Geographic isolation reduces genetic diversity of a wide-ranging terrestrial vertebrate, *Canis lupus*

Salomé A. Frévol[1,2] ⓘ | **Daniel R. MacNulty**[2] | **Morgan Anderson**[3] |
Lindsey E. Carmichael[4] | **H. Dean Cluff**[5] ⓘ | **L. David Mech**[6] | **Marco Musiani**[7]

[1]Université Paris-Saclay, Orsay, France

[2]Department of Wildland Resources and Ecology Center, Utah State University, Logan, Utah, USA

[3]British Columbia Ministry of Forests, Lands, Natural Resource Operations and Rural Development, Prince George, British Columbia, Canada

[4]Department of Biological Sciences, University of Alberta, Edmonton, Alberta, Canada

[5]Environment and Natural Resources, Government of the Northwest Territories, North Slave Region, Northwest Territories, Canada

[6]U.S. Geological Survey, Northern Prairie Wildlife Research Center, Jamestown, North Dakota, USA

[7]Dipartimento di Scienze Biologiche, Geologiche e Ambientali (BiGeA), Università di Bologna, Bologna, Italy

Correspondence
Salomé A. Frévol
Email: salome@frevol.net

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Abstract

Genetic diversity is theorized to decrease in populations closer to a species' range edge, where habitat may be suboptimal. Generalist species capable of long-range dispersal may maintain sufficient gene flow to counteract this, though the presence of significant barriers to dispersal (e.g., large water bodies, human-dominated landscapes) may still lead to, and exacerbate, the edge effect. We used microsatellite data for 2421 gray wolves (*Canis lupus*) from 24 subpopulations (groups) to model how allelic richness and expected heterozygosity varied with mainland–island position and two measures of range edge (latitude and distance from range center) across >7.3 million km^2 of northern North America. We expected low genetic diversity both at high latitudes, due to harsh environmental conditions, and on islands, but no change in diversity with distance to the range center due to the species' exceptional dispersal ability and favorable conditions in far eastern and western habitats. We found that allelic richness and expected heterozygosity of island groups were measurably less than that of mainland groups, and that these differences increased with the island's distance to the species' range center in the study area. Our results demonstrate how multiple axes of geographic isolation (distance from range center and island habitation) can act synergistically to erode the genetic diversity of wide-ranging terrestrial vertebrate populations despite the counteracting influence of long-range dispersal ability. These findings emphasize how geographic isolation is a potential threat to the genetic diversity and viability of terrestrial vertebrate populations even among species capable of long-range dispersal.

KEYWORDS
allelic richness, *Canis lupus*, central-marginal hypothesis, conservation genetics, dispersal, edge effect, expected heterozygosity, genetic diversity, geographic isolation, island effect, wolf

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Salomé A. Frévol and Lindsey E. Carmichael are presently independent researchers.

INTRODUCTION

Genetic diversity is one of three pillars of biodiversity that conservationists seek to maintain, along with species and ecosystem diversity (DeWoody et al., 2021). Populations at the edge of a species' range, which are often smaller and host lower levels of genetic diversity compared with core populations, are particularly vulnerable to stochastic events and genetic drift (Lesica & Allendorf, 1995).

The central-marginal hypothesis (CMH; Eckert et al., 2008), also called the center-periphery hypothesis (Pironon et al., 2016), aims to explain and predict patterns of genetic diversity along the core–edge continuum. The CMH predicts that a decrease in population size and gene flow toward the edges of a species' range increases the relative effect of genetic drift, leading to lower genetic diversity (hereafter "edge effect"; Brussard, 1984; Eckert et al., 2008). Diminished genetic diversity among edge populations might also result from receiving immigrants from fewer source populations (Schwartz et al., 2003) and repeated extinction and recolonization events near the range edge (Mayr, 1942; Volis et al., 2016).

