Commentary Article

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Walking on water: terrestrial mammal migrations in the warming Arctic

Abstract: Caribou and reindeer migrations are the tip of the iceberg when one considers migration among the 70 species of Arctic terrestrial mammals. About 26% of species indeed have migratory individuals, while 33% are non-migratory and 41% are data deficient. Such figures demonstrate the need to both better document and better understand seasonal movements in these vertebrates. Whereas spatiotemporal variations in resources are key drivers of Arctic terrestrial mammal migrations, the changes of water phase around 0°C, from liquid to solid and vice versa, have considerable impacts given that liquid water, snow, and ice differ so strongly in their physical properties. We explore how the interplay between resources and water phase shape Arctic terrestrial mammal migrations, demonstrate that a rich set of research questions emerges from this interaction, and introduce new concepts such as the micro-migrations of small mammals. We also list key questions about the migrations of Arctic terrestrial mammals, with emphasis on the impacts of climate change. We conclude by arguing that the strong exposure of the Arctic to climate change, combined with the quick development of biologging techniques, rapidly increase both the need and the capacity to enhance our knowledge of migration in Arctic terrestrial mammals.

Keywords: Climate change; ice; micro-migrations; movement ecology; snow

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1 Introduction

Nearly 70 species of terrestrial mammals occur in the Arctic at least seasonally [1]. They belong to carnivores, ungulates, shrews, lagomorphs and rodents. Species richness falls dramatically from low to high Arctic, the latter being inhospitable or inaccessible for most species. Terrestrial locomotion is the main mode of movement in Arctic terrestrial mammals. There are no flying species, and swimming is used occasionally but has high energetic cost in cold water [2]. As a result, water bodies such as oceans and large rivers often form species distribution limits [3].

Herbivores comprise the majority of Arctic terrestrial mammals. Small herbivores such as lemmings (*Discrostonyx* sp. and *Lemmus* sp.) are the most abundant, while large herbivores such as caribou and reindeer (*Rangifer tarandus*) are essential food species for Arctic peoples [1]. Plant growth and thus herbivore biomass are low in the tundra (although herbivores can gather in huge numbers at specific times and places), so that terrestrial carnivores are rare, highly mobile and mostly solitary. Some carnivores such as the Arctic wolf (*Canis lupus arctos*) and brown bear (*Ursus arctos*) can compete with humans and receive a high spiritual and cultural value [4]. Some species of Arctic terrestrial mammals attract strong scientific attention because they are keystone species of tundra ecosystems or present conservation concerns [3].

A key characteristic of the Arctic environment is the omnipresence of snow and ice. This has generated many specific adaptations in Arctic terrestrial mammals, including fur structure and color, foot morphology, and behavior [5]. For example, the freezing of water around 0°C allows the smallest species to escape the cold by living under the snow, whereas all species can literally walk on water when ice forms on water bodies. Ice gives animals access to habitats and resources unavailable during summer, such as Arctic foxes (*Vulpes lagopus*) using sea ice as foraging and migrating platform [6], and caribou using it as a bridge to migrate seasonally across habitats [7]. Frozen water is thus key to any discussion about the movement ecology of Arctic terrestrial mammals. However, the quan-

tity and quality of snow and ice are rapidly changing [5], justifying increased attention to the movement ecology of Arctic terrestrial mammals, including their migrations.

Migration is much less prevalent in terrestrial mammals than in birds, given the constraints to long-distance movement generated by terrestrial locomotion. Yet, as shown below, migration does occur in many terrestrial mammals, and millions of individuals rely on migration to complete their annual cycle. We consider migration as one of three dominant movement syndromes [8]: range residency (individuals keep the same home range year-round), nomadism (individuals move unpredictably with little to no site fidelity) and migration (individuals move with persistence from one habitat area to another, bi-directionally and with temporal predictability). Migration distance can be short, allowing individuals to exploit altitudinal gradients or local habitat heterogeneity, but we follow Gnanadesikan et al. [9] in excluding from the definition of migration all movements < 10 times the length of daily movements. Migration within a population can be complete (all individuals migrate) or partial (only some do).

