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Population genetics

Loss of connectivity among island-dwelling Peary caribou following sea ice decline

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Global warming threatens to reduce population connectivity for terrestrial wildlife through significant and rapid changes to sea ice. Using genetic fingerprinting, we contrasted extant connectivity in island-dwelling Peary caribou in northern Canada with continental-migratory caribou. We next examined if sea-ice contractions in the last decades modulated population connectivity and explored the possible impact of future climate change on long-term connectivity among island caribou. We found a strong correlation between genetic and geodesic distances for both continental and Peary caribou, even after accounting for the possible effect of sea surface. Sea ice has thus been an effective corridor for Peary caribou, promoting inter-island connectivity and population mixing. Using a time series of remote sensing sea-ice data, we show that landscape resistance in the Canadian Arctic Archipelago has increased by approximately 15% since 1979 and may further increase by 20–77% by 2086 under a high-emission scenario (RCP8.5). Under the persistent increase in greenhouse gas concentrations, reduced connectivity may isolate island-dwelling caribou with potentially significant consequences for population viability.

1. Introduction

Connectivity is critical for the persistence of natural living populations in dynamic landscapes [1]. By facilitating dispersal, connectivity allows the demographic and genetic rescue of declining populations, alleviating the potential for inbreeding depression and increasing persistence time [2]. Connectivity can indeed facilitate the colonization of suitable habitats that, in a harsh and variable environment, may be crucial to the long-term persistence of populations [2,3]. Doing so, connectivity supports gene flow between populations and enhances local genetic diversity, which reduces inbreeding and eases the effects of genetic drift in small populations [4]. Global warming is expected to have a significant effect on these ecological processes—modifying landscape suitability for species [5] and ushering in rapid changes in connectivity [6,7].