Although the CMH is logically appealing, some researchers have questioned its generality (Dai & Fu, 2011; Eckert et al., 2008). For example, Lira-Noriega and Manthey (2014) found no consistent relationship between genetic diversity and distance from the geographic range center for 40 species including insects, plants, birds, mammals, and worms. Few CMH studies have focused on wide-ranging, highly mobile terrestrial vertebrates (Kyle & Strobeck, 2002; Schwartz et al., 2003), which are notable as they potentially maintain sufficient gene flow across their range such that genetic diversity varies little along the core–edge continuum (Kozakiewicz et al., 2017).

Gray wolves (*Canis lupus*) historically occupied one of the largest ranges of any mammal, spanning much of North America and Eurasia (Young & Goldman, 1944). Currently, North American gray wolves are found from above 80° N in the High Arctic islands and Greenland, through much of continental Canada, Alaska, the Western United States, and Great Lakes area of the Eastern United States (Boitani, 2003; U.S. Fish and Wildlife Service, 2020a). Wolves are highly mobile and disperse long distances across mountains, deserts, and waterways (Jimenez et al., 2017; Linnell et al., 2005; Morales-González et al., 2022; Muñoz-Fuentes et al., 2009), with documented cases of >500-km straight-line dispersal distances (Fritts, 1983; Treves et al., 2009; Wabakken et al., 2007).

Wolves provide the opportunity to determine if terrestrial vertebrate species with high dispersal potential and adaptability to various habitats express patterns of genetic diversity consistent with the CMH. Additionally, the edge effect may interact with the population genetic aspect of the Island Biogeography Theory (MacArthur & Wilson, 1967; Vellend, 2003; Vellend & Geber, 2005), which postulates that loss of genetic diversity to genetic drift, like loss of species diversity, may be substantial in island populations (hereafter "island effect"). Our objective was thus twofold: to determine if geographic patterns of genetic diversity in North American gray wolves are consistent with the CMH, and to assess how the predicted edge effect interacts with the island effect. To that end, we tested how population genetic diversity varies in relation to two indices of the edge effect—latitude (Castellanos-Morales et al., 2014; De Kort et al., 2021; Jenkins et al., 2018; Rodríguez-Rodríguez et al., 2015; Wultsch et al., 2016) and distance to the center of the species' range (Langin et al., 2017; Lima-Rezende et al., 2019; Natesh et al., 2017; Trumbo et al., 2016)—and we evaluated how these relationships are modified by island habitation.

Due to wolves' exceptional dispersal abilities, we predicted that populations at the edge of the species' northern North American range, when measured by distance from the range center, would not have lower genetic diversity than core populations. However, we expected genetic diversity to decrease with increasing latitude due to the increasingly harsh climate conditions and limited prey availability at higher latitudes (Boitani, 2003) that may reduce wolf population densities (Mech, 2005) and limit gene flow from southern populations (Carmichael et al., 2008).

Finally, we expected that genetic diversity would be lowest for island populations (Carmichael et al., 2007; Frankham, 1997; Patiño et al., 2017) and that this island effect would exacerbate the negative effects of distance and latitude on genetic diversity by further reducing dispersal and gene flow.

MATERIALS AND METHODS

Sampling locations and genotyping

We analyzed three previously published datasets (A–C; Carmichael et al., 2007, 2008; McNay, 2006; Musiani et al., 2007) and one new dataset generated for this study (D), for a total of four autosomal microsatellite datasets differing in genetic marker sets (Appendix S1: Figure S1; Frévol et al., 2023). Dataset A includes 1897 wolves from the tundra and boreal zones of Canada and Alaska, and some coastal Pacific and Arctic islands (Carmichael et al., 2007, 2008). Dataset B includes 384 wolves from the central tundra and boreal zones of Canada (Musiani et al., 2007), and Dataset C includes 119 wolves from the boreal zone of interior Alaska (McNay, 2006). Sampling protocols, genetic markers used, and approvals are detailed in each respective study. We did not include samples near

to and south of the Canadian–US border, that is, regions that have been recently recolonized by the species (Boitani, 2003; U.S. Fish and Wildlife Service, 2020a).

