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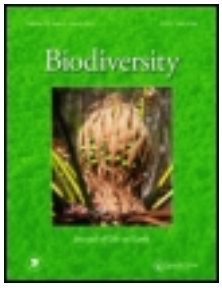

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Ice bridging as a dispersal mechanism for Arctic terrestrial vertebrates and the possible consequences of reduced sea ice cover

Anthony J. Gaston [a], Maria Gavrilo [b] & Christine Eberl [a]

[a] Environment Canada, Carleton University, Ottawa K1A 0H3, Canada

[b] Arctic and Antarctic Research Institute (AARI), 38 Bering Street, Saint-Petersburg, Russia

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Ice bridging as a dispersal mechanism for Arctic terrestrial vertebrates and the possible consequences of reduced sea ice cover

Anthony J. Gaston[a]*, Maria Gavrilo[b] and Christine Eberl[a]

[a]*Environment Canada, Carleton University, Ottawa K1A 0H3, Canada;* [b]*Arctic and Antarctic Research Institute (AARI), 38 Bering Street, Saint-Petersburg, Russia*

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The dispersal abilities of terrestrial mammals are severely constrained by water crossings, resulting in islands generally supporting less diverse mammal faunas than similar continental areas. In ice-affected Arctic regions, seasonal or permanent ice cover provides a bridging mechanism for dispersal, allowing water gaps to be crossed more rapidly and with less energy cost than is entailed in swimming. Consequently, islands that might be out of reach if waters were open become much more readily colonised in the presence of ice. We reviewed the distribution of terrestrial mammals on selected islands throughout the Arctic and analyse historical data for several sites in the Canadian Arctic where mammal populations have undergone extirpation and re-colonisation. We use these data to assess the value of ice for the dispersal of Arctic terrestrial mammals. Given observed dispersal distances we estimate the likely impact of future ice reduction on island faunas. We predict that, as ice cover duration shortens, immigration will decline leading to increased extinctions of island populations and potentially, in the long-term, local genetic differentiation. The eventual disappearance of ice bridges, preventing the immigration of southern species, may leave certain arctic archipelagos as the last refuge for typical Arctic mammals.

Keywords: ice reduction; dispersal; island fauna; Arctic mammals; seasonal ice; adaptation; extinction

Introduction

The dispersal of terrestrial non-flying organisms to islands is a topic of great interest to biogeographers. Limitations on dispersal mean that many islands, especially oceanic islands never connected to continents by land bridges, lack non-flying terrestrial mammals altogether (e.g. Atkinson 1985; Carvajal and Adler 2005; Masseti 2010). For islands not completely inaccessible to terrestrial mammals, the water barrier presents a filter that reduces immigration rates, causing island communities to lack elements of the typical regional mammal fauna and increasing the potential for those mammals that are present to evolve local adaptations (Berry 1996; Loxterman et al. 1998; Cook, Dawson, and MacDonald 2006; Millien 2006). The degree of filtering depends mainly on the distance to source areas (Landry and Lapointe 1999), but is also related to the size of the animal: Large animals can survive swimming journeys for longer than small animals (Lomolino 1984; Peltonen and Hanski 1991). However, small animals are more likely than large animals to be caught up in serendipitous rafting events, sometimes called the 'sweepstake process' (Ali and Huber 2010).

The accessibility of an island to terrestrial mammals is important in the development of the island's ecosystem in several ways: mammalian herbivores (e.g. deer, goats, rabbits) are sometimes important ecosystem architects (Tilghman 1989; Waller and Alverson 1997; Martin et al. 2010); predatory mammals are important in checking the unrestrained increases of mammalian herbivores, and may also be effective deterrents for the breeding of oceanic seabirds (Moors and Atkinson 1984; Terborgh et al. 2006); omnivorous mammals, such as rodents, raccoons, pigs and bears, can be important predators of arthropods and other slow-moving prey, as well as taking the eggs and nestlings of breeding birds (Challies 1975; Moors and Atkinson 1984; Gaston and Masselink 1997).