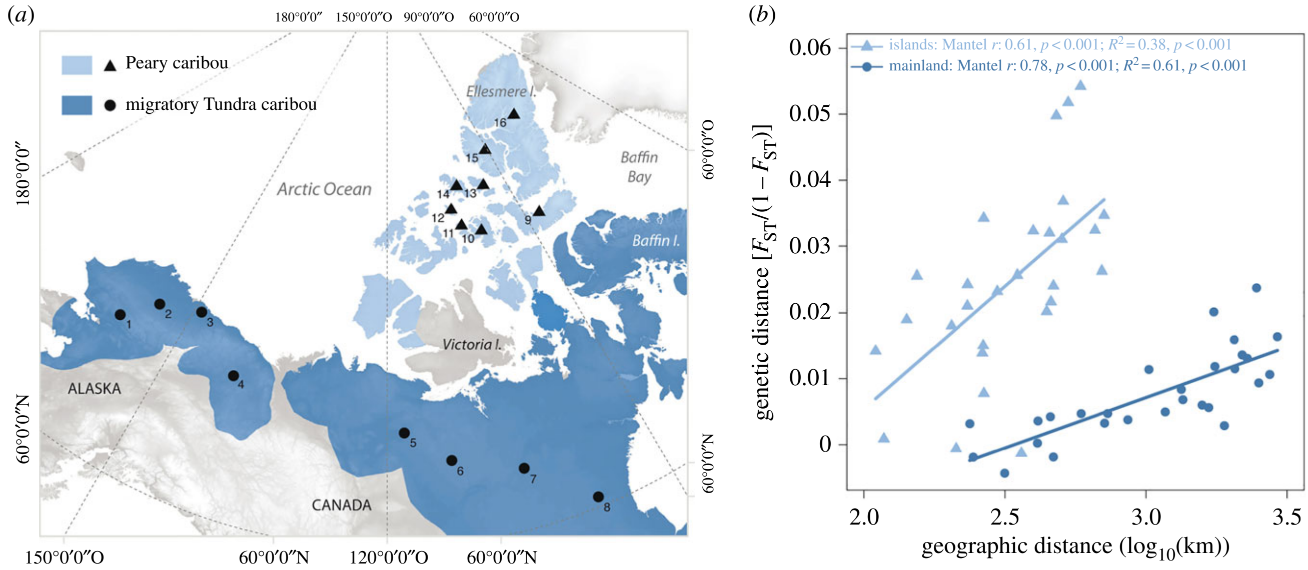

Figure 1. (*a*) Map of the study area. Shaded areas correspond to the range of continental-migratory tundra caribou and island-dwelling Peary caribou. (*b*) Correlation between genetic and geographical distances among caribou populations. Colours correspond to continental (circles; dark blue) and island herds (triangles; light blue), respectively. (Online version in colour.)

Sea ice represents an important bridge for wildlife that use ice as a platform for dispersal and migration [6,7]. Its loss and thinning could impede movement and induce a cascade of unprecedented effects [6]. For Arctic fox (*Vulpes lagopus*), ice allows for long-distance movements, giving rise to a genetically homogeneous population that spans the North American and Svalbard archipelagos [8]. For wolves (*Canis lupus*), it mediates movement among islands and the mainland, allowing for recolonization of extirpated populations [9]. For caribou (*Rangifer tarandus*), sea ice acts as a bridge for seasonal inter-island or island–mainland migrations [10,11]. The long-term viability of island caribou may thus depend on sea-ice connectivity [12].

Compared with herds on the mainland (figure 1), endangered Peary caribou (*R. tarandus pearyi*) occur almost exclusively in the Canadian Arctic Archipelago, which is connected by sea ice most of the year [13]. This subspecies has declined dramatically, driven by extreme, unpredictable weather events and is part of a non-equilibrium grazing system characterized by periodic die-offs and extensive long-distance movements to access forage [14]. Some caribou make extensive and seasonal inter-island movements [10,15]. We surmise that, while island caribou display high levels of connectivity and low genetic distinctiveness among populations, their frequent use of sea ice and low abundance makes them particularly vulnerable to sea-ice loss.

Here we used population genetics, remote sensing and climatic projections to examine how climate change and sea-ice extent modulate population connectivity for island caribou in the most complex archipelago of the Arctic. We asked the following questions: (i) Does genetic structure among Peary caribou differ from migratory tundra caribou on the mainland? (ii) Are genetic exchanges among Peary caribou limited by availability of sea ice for travel between islands? (iii) How will climate change and the retreat of sea ice affect connectivity among caribou in this archipelago? To quantify these relationships, we analysed environmental and genetic patterns across an immense region, spanning most of the North American Arctic.

2. Material and methods

(a) Study area and genetic data

The study area extends across the Canadian Arctic Archipelago and into subarctic Canada and Alaska, USA (figure 1*a*). Genetic samples were obtained from herds of migratory tundra caribou and Peary caribou, and genotyped at 16 microsatellite locus (figure 1*a* and table 1). Pairwise F_{ST} were computed according to Weir & Cockerham [16] (electronic supplementary material).

(b) Analysis of genetic data

We first tested the log-transformed geodesic distances as predictors of genetic differentiation ($F_{ST}/(1 - F_{ST})$) separately among herds of migratory tundra (continental) and Peary caribou (island), referred to as the isolation-by-distance model (IBD). Next, we examined whether current seawater is currently limiting connectivity among Peary caribou, assuming that genetic distances between population pairs increase with cost-weighted distances measured along the optimal least-cost path (LCP) connecting populations. Sea ice should allow caribou movements, while ice-free seawater impedes dispersal among islands [11,17]. We calculated LCP weighted for the presence of seawater using the R package gdistance [18] following a procedure described in [19]. We then contrasted an IBD model (equivalent to a fully permeable landscape), with a model, where land surfaces were assigned a value of 1, while water (with or without ice) was given a lower connectivity value from weak (0.001) to partially permeable (0.9). The connectivity value of water was first evaluated according to an optimization approach (see the electronic supplementary material). To determine which model (IBD or LCP) had the greatest support as a predictor of genetic differentiation, we used three complementary approaches: Mantel tests [20], multiple regressions on distance matrices (MRDM, [21]), and maximum-likelihood population-effects models (MLPE, [22]). We ranked candidate models according to the proportion of explained genetic variance and by calculating Akaike's information criterions (electronic supplementary material).