Dataset D includes 21 wolves sampled from Ellesmere Island (Umingmak Nuna), Nunavut, that have not been previously analyzed. Ellesmere Island is a 196,235-km^2 island in the Canadian Arctic Archipelago that harbors one of the most northerly distributed wolf populations in the world. Samples were collected over three sampling periods in this edge population: 2005, 2009–2010, and 2014–2017. Wolves were captured and handled following protocols in accordance with applicable guidelines from the American Society of Mammalogists (Sikes et al., 2011) and approved by the Utah State University Institutional Animal Care and Use Committee (protocol # IACUC-2365, 2489). During the first two periods, 48 scat samples (2005: 17 adult scats, 2009–2010: 31 pup scats) were collected from around active dens. An additional tissue sample was collected from an adult male wolf fitted with a GPS collar in 2009 (Mech & Dean Cluff, 2011). During the 2014–2017 period, genetic samples were collected from 10 wolves fitted with GPS collars, from ear biopsies, blood, and hair samples. An additional hair sample was collected from a breeding female found dead in 2015 (Anderson et al., 2019).

For Dataset D, DNA was extracted from scat samples using QIAGEN Stool Minikits, and from tissue samples using QIAGEN DNeasy Blood and Tissue Kits, following standard protocol (https://www.qiagen.com/us/resources/resourcedetail?id=68f29296-5a9f-40fa-8b3d-1c148d0b3030&lang=en). A total of 22 dinucleotide microsatellite markers developed from the Dog Genome Project, located on different chromosomes and known to amplify effectively in wolves, were genotyped from these samples: C01.251, C02.30 (Breen et al., 2001; Ostrander et al., 1993), CPH9 (Fredholm & Winterø, 1995), AHT121 (Holmes et al., 2009), REN145P07, REN183B03, REN262I12, REN85N14, REN181L14, REN210D03, REN316E23, REN69B24, REN105L03, REN233H01, REN112G06, REN68B08, REN144A06, REN297N05, REN199O08, REN94H15, REN66E15, and REN106I06 (Breen et al., 2001).

We kept only markers shared between Datasets C and D, both of which were sampled in a relatively small geographic area, to ensure that all markers in all datasets were sampled in at least two geographic locations, which is necessary for identifying trends in genetic diversity (Appendix S1: Figure S1): CPH9, AHT121, REN105L03, REN199O08, REN112G06, REN144A06, REN233H01, REN297N05, REN316E23, REN85N14, REN181L14, REN106I06, REN183B03, REN210D03, and REN66E15. Datasets A (15 markers) and B (13 markers) did not share markers with each other or Datasets C and D, but were both sufficiently expansive to encompass multiple

locations. We recognize that there was some unsampled subspecific variation within our study area, especially in the Arctic islands, but we doubt this affected our results given the otherwise extensive geographic coverage of our sampling (Appendix S1: Figure S1).

Defining wolf groups and species range center

Patterns of population structure for North American gray wolf populations have been elucidated in past studies (Carmichael et al., 2007; Musiani et al., 2007; Schweizer et al., 2016; Sinding et al., 2018; Stronen et al., 2014; Weckworth et al., 2005) with several factors hypothesized to influence the observed genetic clusters: islands (Carmichael et al., 2001), separation at the northern tree line (Musiani et al., 2007), prey specialization and migration linked to migratory caribou herds (*Rangifer tarandus groenlandicus*; Heard & Williams, 1992; Walton et al., 2001), climate (Geffen et al., 2004), and isolation by distance (Geffen et al., 2004).

