rates of birds ranged from 1% to 43% of the local breeding populations.	[34]
(15) Alaska, bird populations at three locations (case study)	Avian malaria was detected in migratory as well as resident species of birds, for the first time documented avian *Plasmodium* transmission in the North American Arctic.	[37]
(16) Wisconsin, USA, Eastern red bat *Lasiurus borealis* (case study)	Migratory bats were found with fungus *Pseudogymnoascus destructans* during June–September, illustrating the potential of detrimental white-nose syndrome to be transferred and dispersed among bats also at northern breeding grounds during summer months.	[81]
(17) Europe, painted lady butterfly *Vanessa cardui* (case study)	Painted lady butterflies are known for seasonal migrations from North Africa and South Europe to temperate and Arctic Europe to avoid high levels of parasitism from numerous Hymenoptera and Diptera parasitoids; however, with rising ambient temperatures, parasitoids-free refuges might shrink.	[82]
(18) Kazakhstan, saiga antelope *Saiga tatarica* (case study)	Saigas are being infected with gastrointestinal nematodes *Marshallagia marshalli* during their seasonal migration by grazing on pastures used by domesticated sheep.	[83]
	Predation	
(19) Global, 111 shorebird species (comparative study)	Significant increases of nest predation were found in the North temperate and Arctic regions during last 70 years, rapid change especially in the Arctic and after year 2000.	[45], Figure 2
(20) Western Europe, five shorebird species (comparative study)	Significant increases of nest predation was detected during four decades until 2006, accompanied by decline in chick survival over the same period.	[47]
(21) Northern Sweden, pied flycatcher *Ficedula hypoleuca* (case study)	Increased nest predation was found over long-term study following higher densities of mustelid predators: in 1965–1986 just 6% of the clutches on average were predated, whilst 26% were in the period 1991–2017.	[84]
(22) Arctic, ducks, geese, gulls and auks (several case studies)	Polar bear *Ursus maritimus*, which with a disappearance of sea ice is now more often trapped on the land, has increased predation pressure on breeding colonies of Arctic birds.	[52,53]
(23) Svalbard, brant geese *Branta bernicla* (case study)	Recorded significant decrease of nests and numbers of young on islands was associated with higher predator impact from polar bears and expanding great skuas *Stercorarius skua.*	[85]

Table 1. (continued)

Location, taxa, and study type	Description of current problems	Refs
(24) Svalbard, common eider *Somateria mollissima* (case study)	Recently observed high egg losses were associated with increasing predator pressure and declining eider populations; but historic predation rates were also high.	I.H. Eldøy, Master thesis, Norwegian University of Science and Technology, 2019
(25) Canadian Arctic, shorebirds (several case studies)	Increased nest predation was indirectly caused by overabundant geese changing vegetation structure and nest detectability for predators.	[65,86]

[a]These examples are illustrative and not exhaustive. Note also that the highlighted interactions may not be disruptive in all contexts. The Arctic and northern temperate regions consist of various environmental mosaics that are highly dynamic in time or space, and local situations at particular locations might counter the global trend. Patterns of high variability are obvious from detailed comparative studies on phenological mismatch [24] or nest predation [45].

birds, for example Arctic ground squirrels (*Urocitellus parryii*) inhabiting Canadian boreal forest were nearly extirpated by increased predation [56].

Responses of migrating animals to changing environmental conditions

Migratory animals can modify their behaviour, life-history, or physiology through phenotypic plasticity or adaptation to account for changes in the profitability of migration. Such changes may ameliorate the consequences of the aforementioned disruptions to migration benefits, particularly chronic stressors. Migratory schedules commonly change, specifically earlier arrival on the breeding grounds, matching phenological advances [19,20,22,57]. However, species can only adjust phenology within certain limits. For example, in migratory birds, flexibility is limited because of the need to build up energetic reserves prior to migration [19,23]. Similarly, caribou can change timing of migration [58], however when tracking frozen water bodies which enhance landscape connectivity, rising temperatures and thinner ice impede caribou migration [17]. Migratory animals can change wintering grounds as well, tracking the altered environmental conditions, where older individuals with more experience can be critical for developing new migration behaviours, as shown for cranes [59]. Migratory routes or the timing of migration may also change in response to predation pressure [60]. Several species of migratory birds have shown long-term reductions in wing length, possibly as an adaptation to improve aerial agility in response to increased predation pressure following recovery of falcon populations [61].