(c) Connectivity changes overtime

To assess changes in connectivity over time, we retrieved monthly Arctic sea-ice extent from 1979 to 2015 available at the

Table 1. Geographical locations of migratory tundra and island-dwelling Peary caribou (Canada, Alaska). Animal manipulations followed guidelines of the Canadian Council on Animal Care.

ecotype	herd	province/state	country	Lat	Long	*N*
migratory tundra	Western Arctic	Alaska	USA	67.52	−158.3	25[a]
	Teshekpuk	Alaska	USA	69.21	−154.79	20[a]
	Central Arctic	Alaska	USA	70.02	−148.95	22[a]
	Porcupine	Yukon	Canada	67.67	−141.04	29[a]
	Bluenose East	NW Territories	Canada	66.13	−117.85	31[a]
	Bathurst North	NW Territories	Canada	64.44	−112.42	28[a]
	Ahiak/Beverly	Nunavut	Canada	63.255	−104.44	50[a]
	Qamanirjuaq	Nunavut	Canada	60.52	−97.94	22[a]
Peary caribou	Devon Is.	Nunavut	Canada	75.44	−87.63	10[b]
	Bathurst Is. Complex	Nunavut	Canada	75.92	−100.17	20[b,c]
	Cameron Is.	Nunavut	Canada	76.48	−103.91	22[b]
	Lougheed Is.	Nunavut	Canada	77.42	−105.21	42[b]
	Amund Ringnes/Cornwall Is.	Nunavut	Canada	78.08	−95.86	6[b]
	Ellef Ringnes/King Christian Is.	Nunavut	Canada	78.54	−102.29	16[b]
	Axel Heiberg Is.	Nunavut	Canada	79.68	−91.20	20[b]
	Ellesmere Is.	Nunavut	Canada	80.30	−78.10	41[b]
Total						404

[a]Ref. [5].
[b]This study.
[c]Environment and Natural Resource. 2014. Peary caribou DNA sample collections, Bathurst Island Complex, July 1998. Unpublished Data. Government of NWT, Yellowknife, NT.

National Snow and Ice Data Center (University of Colorado, Boulder, CO, USA). Future sea-ice predictions were extracted from the climate EC-Earth model assuming two different emission scenarios, RCP4.5 (moderate) and 8.5 (high), every 10 years, from 2016 to 2086 [23]. We predicted a decrease in connectivity among locations adversely affected by sea-ice decline, owing to longer ice-free seasons. Connectivity was estimated in the past (for each month from 1979 to 2015) and to the future with LCPs calculating: (i) among the eight Peary caribou populations, (ii) on 1000 occurrence points randomly sampled across the Peary caribou range, and (iii) only considering the shortest straight lines between islands. To estimate connectivity change over the years, we next averaged monthly LCP estimates. Based on observations that caribou are reluctant long-distance swimmers [17,24], we followed the protocol above giving sea ice and land mass a value of 1, while ice-free waters were considered not permeable to movement. Because LCPs were all highly correlated (all Pearson's $r > 0.86$), we only presented results based on random occurrences that we considered most representative of connectivity changes in the entire region.

3. Results and discussion

The strong linear correlation between genetic and geodesic distances for both Peary caribou (Mantel's $r = 0.61$, $p < 0.001$; MRDM $R^2 = 0.38$, $p < 0.001$) and continental caribou herds (Mantel's $r = 0.78$, $p < 0.001$; MRDM $R^2 = 0.61$, $p < 0.001$) suggests that populations are isolated by distance irrespective of landscape features (figure 1*b*; table S2). All three statistical methods used to rank models indicated that adding a weight to the water did not explain more genetic variance in comparison with a simple IBD model (ΔAICc < 2; electronic supplementary material, table S2). Caribou are able to swim and cross up to 3–10 km [24], rarely more [17], but swimming is much less efficient and more energetically costly than walking on ice or land mass (see [17] and references therein). Observations of caribou trips of several hundred kilometres on sea ice are regularly recorded, up to a 380 km walk [10]. We observed linear IBD, suggesting that sea ice was an effective corridor allowing connectivity among Peary caribou populations. Additionally, the differences in slope for Peary caribou and migratory tundra caribou can partially be explained by differences of population densities ([25], see electronic supplementary material).