We identified 24 possible wolf subpopulations (hereafter "groups"; Figure 1) based on prior knowledge of genetic cluster delimitations (Carmichael et al., 2007; Schweizer et al., 2016), ecotypes (Carmichael et al., 2007; Musiani et al., 2007; Schweizer et al., 2016), land cover (e.g., forest or tundra), island delineations, and caribou herd migration patterns (Carmichael et al., 2007; Musiani et al., 2007). We also used country and province borders to separate particularly large groups, or in the absence of these (e.g., Baffin Island), split a group in the middle to account for isolation by distance (Geffen et al., 2004), such that geographic measures such as latitude more accurately represented sampled individuals.

Patterns of genetic diversity along the core–edge continuum may be expected to interplay with other patterns of variation such as differentiation between the wolf ecotypes described in the study area. However, genetic diversity does not appear to differ between mainland ecotypes (Carmichael et al., 2007; Musiani et al., 2007; Schweizer et al., 2016), and our use of neutral markers (rather than genes under selection) may reflect patterns of genetic diversity present in groups regardless of their subdivision into subspecies or ecotypes.

We used QGIS 3.16 to determine (1) the spatial boundaries and geographic centroid of each group (Figures 1 and 2), and (2) the geographic centroid of the group centroids (Figure 2). The latter corresponds to the center of the sampled range (i.e., the geographic center of our study area), and represents our proxy for the species' range center. The true center of the species' North American range is probably some distance south of our
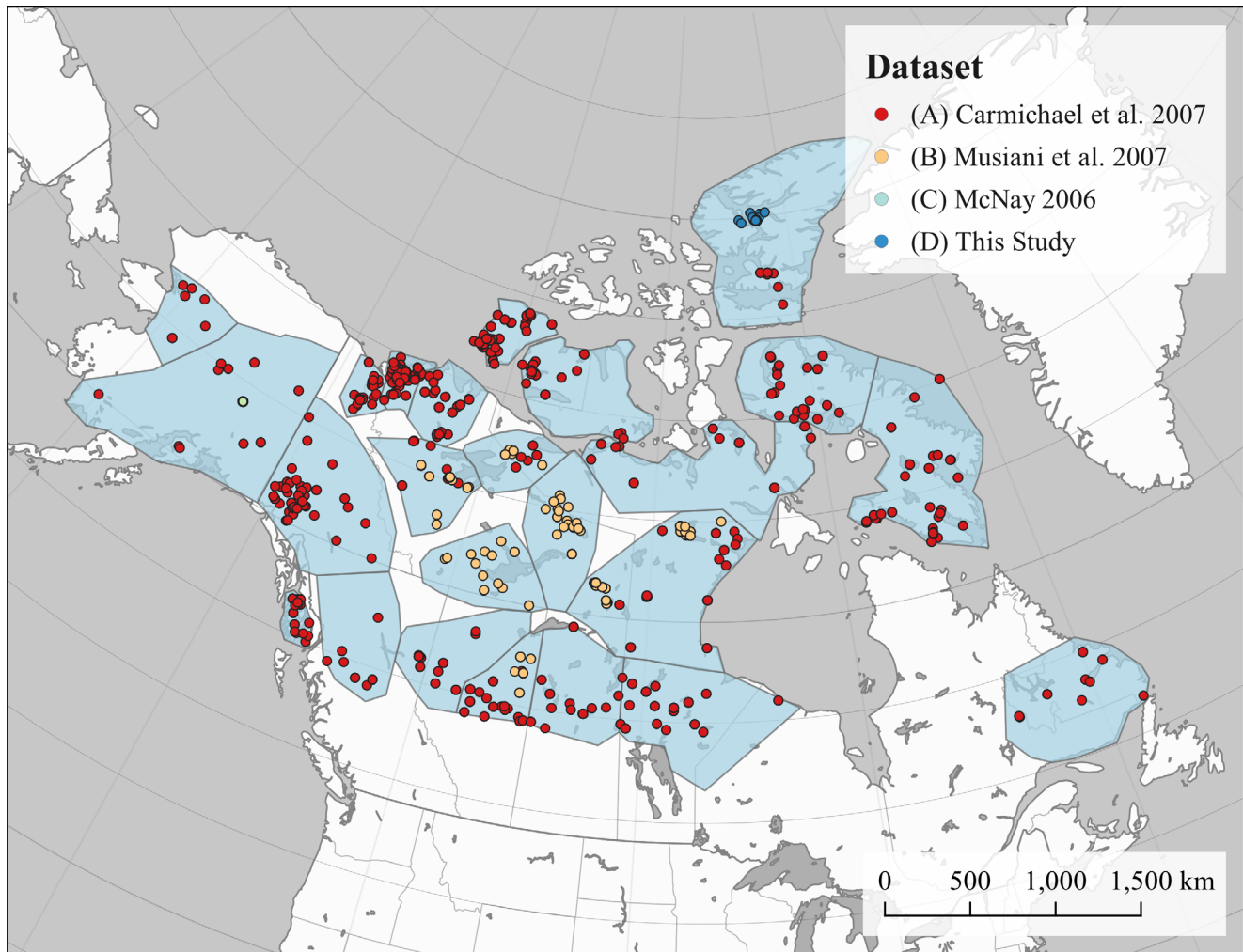
FIGURE 1 Geographic distribution of 24 putative North American gray wolf groups (blue polygons) and four autosomal microsatellite datasets included in this study (A–D). Points may represent ≥1 sampled individual (see Appendix S1: Figure S1 for dataset sampling extents).