Where the sea is subject to seasonal ice cover, islands are much more accessible to terrestrial mammals. Those animals that remain active during winter can cross over the ice, allowing a much greater over-water dispersal range (Crowell 1986; Lomolino 1988, 1993, 1994). Like swimming, such dispersal will depend on the distance to be traversed and on the endurance capacity of the animal, but for non-aquatic mammals walking is more efficient, in terms of energy/distance, than swimming (Schmidt-Nielsen 1972), while thermoregulation requires less energy expenditure in air than in water (Dawson, Roemer, and Horvath 1970; MacArthur 1984). Consequently dispersal across ice is generally easier than dispersal across water,

*Corresponding author. Email: tony.gaston@ec.gc.ca

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especially where ice cover is continuous and immobile (Lomolino 1994; Ehrich et al. 2001; Belant and Van Stappen 2002).

The role of ice in allowing access for terrestrial mammals to otherwise inaccessible islands was recognised long ago (Jackson 1920; Rausch 1953; Banfield 1954; Denman 1965). Many species in the Arctic that, in the absence of ice, would have had difficulty accessing offshore islands are widely distributed on islands well beyond their normal swimming range (e.g. Banfield 1954; distributions in Banfield 1974). In addition, where ice cover is irregular, rather than annually predictable, periodic ice bridging or ice-rafting leads to the unpredictable arrival of mammalian predators on islands where breeding birds may not be accustomed to their presence, leading to periodic large-scale breeding failures of ground-nesting birds (e.g. Birkhead and Nettleship 1995; Burke et al. 2011).

The extent of minimum ice cover in the Arctic has diminished sharply over the past two decades (Comiso et al. 2008; Parkinson and Cavalieri 2008; Perovich and Richter-Menge 2009), with an overall rate of change in September ice cover of 28.5% per decade between 1981 and 2010 (ftp://sidads.colorado.edu/DATASETS/NOAA/G02135/Sep/, last accessed 24 August 2011). This trend has been accompanied by an advance in the date of ice breakup and clearance and a retreat of the date of freeze-up (Gagnon and Gough 2005; Dumas, Flato, and Brown 2006; Hochheim, Barber, and Lukovich 2010). Consequently, the open water season has lengthened (e.g. by ~40 days in northern Hudson Bay; Gaston, Smith, and Provencher 2012), potentially reducing the opportunity for terrestrial mammals to disperse across ice.

In this paper, we examine the distribution of non-aquatic mammals on Arctic islands, especially those in Canada and the Russian Arctic. We use actual observations of ice-crossings, records of sudden arrivals on islands well beyond normal swimming range, and historical distributions, to assess the likely over-ice dispersal range of Arctic land mammals. Based on this information, we assess the likely effect of future changes in Arctic sea ice conditions on the distribution and connectivity of Arctic terrestrial mammal populations and discuss the potential consequences of these changes for Arctic island ecosystems.

Methods

Terrestrial mammals on Arctic islands

The distributions of mammals among islands of the Canadian and Russian Arctic were obtained from the literature, from North American museum specimen records and from observations by AJG (Canada) and MG (Russia) and colleagues over the past several decades. Details of sources are given in Appendix 1 (online). For each island, the total area was obtained from gazetteers, or measured using MapInfo Professional v 6.5 (MapInfo Corp. 1985–2001) and ADC Worldmap v2 (ADC 1993–1998) and distance from potential sources of colonisation was measured using the measuring tool of MapInfo Professional in two ways: (1) from the nearest continental mainland; (2) across the longest water-crossing involved in a chain of connecting islands from either the continental mainland, or in Canada from Baffin or Somerset islands (maximum inter-step distance, MID). Islands were only considered potential stepping-stones if they exceeded 1 km^2 in area. For many Arctic islands the amount of biological survey work is insufficient to be certain of the presence/absence of all mammal species. For Canada, we considered only islands where a biological survey party was known to have visited and either (1) collected specimens, or (2) reported mammal records. In the case of Lemmings, where population cycles make determination of presence difficult in low years, we took an absence of lemming predators (long-tailed jaegers *Stercorarius longicaudus*, snowy owls *Bubo scandiacus*, rough-legged hawks *Buteo lagopus*) over several years as evidence that Lemmings were not present.