Based on the time series of remote sensing detection of Arctic sea ice, our LCP analysis estimates that landscape resistance in the Canadian Arctic Archipelago increased by roughly 15% between 1979 and 2015, owing to a broader seasonal window without sea ice (figure 2). Our results indicate that the loss of sea ice will translate into an increase in landscape resistance of 20% by 2086 according to the moderate RCP4.5 emission scenario and by up to 77% according to the RCP8.5 scenario (figure 2*a*). This more resistant landscape may adversely affect population connectivity by hampering dispersal, annual migrations and escape from unpredictable but reoccurring episodes of severe weather [10].

In the past, the annual landscape resistance was maximal during the sea ice–free season (mostly September) and minimal the rest of the year (figure 2*b*,*c*). Following RCP projections, the ice-free season will increase in the future, especially according to the RCP8.5 model that predicts an increase of approximately 150% in landscape resistance from July to November (figure 2*b*,*c*).

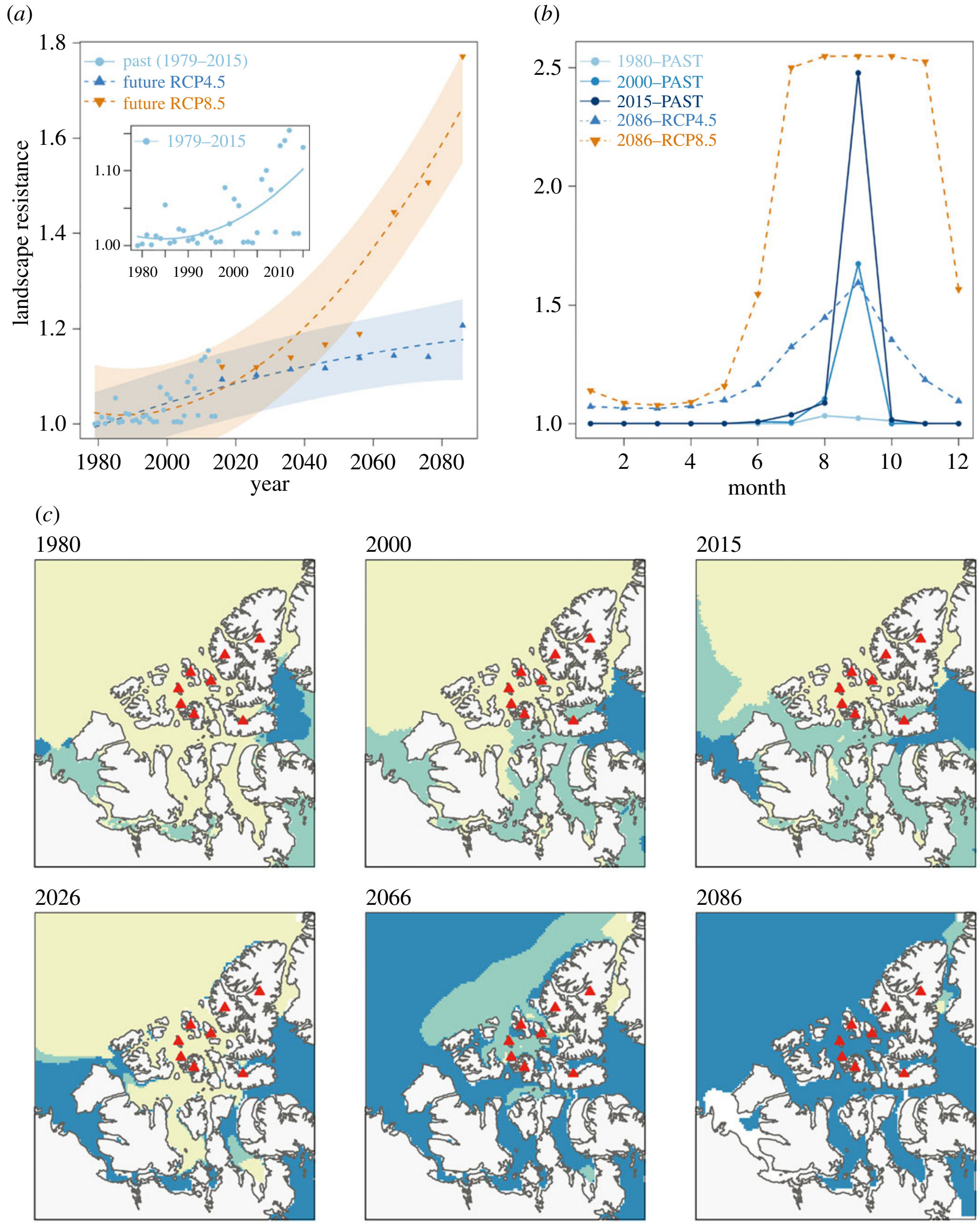

Figure 2. (*a*) Connectivity changes overtime in the Canadian Arctic region for the past (1979–2015) and the next 70 years following the RCP4.5 and RCP8.5 models. The inset details the connectivity trend over 1979–2015. Trend lines and 95% CI of the predicted connectivity changes are represented with solid and shaded areas, respectively; (*b*) monthly connectivity changes over time for selected years between 1980 and 2015 and in 2086 following the RCP8.5 and RCP4.5 models; (*c*) observed (past) and forecasted (future) maximum sea-ice extent in the Canadian Arctic region for selected years between 1979–2015 and 2026–2086 following the RCP8.5 models. Blue: December, green: July, yellow: September. Note that colours overlap and sea-ice extent is always at its maximum in December. Red triangles correspond to sampling location for Peary Caribou. (Online version in colour.)