proxy range center given that our data do not include wolves living near or south of the Canadian–US border.

Measuring geographic isolation

We defined two continuous indices of geographical isolation for each group: latitude of the group center and distance of the group center from the sampled range center (Figure 2; Table 1). We also defined a categorical variable (Location) with two levels (mainland and island) that classified each group according to whether it inhabited the mainland or any of the Arctic or Pacific Coast islands.

Genetic diversity modeling

We identified scoring errors and the presence of null alleles using MICROCHECKER v2.2.3 for each wolf group (Van Oosterhout et al., 2004). We also tested markers in each

dataset and group for deviations from Hardy–Weinberg equilibrium and for linkage disequilibrium using the exact probability test in Genepop v4.2 (Rousset, 2008; Appendix S2). Error rates were adjusted using a Bonferroni correction adapted to the number of markers per dataset.

We used the well-established allelic richness (AR) and Nei's unbiased expected heterozygosity (H_e; Nei & Roychoudhury, 1974) as measures of group genetic diversity. We used both measurements because AR measures the number of alleles in a population standardized by sample size and is a measure of the raw amount of variation at loci, whereas H_e accounts for both the number of alleles and the evenness of allele frequencies. We calculated AR using the rarefaction method implemented in FSTAT v2.9.4 (Goudet, 2003) and obtained H_e using Genetix v4.05.2 (Belkhir et al., 2004).