We have not included over-ice dispersal distances for Polar Bear or Arctic Fox, as both these species are known to live and travel extensively on sea ice during winter (Stirling 1988; Geffen et al. 2007; Tarroux, Berteaux, and Bety 2010; Noren et al. 2011). Nor have we included Greenland as an island. In assessing over-ice dispersal distances, we excluded islands connected to the mainland by land bridges since the Pleistocene (e.g. Wrangel Island, New Siberian Islands, islands in the Beringean land-bridge). Islands were assessed as (1) species recorded, (2) biological survey but species not recorded, (3) no information.

Observations of immigration and emigration

Observations were made during visits of 2–12 weeks over >10 seasons at three islands in the Canadian Arctic: Coats Island (62° N, 82° W; 5687 km^2, 68 km from the potential source area of Southampton Island, total days of field work >1000), Digges Island (62° 40′ N, 77° 45′ W; 40 km^2, 4.5 km from mainland Quebec, 260 field days) and Prince Leopold Island (74° 05′ N, 90° 00′ W; 68 km^2, 9.5 km from Somerset Island, 590 field days). Daily records were kept of all mammals recorded, both sightings and signs (tracks, hairs, dens, etc.). All three islands are connected to adjacent potential source areas by winter ice cover.

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Dispersal distances over ice

To estimate likely maximum trans-ice dispersal distances we collated information from (1) eyewitness accounts of the arrival of mammals on previously unoccupied islands; (2) records of intermittent presence and absence; (3) maximum inter-step distances from potential source areas. Data and sources are given in Appendix 1 (online).

Results

Terrestrial mammals on Arctic islands

The most distant Arctic islands and archipelagos supported no terrestrial mammals, other than Arctic Fox and Polar Bear, before the arrival of people (e.g. Bear Island [Bjornoya], Iceland, Jan Mayen, Figure 1). Nearly all other islands $>100\,km^2$ in extent supported at least one species of terrestrial mammal, but the most isolated islands supported only the largest Arctic herbivore, the Reindeer/Caribou, *Rangifer tarandus*, (see Appendix 2a online; Spitzbergen; Coats and Mansel islands in Nunavut; Reindeer became extinct on Franz Josef more than a millennium ago [Zale, Glazovskiy, and Naslund 1994]). Musk Ox, *Ovibos moschatus*, is less widely distributed than Caribou, being present only on the islands of the Canadian Arctic west/northwest of Baffin Island (Banfield 1974). The Arctic Hare, *Lepus arcticus*, is found on most islands in northern Canada (see Appendix 2b online), but its congener in Eurasia, the mountain hare (*Lepus timidus*) does not reach any offshore islands, except for occasional records on southernmost island of the Severnaya Zemlya, Novaya Zemlya and New Siberian archipelagos. Lemmings, *Dicrostonyx* and *Lemmus* spp., are found on all the larger islands in the Canadian Arctic for which we obtained credible records, apart from Coats, Mansel, Salisbury and Akpatok, and on Novaya Zemlya, Severnaya Zemlya, the New Siberian Islands and Wrangel Island, but not on Kolguyev Island or Franz Josef (see Appendix 2c online). Arctic Ground Squirrels, *Spermophilus parryii*, occur to 70 N in North America (Banfield 1974), but do not occur on any islands.

Among carnivores, Wolf, *Canis lupus*, is found on larger islands throughout the Canadian Arctic archipelago; and on all the Russian archipelagos except Franz Joseph, although only a rare vagrant on Severnaya Zemlya (see Appendix 2d online). On the New Siberian Islands it may form a distinct local population. Red Fox, *Vulpes vulpes*, although absent from many islands in the western Canadian Arctic, has been expanding northwards on Baffin Island since appearing there in the early part of the twentieth century and has been reported from Cornwallis and Ellesmere islands, north of Parry Channel