Here we comment on 1) the occurrence of migration in Arctic terrestrial mammals, 2) the factors shaping these migrations, with special emphasis on the role of water properties, and 3) priority research directions regarding Arctic terrestrial mammal migrations, with emphasis on the impacts of climate change.

2 Occurrence of migration in Arctic terrestrial mammals

Gnanadesikan et al. [9] categorized 5,420 extant mammal species as migratory, possibly migratory, non-migratory, or data deficient. We extracted from this list the 70 species recognized as Arctic terrestrial mammals by Reid et al. [3], who used the definition of the Arctic adopted by the Arctic Biodiversity Assessment [10]. This definition follows the Circumpolar Arctic Vegetation Map [11] and does not include the tree-covered sub-Arctic habitats. We updated Gnanadesikan et al.'s categorization based on recent literature and our expert knowledge (Table 1, Appendix 1). This yielded 18 (26%) species with confirmed (14 species) or suspected migration (4 species), 23 (33%) species classified as non-migratory, and 29 (41%) species being data deficient (Table 1).

Species with confirmed or possible migration belong to 8 (57%) of the 14 families of Arctic terrestrial mammals (Table 1). All Arctic ungulates have migratory popula-

tions, which is not surprising since ungulates as a group are highly migratory [9]. Among them, caribou are well-known long-distance migrants [12, 13]. Several carnivores also migrate. Wolverines (*Gulo gulo*) can shift from high elevations in summer to low elevations in winter [14, 15]. Other carnivores may move over large areas during winter, following migratory herds of caribou (wolf *Canis lupus* [16]) or foraging on the sea ice before returning to their den in spring (Arctic fox [17]). Some rodents (*Lemmus* sp. and *Adodemus* sp.) migrate over a few kilometers. Norwegian lemmings (*Lemmus lemmus*) migrate in autumn to alpine tundra where they overwinter in snowbed habitats, and move in spring to forested moist habitats located up to 3 km away and 200 m lower [18, 19]. Similarly, brown lemmings (*Lemmus trimucronatus*) use low-lying wet tundra during summer and mesic tundra during winter [20]. These micro-migrations are often overlooked in studies of mammal migration (e.g., [21]), although they perfectly fit most definitions of migration as long as movements across habitats are performed by individuals and not only observed across generations. At large or small scales, terrestrial migrations are therefore relatively common in Arctic mammals.

A major difference between most Arctic breeding birds and Arctic terrestrial mammals is that mammalian migration appears to be a flexible conditional tactic (rather than a genetically fixed strategy), where individuals migrate or not depending on a complex combination of genetic, environmental, and demographic correlates [21, 22]. Facultative or partial migration seem very common in Arctic terrestrial mammals, since ≥14 (77%) of the 18 migratory or possibly migratory species include populations with facultative or partial migration (Appendix 1). The proportion of migratory individuals may vary widely across populations (likely increasing with latitude), and some individuals may show migratory plasticity by alternating between seasonal migration and year-round residency [17, 23, 24]. Such plasticity, combined with the technical hurdles of studying movement in small species, explains why > 40% of species are still data deficient.

3 Mammal migrations shaped by resources and water properties

Building on the classic work of ornithologists such as Lack [25], MacArthur [26] and Alerstam et al. [27], a formalized view of the evolution of mammal migration was proposed by Holt and Fryxell [28] and Fryxell and Holt [29]. This view predicts the existence of migration or partial migra-

Table 1. Number of species in each of the 14 families (5 orders) of Arctic terrestrial mammals for which migration is confirmed or suspected (Migratory, n=18), absent (Non-migratory, n=23), or unknown because of lack of data (Data deficient, n=29). Migration is considered confirmed or suspected for a given species when occurring or suspected in ≥ 1 population. The list and classification of Arctic terrestrial mammals follows Reid et al. [3] and the data presented were updated from Gnanadesikan et al. [9]. See Appendix 1 for species data, supporting references, and updates provided by this study.