Using different datasets with differing markers sampled could hinder direct statistical comparison (de Groot et al., 2016). All microsatellite allele data were derived using the same capillary electrophoresis technique, but
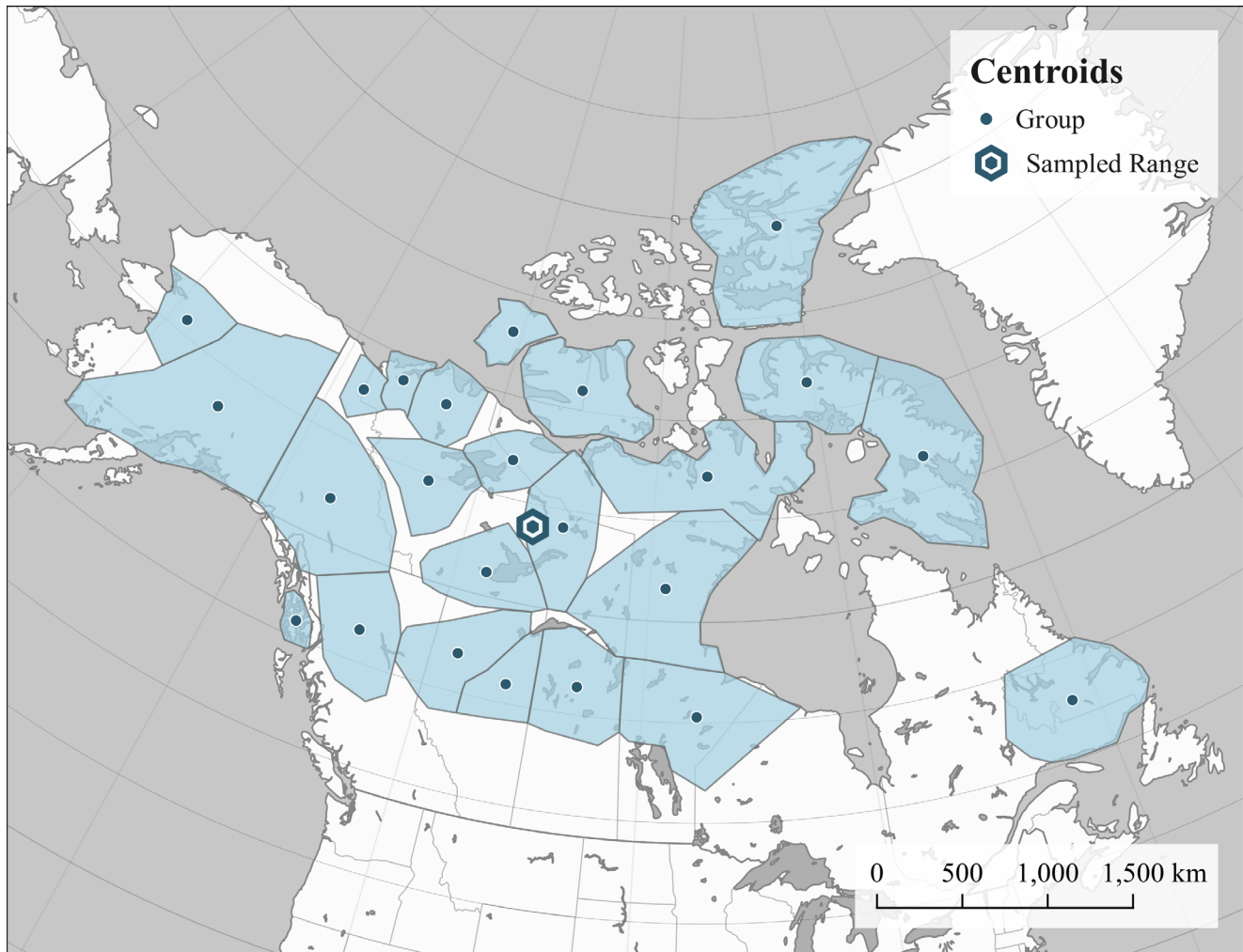
FIGURE 2 The degree of geographic isolation of wolf groups in northern North America was measured as the latitude and Euclidean distance between each group centroid and the sampled range centroid.

TABLE 1 Indices of geographic isolation hypothesized to reduce genetic diversity of wolf groups in northern North America.

Variable	Definition
Distance	Distance of the group centroid to species' sampled range centroid
Latitude	Latitude of the group centroid
Location	Mainland or island habitation

between-dataset calibration was not possible due to differences in focal markers and laboratories performing genotyping. Thus, we analyzed AR, which is sensitive to marker identity (Bashalkhanov et al., 2009), using only the dataset with the greatest spatial extent (Dataset A). We used linear mixed models (LMMs) in R package lme4 (Bates et al., 2015) to analyze AR after checking that it approximated a normal distribution. All LMMs included marker identity as a random intercept (Bolker et al., 2009).