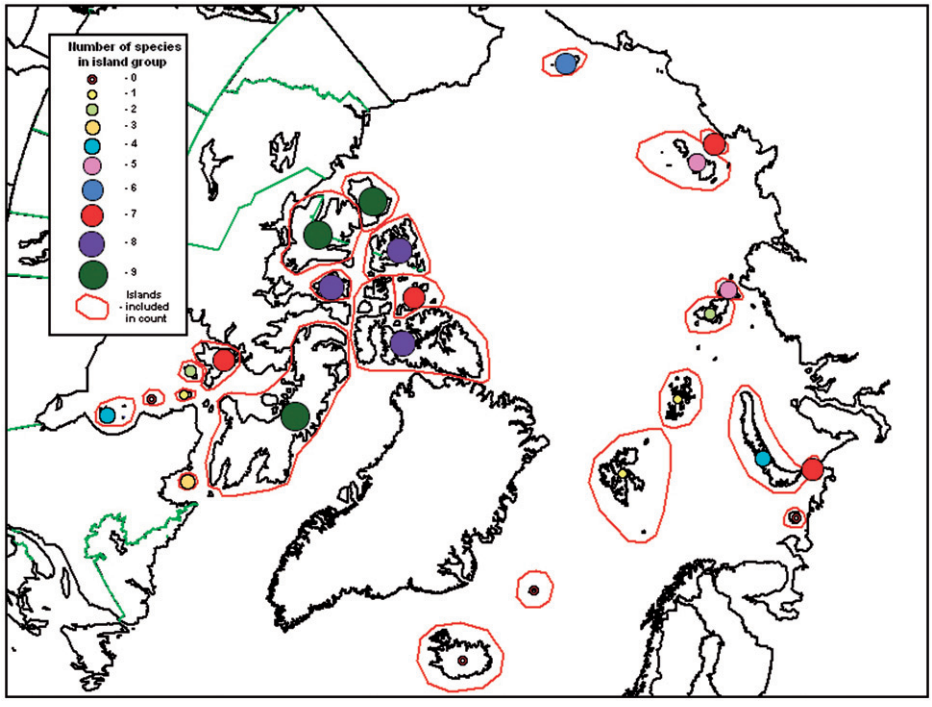

Figure 1. Distribution of terrestrial mammal species present on different islands and island groups in Arctic marine waters (excluding Greenland). For sources, see Appendix 1 (online).

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(Banfield 1954; MacPherson 1964). The Ermine, *Mustela erminea*, has been recorded on all the larger islands where Lemmings occur and on some smaller islands (see Appendix 2e online) where it sometimes preys on birds (Cairns 1985). Wolverine, *Gulo gulo*, although very sparse, has been recorded throughout the larger Canadian Arctic islands except the most remote, and on Wrangel Island (see Appendix 2f online).

Observations of immigration and emigration

At Digges Island, where observers were present in 12 summers between 1979 and 2009, Caribou (1990 onwards), Collard Lemming (all but one year), Red Fox (5 years) and Ermine (1 year) were recorded. Caribou visited the island from 1986 onwards, after they became common on the adjacent mainland coast (A. Mangiuk pers. comm. 1992). Red Fox was present in 1980–1982, and 1992–1994, but not seen in 1985 and 1990.

In 17 years of summer field camps at Prince Leopold Island, caribou, Arctic Hare, *Lepus arcticus*, and Collard Lemming were recorded. Only Arctic Hare, recorded in three years, was recorded more than once. Caribou were seen only in 1984, but antlers found in 2000 suggested a visit sometime between 1993 and 2000. Collared Lemming was seen only in 2009.

Coats Island was visited in 29 seasons, with Caribou recorded every year, but no records by camp personnel of any of our other study species. Coats Island is 68 km from the larger Southampton Island which, in turn, is 20 km from the mainland. Arctic Hare, Lemmings (both *Lemmus* and *Dicrostonyx*) and Ermine are present on Southampton Island (Sutton 1932). In the 1930s wolves were present on Southampton Island but died out after caribou were extirpated from the island in 1953 (Heard and Ouellet 1994). Subsequently, there have been several records of wolves on Southampton Island, indicating periodic immigration from the mainland (T. Alogut pers. comm.).

Dispersal distances over ice

Caribou show evidence of the greatest dispersal range (<380 km) by far, which accounts for their presence on Spitzbergen and their previous Holocene occurrence on Franz Josef (Zale, Glazovskiy, and Naslund 1994). Among other species, only the Grizzly Bear, *Ursus arctos*, has definitely dispersed >100 km across ice (Doupé et al. 2007). However, even the smallest (Lemmings) can disperse over >10 km of ice (Figure 2) and the Arctic Hare appears capable of dispersing up to 50 km. In the Canadian Arctic the presence or absence of Lemmings on islands can be related both to island MID and island area, with the two variables being significantly correlated (Figure 3; $r_{43}=0.46$, $P=0.001$) as predicted by island biogeographic theory (McArthur and Wilson 1967; Lomolino and Weiser 2001). Among islands without Lemmings, 63% ($N=11$) had a greater MID than the 95% confidence ellipse for islands with Lemmings (Figure 3). The slope of the MID on island area relationship for islands without Lemmings was similar to that for islands with Lemmings, although it did not differ significantly from zero. All of the estimated dispersal distances across ice are far in excess of those