Order	Family	N species	Migratory	Non-migratory	Data deficient	Confirmed and suspected migratory species
Carnivora	Canidae	4	3	1	0	*Canis lupus*, *Vulpes lagopus*, *V. vulpes*
	Felidae	2	0	2	0	
	Mustelidae	5	1	4	0	*Gulo gulo*
	Ursidae	2	2	0	0	*Ursus americanus*, *U. arctos*
	Total	13	6	7	0	
Cetartiodactyla	Bovidae	3	3	0	0	*Ovibos moschatus*, *Ovis dalli*, *O. nivicola*
	Cervidae	3	3	0	0	*Alces alces*, *A. americanus*, *Rangifer tarandus*
	Total	6	6	0	0	
Eulipotyphla	Soricidae	14	0	6	8	
Lagomorpha	Leporidae	4	2	1	1	*Lepus arcticus*, *L. timidus*
	Ochotonidae	3	0	2	1	
	Total	21	2	9	10	
Rodentia	Castoridae	1	0	1	0	
	Cricetidae	24	3	3	18	*Lemmus lemmus*, *L. sibericus*, *L. trimucronatus*
	Dipodidae	1	0	0	1	
	Muridae	1	1	0	0	*Apodemus sylvaticus*
	Sciuridae	3	0	3	0	
	Total	30	4	7	19	
	Grand total	70	18	23	29	

tion in a wide variety of ecological conditions, as long as two available habitats show seasonal variation in fitness and the benefits of migration exceed its costs. Interestingly, the model also predicts the common coexistence of several strategies, such as migration and residency. Avgar et al. [21] followed up in suggesting that benefits of mammal migration belong to four categories : energy intake (increased food quantity or quality, decreased conspecific food depletion), energy expenditure (increased thermoregulation, decreased parasitism), predation (decreased adult or juvenile predation), and mating (increased mate finding). However, a good understanding of mammal migration must also integrate Nathan et al.'s conceptual framework for movement ecology [30], where four mechanistic components (external factors, navigation capacities, internal state, motion capacities; Figure 1) interact to generate movement, and thus migration. How can the above theory help us think about Arctic terrestrial mammal migrations, and the impacts of climate change on such migrations?

We have explained in Berteaux et al. [5] the main characteristics, seasonal changes, and longer-term changes of snow and ice in the Arctic tundra. We have also reviewed the mechanisms linking the permafrost system (including snow and ice) to the ecology of tundra wildlife, with emphasis on the impacts of water phase transitions

around 0°C. Case studies provided in [5] highlight that critical places and times play a disproportionate role in the ecology of tundra wildlife, because these places and times are characterized by water phase transitions. For example, spring snowmelt has strong effects on small mammal ecology because of dramatic changes in thermoregulation and predation risk. Berteaux et al. [5] did not focus on mammal movement, however. Our central point here is therefore that one category of external factors, namely the state and properties of water, disproportionately affects the costs, benefits, and mechanisms of migration in mammal species living in the Arctic. In short, we propose the general hypothesis that most effects of climate change on Arctic mammal migration involve the changing Arctic cryosphere.

The importance of the cryosphere for northern wildlife is well recognized [5, 31, 32], but the specific links between water state and Arctic terrestrial mammal migration have never been reviewed. Figure 1 (top left) lists most characteristics of liquid and frozen water with potential cascading effects on the mechanisms of animal movement. These factors can all impact the navigation capacities, internal state, or motion capacities of individuals, as illustrated in Figure 1 (light-yellow boxes) and below.