Due to the rapid pace and complexity of recent changes at breeding grounds (Table 1 and Figure 3), migratory animals may not have developed suitable responses to all novel threats. Current migratory behaviour might become less advantageous or even maladaptive (see Figure S2 in the supplemental information online). In the worst-case scenario, breeding locations in the Arctic tundra, as well as in boreal and North temperate zones, could now represent **ecological traps** with lower profitability than alternative locations [62,63] or **degraded environments** with no better alternatives in the surrounding landscape for migrating animals (see Figure S3 in the supplemental information online).

Implications for population dynamics

Migratory behaviour presumably evolved as an adaptive strategy to maximise fitness as a trade-off between reproductive success and adult mortality in seasonal environments [5,6]. However, conditions on breeding grounds are changing, with potential to reduce reproductive success, lowering the profitability of migration. Negative consequences are likely for individual fitness, population trends and recovery from perturbations (Figure 3 and Table 1). The breeding ranges of migratory birds may track the distributions of predators and alternative prey species [4,64], suggesting that some species might avoid breeding grounds with high nest and chick predation if more suitable alternatives are available. Similar predator avoidance at larger scales would be more difficult for ground-travelling mammals, for example, caribou, which prefer remote calving grounds with lower predation pressure [17]. Conversely, regions with high predation pressure, or sites with lack of alternative prey, could experience local extinction of migratory animals [4,64] and thereby initiate significant alterations in predator–prey interactions, changing trophic food webs with cascading effects for the ecosystem.

Responses vary across different species or populations. For example, North American shorebirds that feed on invertebrates are generally declining whereas herbivorous geese are increasing [65,66]. In these cases, the complex drivers are different: multiple factors are responsible for declines in shorebirds, whereas increases in numbers of geese are mainly driven by changes in agriculture practices and improvements in winter habitat quality [67], regardless of possible changes in the profitability of migration.

Many temperate species have shifted ranges northward following global warming. However, High Arctic migratory animals usually cannot extend their northward distribution owing to the geographic barrier of the Arctic Ocean [40]. Migratory species often have inflexible life-history strategies and hence are particularly at risk from any environmental changes [19,40]. The life-cycle of migratory animals typically consists of distinct stages in different environments, each with different limiting factors. Serious disruption at any stage of the life-cycle could lead to a steep decline of the whole population [16,68]. Traditional harvest of migratory ungulates and birds remains important for many groups of indigenous people [17,69], consequently reduced populations of migratory animals could also socioeconomically impact human communities.

Implications for conservation

It will be challenging to directly mitigate the large-scale impacts of climate change for migratory species that are dependent on multiple environments distributed across several regions of the globe. Conservation efforts at all spatial and temporal scales are important, starting from local direct nest protection to regional habitat management. However, large-scale conservation projects are essential to secure future for migratory animals (see Figure S3 in the supplemental information online), including the development or expansion of international networks of protected areas [70,71].

Climate change is most pronounced in Arctic regions where suitable habitats are changing rapidly [19,40]. Environmental protections in the Arctic require cooperation among governments and indigenous peoples [69] in the face of economic incentives for development of mining and oil drilling and to manage exploitation of natural resources and wildlife. Growing Arctic settlements need proper waste disposal systems to avoid supplemental feeding of generalist predators [54]. New trading routes, currently opening across the more ice-free Arctic Ocean [72], need to be carefully planned and well controlled from the start to minimize their impact on the Arctic ecosystems, especially when many Arctic regions still remain largely unprotected [73]. Issues encountered by migrating animals at the northern temperate breeding grounds are more complex, involving climate change, habitat degradation due to intensification of agriculture and forestry production or urban areas spreading, direct persecution, disturbance or increased predation pressure [45,47,74], requiring coordinated conservation activities across large scales (see Figure S3 in the supplemental information online). Moreover, it is important to maintain landscape connectivity by reducing obstacles in traffic corridors such as telecommunication towers, wind turbines, and powerlines for migrating bats and birds or gas pumpjacks and fence-lines for migrating ungulates [74].