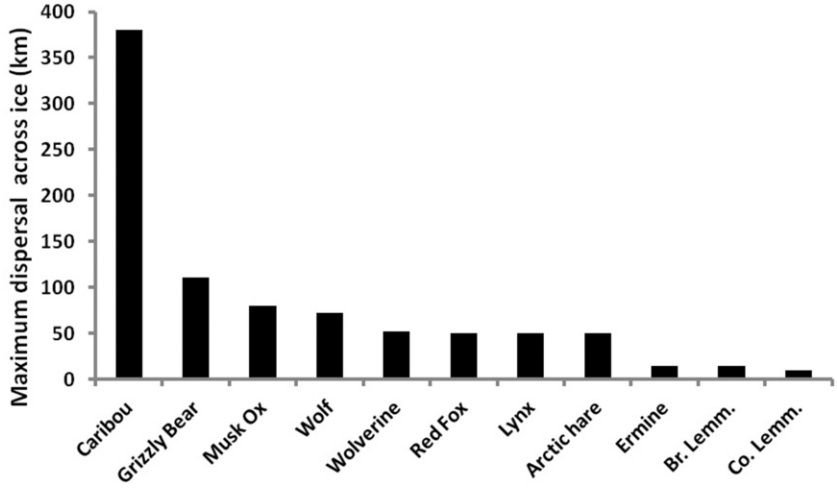

Figure 2. Maximum dispersal distances over ice, based on direct observations and on inferences from current distributions, assuming that the most distant dispersal events in the Arctic all occur over ice, rather than by swimming. Polar Bear and Arctic Fox are omitted because they are ubiquitous.

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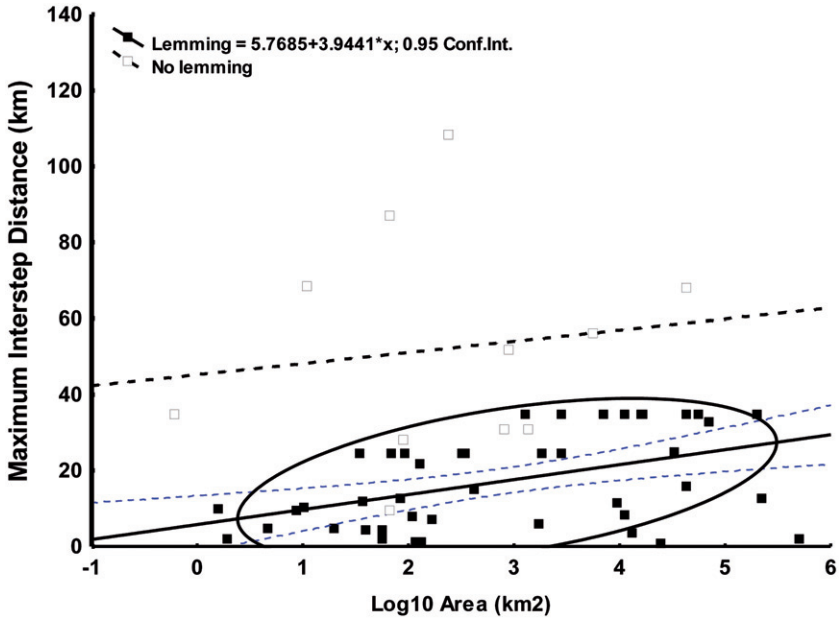

Figure 3. MIDs (the maximum distance between potential stepping-stone islands connecting a given island with the North American mainland, or with Baffin or Ellesmere islands) for islands in the Canadian Arctic with and without Lemmings in relation to island area. For sources, see Appendix 1 (online).

reported for similar-sized mammals swimming (< 3 km; King 1984; Russell, Clout, and McArdle 2004).