Navigation capacity – Changes in water phase frequently offer navigation cues used to determine the timing
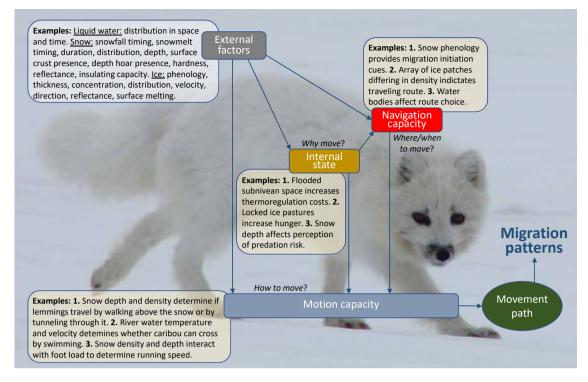
Examples: Liquid water: distribution in space and time. Snow: snowfall timing, snowmelt timing, duration, distribution, depth, surface crust presence, depth hoar presence, hardness, reflectance, insulating capacity. Ice: phenology, thickness, concentration, distribution, velocity, direction, reflectance, surface melting.

External factors

Examples: 1. Snow phenology provides migration initiation cues. **2.** Array of ice patches differing in density indictates traveling route. **3.** Water bodies affect route choice.

Navigation capacity

Why move?

Internal state

Where/when to move?

Examples: 1. Flooded subnivean space increases thermoregulation costs. **2.** Locked ice pastures increase hunger. **3.** Snow depth affects perception of predation risk.

Migration patterns

How to move?

Examples: 1. Snow depth and density determine if lemmings travel by walking above the snow or by tunneling through it. **2.** River water temperature and velocity detemines whether caribou can cross by swimming. **3.** Snow density and depth interact with foot load to determine running speed.

Motion capacity

Movement path

Figure 1. Conceptual framework for the movement ecology of Arctic terrestrial mammals, modified from Nathan et al. [30] and Morelle et al. [45]. External factors (biotic and abiotic), navigation capacity (cognitive and sensory machineries processing information), internal state (affecting motivation and readiness to move), and motion capacity (individual characteristics enabling movement) interact to determine the movement path, and ultimately migration patterns. Blue arrows indicate processes at play in the movement (feedback processes not represented). Examples of external factors linked to water state and characteristics are provided in the white box, while examples of water-related processes affecting navigation capacity, internal state, and motion capacity of individuals are provided in the light-yellow boxes. Picture of traveling Arctic fox: Clément Chevallier.

and direction of movement. For example, the spring melt of snowbeds, which floods underground tunnels, triggers lemming movements to summer habitats [19]. Conversely, the first substantial snowfalls in autumn trigger small mammal movements to the sites where winter nests can be established [33]. The receding edge of the melting snow acts as an environmental cue tracked by some caribou populations, allowing them to reach calving grounds on time to synchronize parturition with the peak of plant growth [34].

Internal state –Phenotypic traits, physiology, or motivation can interact with snow and ice conditions to influence migration parameters. For example, physiological condition may change with age and impact migration costs, as seen in moose (*Alces alces*) where propensity to migrate and migration distance decline in older individuals inhabiting areas where snow depth is high (and thus movement and thermoregulation costs are important) [23]. Nutritional stress induced by icing events rendering forage inaccessible ("locked pastures") may induce range displacement in normally sedentary Svalbard reindeer (*R.*

tarandus plathyrynchus) [24], although migration was not demonstrated in this particular example.

Motion capacities – Water state strongly impacts locomotion mode and speed. Although terrestrial migrants can cross open water by swimming, they clearly prefer to get around [35] or use ice bridges [2]. As such, caribou from the Dolphin and Union herd migrating from Victoria Island to the mainland may be forced to stage along the coast during several weeks, until suitable sea ice is formed [7]. Small mammals may travel a few kilometers by running on top of the snowpack or by digging tunnels through the snowpack, potentially depending on snow depth and hardness [36].

Published correlations between water characteristics and animal movement do not always indicate which mechanisms are at play. For example, snow depth variation along a 1,100-km latitudinal gradient best explains the proportion of migratory moose in Swedish populations [23], but multiple processes could link snow depth to annual movement strategy. Also noteworthy is the strong bias of Arctic ecology away from the frozen season, due to logistic difficulties and the reduced primary production

and animal activity. As a result, the links between water properties and Arctic terrestrial movements are largely understudied, despite their importance in a rapidly changing climate.