We suggest that Arctic and northern temperate breeding grounds need substantial conservation attention, in addition to well-recognised problems at stopover sites and wintering areas of migratory species [12,16,74]. Targeting only one or two stages may be not enough [45], therefore integrated conservation measures based on international cooperation will be essential to cover the entire life-cycle, and the critical areas used by migratory animals throughout the year.

Concluding remarks and future perspectives

Ecological conditions at Arctic and northern temperate breeding grounds may be deteriorating for many migrating animals owing to recent changes in the availability of food resources, prevalence of pathogens and parasites, and increased predation rates. Animals adapted for migration to the Arctic and northern temperate regions may face dual threats from low breeding productivity at breeding grounds and deteriorating adult survival during their migratory movements [45]. This double jeopardy for long-distance migrants could further intensify the negative population trends of migratory species.

When mitigating impacts of chronic stressors at larger scales, it is vital to rank habitats by their quality, although challenging to be able to recognise: (i) habitats supporting sufficient reproductive output and likely maintaining good source populations of migratory species; (ii) disturbed habitats, which are still advantageous for migrating animals, only less than they used to be; and (iii) ecological traps or degraded environments with negative consequences for reproductive output and subsequent population trends (see Figures S2 and S3 in the supplemental information online). The distinction will be essential for effective targeting of conservation measures, mitigating the impacts of current human pressure and climate-change-induced pulse or press stressing events. More extensive and well-connected networks of protected areas, building on previous efforts such as Ramsar Wetlands or Natura 2000 sites across breeding, migratory and wintering areas, as well as population-specific protective measures, will be essential (see Outstanding questions). Last, recent developments in tracking technologies facilitating effective tracking of complete journeys and life cycles of individuals, represent a breakthrough for studies of migratory connectivity and population dynamics.

Outstanding questions

Which levels of predation, pathogen prevalence or reduced food supply (acute or chronic stressors) at breeding grounds represent ecological traps, or degraded environments, with declining populations? Which sites remain advantageous for migration but are less profitable than before? Which limiting factors are most influential in driving global population trends? Are these effects independent or do they have synergistic interactions? Are there common patterns within a community, or are the ecological drivers different for each species or population?

Which species are best able to cope with novel conditions at breeding grounds and which are more likely to be vulnerable? How do life-history traits and social behaviour influence the species adaptability to novel environmental changes? How are the challenged advantages for the long-distance animal migration in the north relevant to: (i) short-distance or partial migrants, nomadic and resident species; (ii) other geographical regions such as mammals in sub-Saharan Africa; and (iii) to nonterrestrial taxa such as fish or cetaceans?

Is there currently more or less intense competition among migrating animals in the northern latitudes in comparison with earlier decades? Given the declining numbers of many migrating animals nowadays, density-dependent competition could be reduced if resources are unchanged. However, sources and habitat carrying capacity have probably changed, and interspecific competition with new species spreading poleward could offset any additional advantages for long-distance migration to the north.

Developing effective conservation strategies for populations of migratory animals will be a crucial task for coming decades. But what are the most efficient protective measures for migratory species with complex life histories? Inevitably, there will be need for prioritisation, and we need to understand well the main drivers of global population trends in migratory species, and we need to apply correctly large-scale conservation measures as well as species-specific rescue action plans.

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Author contributions

All authors conceived the study; V.K. compiled the data with help from B.K.S. and R.P.F. V.K. wrote the manuscript with inputs from all coauthors.

Declaration of interests

No interests declared.

Supplemental information

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