Discussion

In the Canadian Arctic, Arctic Hare, Ermine and Collared Lemming occur on Ellesmere and Axel Heiberg islands and many of the Queen Elizabeth Islands. However, it is likely that Arctic Hares and Collared Lemmings persisted in a Canadian high Arctic refugium north of Parry Channel during the Pleistocene glaciations (Fedorov and Stenseth 2002; Waltari and Cook 2005), in which case presumably Ermine could have done so too. Several Canadian islands which lack Lemmings, Ermine and Arctic Hare are more isolated than those north of Parry Channel (Akpatok MID 52 km, Mansel 56 km, Coats 68 km), while Salisbury and Nottingham islands, although having MID of 31 km, are surrounded by waters where pack ice remains mobile in winter, unlike the ice over much of Parry Channel and among the high Arctic islands (Danielson 1971). The absence of Lemmings and Arctic Hare from islands capable of supporting self-sustaining populations of caribou suggests that their absence is the result of a very low likelihood of dispersal across more than 50 km of ice, rather than unsuitability of the islands to support herbivores. Conversely, a periodic appearance of Arctic Hare and Collared Lemming on Prince Leopold Island (MID 10 km) demonstrates that these species are capable of regularly crossing shorter distances over ice. The absence of Red Fox from Coats Islands probably reflects the absence of a suitable prey base, rather than an inability to immigrate, as Red Fox is known to have crossed Hudson Strait and Parry Channel within historic times (Banfield 1954), as well as once being trapped on Coats Island itself (Gaston and Ouellet 1997). The absence of ground squirrels from all islands is presumably related to their hibernation during winter, reducing the opportunity to disperse during the ice-bridge season (Crowell 1986).

There are many small, scattered island groups in eastern Hudson Bay, of which the most extensive is the Belcher Islands. Many of the islands are very small and there are numerous reefs. MIDs are difficult to assess in this situation because it is hard to know what size of island might make an effective stepping-stone. Lemmings have been recorded on some of the island groups (Belchers, King George), but not on others similarly situated (Ottawa, Sleeper islands; Manning 1976). If we assume that islands $< 1\,km^2$ in extent cannot provide suitable stepping stones, then the King George Islands have a MID of 26 km, possibly the farthest crossing made by Lemmings since the Pleistocene.

Currently, climate change is causing diminishing Arctic sea-ice. If, as predicted (Sou and Flato 2009), this trend continues, lengthening of the open water

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season and in particular reduction in ice cover during summer will reduce the opportunity for over-ice dispersal. This will alter the balance of immigration and extinction, increasing the number of islands where species are absent and hence reducing the mean diversity of island mammal faunas (Figure 4). For Lemmings, we can predict increased isolation of island populations (Figure 3), leading to reduced immigration and increased local extinction, the latter process being linked to island area (Figure 5).

The terrestrial mammals of various archipelagoes off Siberia, especially Novaya Zemlya, Severnaya Zemlya and New Siberian Islands could eventually become totally isolated from the Asian continent, as most require dispersal across >30 km of sea which is probably beyond the swimming capacity of any Arctic mammals except Bear and Caribou. Local populations of Lemmings and Ermine may commence diverging from source populations through local adaptation and genetic drift (Berry 1996). The same would apply to populations of the smaller mammals on the islands of eastern Hudson Bay (e.g. Belchers, King George, Digges). Islands to the north of Parry Channel will eventually be isolated from those to the south. However, this is a more distant prospect, given that ice is predicted to persist in this area longer than elsewhere (Sou and Flato 2009). On the smaller islands local populations will begin to 'wink out', as stochastic processes take effect (Lomolino 1994).

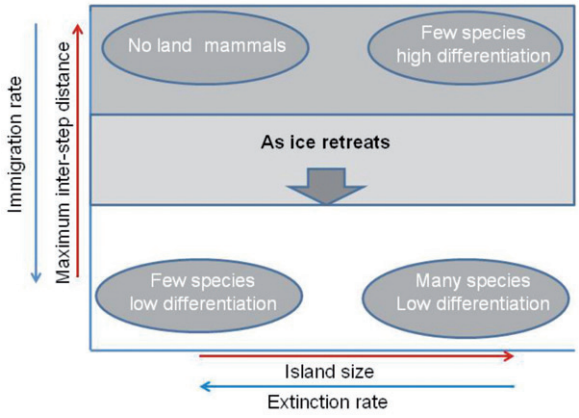

Figure 4. Hypothetical diagram illustrating how mammalian diversity and genetic differentiation are related to MID (assuming isolation increases with MID) and island area (assuming extinction probability is inversely related to island size). As the duration of ice cover in surrounding water decreases (as ice retreats), isolation is assumed to increase, reducing immigration and increasing population differentiation.