In closing this section, we note that although we emphasized the effects of the cryosphere on the mechanisms of animal movement, the conditions of the cryosphere also strongly impact the difference in fitness realized by migrating animals between the two seasonal habitats. As such, how the cryosphere influences both the origin and destination of a migratory event is critical. We provided a few examples focused on the origin (e.g., spring melt floods underground tunnels) rather than the destination of migration, but both must be considered as important.

Table 2. Priority research (with emphasis on climate change effects) regarding the description, understanding, forecasting, and management of migration in Arctic terrestrial mammals. Research directions are sorted into: 1) techniques and methodology, 2) research at the population or species level, and 3) research requiring integration of knowledge across species. Research most directly linked to water properties (particularly water phase) is identified with a star.

Priority research regarding migration in Arctic terrestrial mammals	Description	Understanding	Forecasting	Management
Techniques and methodology				
• Develop tracking devices allowing the study of small mammal micro-migrations.	X	X		
•* Develop biologging techniques allowing the integrated recording of animal movement and snow properties, particularly depth and hardness.	X	X		
•* Develop some experimental protocols to assess the costs and benefits of movement under varying snow and ice conditions.		X	X	
•* Enhance modeling and prediction of snow properties over large areas using remotely sensed data.		X	X	
• Further develop online platforms and data repositories, such as the Arctic Animal Movement Archive in Movebank [44] to facilitate the management, sharing, analysis, and archiving of animal movement data.	X	X		X
Population or species level				
• Complete the inventory of migrating populations of Arctic terrestrial mammals.	X			
•* Assess which of the main migratory routes of long-distance migrants rely on seasonal ice bridges.	X	X		X
•* Evaluate whether some of these ice bridges are at risk of rapid degradation from climate change and ship traffic, and how can management mitigate the problem.			X	X
• Examine the demographic effects (if any) of loss of migration.		X		X
•* Better assess the navigation cues, including the phenology of water phase transitions, used by migrating Arctic terrestrial mammals.		X	X	
• *Assess via non-lethal methods how snow and ice conditions affect the internal state of animals (e.g., stress level, energetic state, metabolic rate) and ultimately their migratory patterns.		X	X	
• Develop flexible management regimes to accommodate changing migration routes or summer and winter grounds, particularly in long-distance migrants.				X
• Clarify the roles of learning and genetics in driving individual migrations.		X		X
• Identify differences (ontogeny, fitness, etc.) between migrants and residents in populations with partial migration.	X	X		
Integration of knowledge across species required				
• Assess the biological significance of the high frequency of partial migration in Arctic terrestrial mammals.		X	X	
• Determine whether there are currently some generalized shifts in the distribution of summer grounds, winter grounds, or migration routes.	X	X	X	X
• Determine the extent to which spring and fall migration phenology is shifting, and what is the variability across populations.	X	X	X	X
•* Assess whether some populations are developing mismatches between their phenology of migration and the phenology of resources, snow and ice.	X	X	X	X

4 Priority research directions given climate change

We generated priority research directions regarding migration of Arctic terrestrial mammals, after considering 1) our current knowledge on the occurrence and characteristics of migration in of Arctic terrestrial mammals, 2) our understanding of the role of temperature-dependent water properties in shaping Arctic wildlife ecology, 3) the extraordinary exposure of the Arctic to climate change, and 4) the technical advances in biologging currently revolutionizing movement ecology (Table 2).

We recognize that evaluating priority research is a subjective exercise biased by the authors' experience, in our case ecological research on small and medium-sized Arctic terrestrial herbivorous and carnivorous mammals. For example, many questions dealing with the ecophysiology of migration in Arctic terrestrial mammals, or the importance of learning for efficient navigation, are also highly relevant but we are not qualified to list them. Our list of research directions thus mostly offers a stimulus and framework for additional thinking.

5 Conclusion

The Arctic Biodiversity Assessment [1] made clear that climate change is by far the most serious threat to Arctic biodiversity and exacerbates all other threats. Changing air temperatures indeed have considerable impacts on snow and ice [37], with extensive effects on ecological systems, including wildlife [38–40]. Our review also makes clear that migration is common in Arctic terrestrial mammals, more so than often thought, and that its parameters depend strongly on water state and snow and ice characteristics. In a global context where remnant long-distance terrestrial mammal migrants are disappearing at an alarming rate and are thought to have poor long-term prospects [41, 42], the question thus arises: How will migrations of Arctic terrestrial mammals fare in the next 100 years?