For Peary caribou, a temporal and spatial shift in sea-ice extent may be adversely critical. Some caribou show fidelity to wintering and calving grounds with access based on inter-island migrations associated with land-fast sea ice [10,15]. Although movement data are limited, spring migration has been recorded in April–June, while autumn movements occurred in September–November [10,15]. Predicted delays in sea-ice formation or early break-up could alter or prevent such migration, with detrimental effects on calving success, body condition and survival. In areas where anthropogenic activities have compromised sea-ice structure (e.g. ice breaking transits), caribou halt migration and aggregate (along the shoreline) until freeze up occurs [12]. Hence, our connectivity estimates are conservative and probably underestimate the impact of sea-ice change on wildlife. Based solely on sea-ice occurrence, they did not include sea-ice quality or structure, which may further influence movement patterns and energetics [15,26]. Compared with species (e.g. Arctic fox) that can use floating sea ice, caribou may only be able to cross when sea ice is stable and continuous. Mortalities, due to drowning or exposure after breaking though ice, have been documented [11–13]. Thus over the long term, the collapse of sea-ice connectivity could increase demographic and genetic isolation, undercutting population viability and persistence.

Data accessibility. Data for this study are available on Dryad [27] or in the electronic supplementary material.

Authors' contributions. L.P. and G.Y. conceived the study. D.A.J., J.A.S., N.L., S.D.C. and G.Y. acquired the genetic data. S.M.O. and D.S. (polar oceanographers) provided oceanographic data. D.A.J., G.Y. and L.P analysed the data, contributed to the interpretation of the results and writing of the paper. All co-authors contributed to the text and interpretation of the results. All authors gave final approval for publication and agreed to be accountable for all aspects of the content therein.

Competing interests. We have no competing interests.

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