With the demise of local lemming and hare populations we can expect changes in vegetation towards less herbivore-resistant plants and the disappearance of predators which specialise on Lemmings, such as Long-tailed Jaegers, *Stercorarius longicaudus*, and Pomarine Jaegers, *S. pomarinus*, (Furness 1987) and Snowy Owls (Gilg, Sittler, and Hanski 2009), leading to a simplification of local food webs. At the same time, decreased accessibility to Arctic Foxes may enable the establishment or increase of ground-nesting birds on small, offshore islands, especially colonial seabirds, such as Atlantic Puffin, *Fratercula arctica*, and Common Murre, *Uria aalge*. As commented by Lomolino (1994) '*Actions disrupting ice cover . . . may severely reduce the diversity of mammalian communities*'. To this we can add 'and substantially alter other ecosystem elements'.

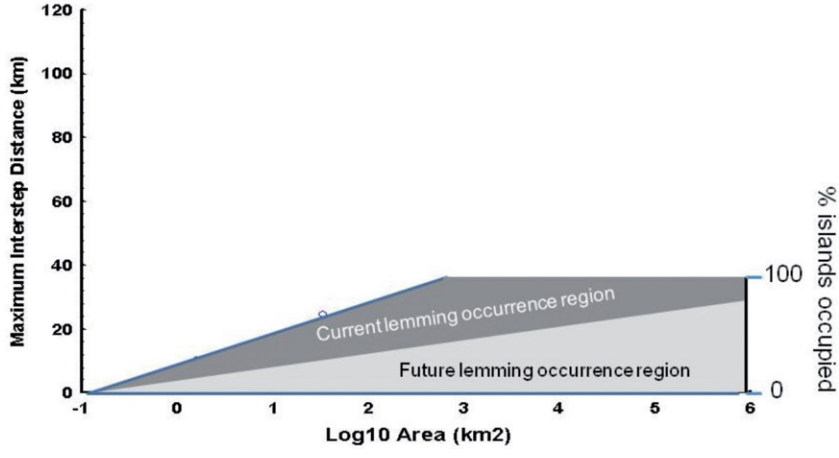

Figure 5. Diagrammatic representation of changes predicted in lemming distributions following reductions in sea ice cover and duration, based on the MID/island area relationship shown in Figure 3. Currently, all islands >1000 km^2 and with an MID of <40 km are occupied (dark grey and light grey areas). As immigration becomes more difficult, the proportion of islands occupied at a given time will diminish so that occupied islands become confined to the light grey area of the diagram.

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We can make one further prediction that, although speculative, could be an important element in constructing a conservation programme for the high Arctic fauna. The gradual disappearance of ice bridges to Arctic islands should inhibit the northward migration of southern predators and competitors of the present Arctic mammal fauna. It may be that at some future time the Arctic islands, especially those of the Canadian Arctic Archipelago, Severnaya Zemlya, the New Siberian Islands and Novaya Zemlya, all rich in Arctic mammals at present and by then surrounded by permanent open water, will provide the last refuge for species such as Lemmings, characteristic of the Pleistocene glacial epoch. In fact there is evidence that at least one island in Severnaya Zemlya retains a relict population of *Dicrostonyx torquatus* characteristic of late-Pleistocene forms (Abramson, Smirnov, and Tikhonova 2004). Many processes other than change in ice cover will influence ecosystem changes under global warming and this makes predicting future ecosystem changes extremely uncertain. Nevertheless, given the substantial dispersal barrier created by open water, we believe that if the Pleistocene fauna is to survive anywhere, it has the best chance to do so on Arctic islands far offshore from the continents. Measures to prevent the immigration of southern species into such islands by means of human agency, either deliberate or accidental should be carefully considered.

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