A first step to answer this question is to better document and monitor migrations in Arctic terrestrial mammals. The existence of migration is still not adequately tested in many species (Figure 2), variation in movement patterns across populations is usually unknown, and micro-migrations of small mammals are

Figure 2. The existence of seasonal migrations is strongly suspected but still not demonstrated in some Arctic terrestrial mammals. Such is the case for these Arctic hares photographed in late October 2020 at Canadian Forces Station Alert (Ellesmere Island, Canada), 817 km from the North Pole. Picture: CFS Alert personnel.

often overlooked. Technical solutions to track individuals year-round are quickly spreading, which offers one obvious direction for progress. A second step is to better understand and model how the changing cryosphere impacts Arctic terrestrial mammal migrations, knowing that perfect projection of the effects of climate change on mammals is out of reach [43]. A third step consists in identifying management options that can help sustain Arctic terrestrial mammal migrations. Options are likely few but mitigation may exist for specific populations facing clear migration constraints in environments that can be manipulated by humans. Finally, all the above highlights once again the importance of relentlessly promoting the rapid halt of climate warming through the stabilization and then decline of greenhouse gas concentrations. Perhaps ironically, Arctic mammals, which are marvels of adaptation to life in the cold, snow and ice, offer useful examples of what is at stake if we continue to mismanage our planet.

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References

[1]   CAFF, Arctic Biodiversity Assessment. Status and trends in Arctic biodiversity, Conservation of Arctic Flora and Fauna, Akureyri, Iceland, 2013

[2]   Gaston A.J., Gavrilo M., Eberl C., Ice bridging as a dispersal mechanism for Arctic terrestrial vertebrates and the possible consequences of reduced sea ice cover, Biodiversity, 2012, 13, 182–190

[3]   Reid D.G., Berteaux D., Laidre K.L., (Lead authors), and 32 Contributing Authors, Chapter 3 - Mammals, In: Arctic Biodiversity Assessment: Status and Trends in Arctic Biodiversity, Conservation of Arctic Flora and Fauna (CAAF), Arctic Council, Iceland, 2013, 78–141

[4]   Dickman A.J., Macdonald E.A., Macdonald D.W., Biodiversity Conservation and Poverty Traps Special Feature: A review of financial instruments to pay for predator conservation and encourage human-carnivore coexistence, Proc. Natl. Acad. Sci., 2011, 108, 13937–13944

[5]   Berteaux D., Gauthier G., Dominé F., Ims R.A., Lamoureux S.F., Lévesque E., et al., Effects of changing permafrost and snow conditions on tundra wildlife: critical places and times, Arct. Sci., 2017, 3, 65–90

[6]   Lai S., Bêty J., Berteaux D., Spatio–temporal hotspots of satellite–tracked arctic foxes reveal a large detection range in a mammalian predator, Mov. Ecol., 2015, 3, 37

[7]   Poole K.G., Gunn A., Patterson B.R., Dumond M., Sea ice and migration of the Dolphin and Union caribou herd in the Canadian Arctic: an uncertain future, Arctic, 2010, 63, 414–428

[8]   Abrahms B., Seidel D.P., Dougherty E., Hazen E.L., Bograd S.J., Wilson A.M., et al., Suite of simple metrics reveals common movement syndromes across vertebrate taxa, Mov. Ecol., 2017, 5

[9]   Gnanadesikan G.E., Pearse W.D., Shaw A.K., Evolution of mammalian migrations for refuge, breeding, and food, Ecol. Evol., 2017, 7, 5891–5900

[10]   Meltofte A., Barry T., Berteaux D., et al, Arctic Biodiversity Assessment: Status and Trends in Arctic Biodiversity – Full Report, Conservation of Arctic Flora and Fauna (CAAF), Arctic Council, Iceland, 2013

[11]   Walker D.A., Raynolds M.K., Daniëls F.J.A., Einarsson E., Elvebakk A., Gould W.A., et al., The Circumpolar Arctic vegetation map, J. Veg. Sci., 2005, 16, 267–282

[12]   Fancy S.G., Pank L.F., Whitten K.R., Regelin W.L., Seasonal movements of caribou in arctic Alaska as determined by satellite, Can. J. Zool., 1989, 67, 644–650

[13]   Gurarie E., Hebblewhite M., Joly K., Kelly A.P., Adamczewski J., Davidson S.C., et al., Tactical departures and strategic arrivals: Divergent effects of climate and weather on caribou spring migrations, Ecosphere, 2019, 10, e02971

[14]   Whitman J.S., Ballard W.B., Gardner C.L., Home range and habitat use by wolverines in Southcentral Alaska, J. Wildl. Manag., 1986, 50, 460–463

[15]   Landa A., Strand O., Linnell J.D.C., Skogland T., Home-range sizes and altitude selection for arctic foxes and wolverines in an alpine environment, Can. J. Zool., 1998, 76, 448–457

[16]   Walton L.R., Cluff H.D., Paquet P.C., Ramsay M.A., Movement patterns of barren-ground wolves in the Central Canadian Arctic, J. Mammal., 2001, 82, 867–876

[17]   Lai S., Bêty J., Berteaux D., Movement tactics of a mobile predator in a meta-ecosystem with fluctuating resources: the arctic fox in the High Arctic, Oikos, 2017, 126, 937-947

[18]   Tast J., Will the Norwegian lemming become endangered if climate becomes warmer?, Arct. Alp. Res., 1991, 23, 53–60

[19]   Henttonen H., Kaikusalo A., Lemming movements, Biol. Lemmings, 1993, 157–186

[20]   Duchesne D., Gauthier G., Berteaux D., Habitat selection, reproduction and predation of wintering lemmings in the Arctic, Oecologia, 2011, 167, 967–980

[21]   Avgar T., Street G., Fryxell J.M., On the adaptive benefits of mammal migration, Can. J. Zool., 2014, 92, 481–490

[22]   Berg J.E., Hebblewhite M., St. Clair C.C., Merrill E.H., Prevalence and mechanisms of partial migration in ungulates, Front. Ecol. Evol., 2019, 7, 325

[23]   Singh N.J., Börger L., Dettki H., Bunnefeld N., Ericsson G., From migration to nomadism: movement variability in a northern ungulate across its latitudinal range, Ecol. Appl., 2012, 22, 2007–2020

[24]   Loe L.E., Hansen B.B., Stien A., D. Albon S., Bischof R., Carlsson A., et al., Behavioral buffering of extreme weather events in a high-Arctic herbivore, Ecosphere, 2016, 7, e01374

[25]   Lack D., The significance of migration, In: The Natural Regulation of Animal Numbers, Oxford University Press, Oxford, 1954, 243–254

[26] MacArthur R.H., On the breeding distribution pattern of North American migrant birds, The Auk, 1959, 76, 318–325

[27] Alerstam T., Hedenström A., Åkesson S., Long-distance migration: evolution and determinants, Oikos, 2003, 103, 247-260

[28] Holt R.D., Fryxell J.M., Theoretical reflections on the evolution of migration, In: Animal Migration, E.J. Milner-Gulland, J.M. Fryxell, and A.R.E. Sinclair, Oxford University Press, New York, 2011, 17–32

[29] Fryxell J.M., Holt R.D., Environmental change and the evolution of migration, Ecology, 2013, 94, 1274–1279

[30] Nathan R., Getz W.M., Revilla E., Holyoak M., Kadmon R., Saltz D., *et al.*, A movement ecology paradigm for unifying organismal movement research, Proc. Natl. Acad. Sci., 2008, 105, 19052–19059

[31] Boelman N.T., Liston G.E., Gurarie E., Meddens A.J.H., Mahoney P.J., Kirchner P.B., *et al.*, Integrating snow science and wildlife ecology in Arctic-boreal North America, Environ. Res. Lett., 2019, 14, 010401

[32] Slatyer R.A., Umbers K.D.L., Arnold P.A., Ecological responses to variation in seasonal snow cover, Conserv. Biol., 2021

[33] Reid D.G., Bilodeau F., Krebs C.J., Gauthier G., Kenney A.J., Gilbert B.S., *et al.*, Lemming winter habitat choice: a snow-fencing experiment, Oecologia, 2012, 168, 935–946

[34] Laforge M.P., Bonar M., Vander Wal E., Tracking snowmelt to jump the green wave: phenological drivers of migration in a northern ungulate, Ecology, 2021, 102, e03268

[35] Leblond M., St-Laurent M.-H., Côté S.D., Caribou, water, and ice - fine-scale movements of a migratory arctic ungulate in the context of climate change, Mov. Ecol., 2016, 4, article 14

[36] Poirier M., Gauthier G., Domine F., What guides lemmings movements through the snowpack?, J. Mammal., 2019, 100, 1416–1426

[37] Vaughan D.G., Comiso J.C., Allison I., Carrasco J., Kaser G., Kwok R., *et al.*, Observations: cryosphere, Clim. Change 2013 Phys. Sci. Basis Contrib. Work. Group Fifth Assess. Rep.

Intergov. Panel Clim. Change Stock. TF Qin G-K Plattner M Tignor SK Allen J Boschung Nauels Xia V Bex PM Midgley Eds Camb. Univ. Press Camb. U. K. N. Y. NY USA, 2013, 317–382

[38] Post E., Forchhammer M.C., Bret-Harte M.S., Callaghan T.V., Christensen T.R., Elberling B., *et al.*, Ecological dynamics across the Arctic associated with recent climate change, Science, 2009, 325, 1355–1358

[39] Hansen B.B., Aanes R., Herfindal I., Kohler J., Sæther B.-E., Climate, icing, and wild arctic reindeer: past relationships and future prospects, Ecology, 2011, 92, 1917-1923

[40] Gauthier G., Bêty J., Cadieux M.C., Legagneux P., Doiron M., Chevallier C., *et al.*, Long-term monitoring at multiple trophic levels suggests heterogeneity in responses to climate change in the Canadian Arctic tundra, Phil Trans R Soc B, 2013, 368, 20120482

[41] Berger J., The last mile: How to sustain long-distance migration in mammals, Conserv. Biol., 2004, 18, 320–331

[42] Kauffman M.J., Cagnacci F., Chamaillé-Jammes S., Hebblewhite M., Hopcraft J.G.C., Merkle J.A., *et al.*, Mapping out a future for ungulate migrations, Science, 2021, 372, 566–569

[43] Berteaux D., Humphries M.M., Krebs C.J., Lima M., McAdam A.G., Pettorelli N., *et al.*, Constraints to projecting the effects of climate change on mammals, Clim. Res., 2006, 32, 151–158

[44] Davidson S.C., Bohrer G., Gurarie E., LaPoint S., Boelman N.T., Eitel J.U.H., *et al.*, Ecological insights from three decades of animal movement tracking across a changing Arctic, Science, 2020, 370, 712–715

[45] Morelle K., Lehaire F., Lejeune P., Is wild boar heading towards movement ecology? A review of trends and gaps, Wildl. Biol., 2014, 20, 196–205

Supplementary Material

The Excel file named "Berteaux and Lai_SuppMat" contains two sheets in addition to the ReadMe sheet. The sheet named "Movement type categorization" shows the movement type (M = migratory, N = non-migratory, U = unclear movement pattern but possibly migratory, D = data deficient) of the 70 species of Arctic terrestrial mammals recognized by Reid et al. [3]. Data come from Gnanadesikan et al. [9], expect for updates made by us which appear in red characters. Red characters in the Movement type column indicate both our updated data and, in parentheses, the original data from Gnanadesikan et al. [9]. References cited in the "Movement type categorization" sheet are available in the "References" sheet.