Expected heterozygosity is less sensitive to marker identity because it is defined by relative allele frequencies as well as number of alleles. Thus, we scaled H_e estimates from 0 to 1 following Smithson and Verkuilen (2006) and analyzed these scaled estimates across all four datasets using generalized linear mixed models (GLMMs) with a beta family and logit link in R package glmmTMB (Brooks et al., 2017; Appendix S3). GLMMs included marker identity as a random intercept, which accounted for differences in genetic diversity among markers and unmeasured differences among datasets (including differences among personnel who completed microsatellite calling), as each consistently used a specific set of markers.

We compared multiple models for AR and H_e, including intercepts-only null models (Appendix S3: Table S1). In models including the Location variable, mainland was the reference category. Models including interaction terms also included the main effects in the interaction. The best models explaining AR and H_e were selected

using the Akaike information criterion corrected for small sample size (AIC$_c$; Konishi & Kitagawa, 2008) and the Akaike weight (W; Wagenmakers & Farrell, 2004), which represents the relative likelihood of a model given the candidate set of models. We identified biologically significant variables in our regression models if the estimated 95% CI for the corresponding coefficient excluded zero. We plotted predicted values and CIs for the best fit models of AR and H$_e$ using R package ggplot2 (Wickham, 2016) and compiled graphs with R package gridExtra (Auguie, 2017).

RESULTS

Allelic richness

Two equally competitive models (ΔAIC$_c$ < 2) best explain variation in AR (Table 2). Both include covariates for a wolf group's distance from the sampled range center (Distance) and for geographic location indicating whether the group inhabited an island or the mainland (Location; Table 1). The top model includes an additive effect of Distance and Location (ΔAIC$_c$ = 0) but the model that includes an interactive effect between Distance and Location is equally competitive (ΔAIC$_c$ = 0.43). The null model fits the data poorly (ΔAIC$_c$ = 179.64), implying that the overall influence of the edge and island effects on AR was strong.

Coefficients for the Distance × Location model (Table 3a) and the Distance + Location model (Table 3b) indicate that a group's AR decreased with its distance from the sampled range center and according to whether the group inhabited an island (Figure 3a). The Distance × Location interaction suggests that the island effect strengthened the negative effect of distance from the sampled range center, although the 95% CI for the interaction term overlaps zero.

TABLE 2 Model selection results for linear mixed models describing the effects of geographic isolation on allelic richness of wolves in northern North America.

Model	LL	K	AIC$_c$	ΔAIC$_c$	W
Distance + Location	**−397.76**	**4**	**803.61**	**0.00**	**0.55**
Distance × Location	**−396.95**	**5**	**804.04**	**0.43**	**0.44**
Latitude × Location	−400.87	5	811.88	8.27	0.01
Latitude + Location	−403.11	4	814.31	10.70	0.00
Location	−404.16	3	814.38	10.76	0.00
Latitude	−465.18	3	936.42	132.80	0.00
Distance	−475.70	3	957.46	153.84	0.00
Null	−489.61	2	983.25	179.64	0.00

Note: Log-likelihood (LL), number of parameters (K), corrected Akaike information criterion (AIC$_c$), differences in AIC$_c$ compared to the best scoring model (ΔAIC$_c$), and AIC$_c$ weights (W) are given for each model. Models that are plausibly the best (ΔAIC$_c$ < 2) appear in boldface.

TABLE 3 Best fit linear mixed models for the effects of geographic isolation on allelic richness of wolf groups in northern North America.

Model/parameter	β	SE	t	95% CI
(a) Distance + Location				
Intercept	5.19	0.19	27.21	4.82, 5.57
Distance	−0.15	0.04	−3.60	−0.24, −0.07
Location:island	−1.36	0.10	−14.16	−1.55, −1.17
(b) Distance × Location				
Intercept	5.20	0.19	27.22	4.82, 5.57
Distance	−0.13	0.05	−2.81	−0.22, −0.04
Location:island	−1.32	0.10	−12.98	−1.52, −1.12
Distance × Location:island	−0.15	0.12	−1.27	−0.38, 0.08

Note: Model coefficient (β), SE, and t value (t) are given for each model variable. The reference location is mainland.
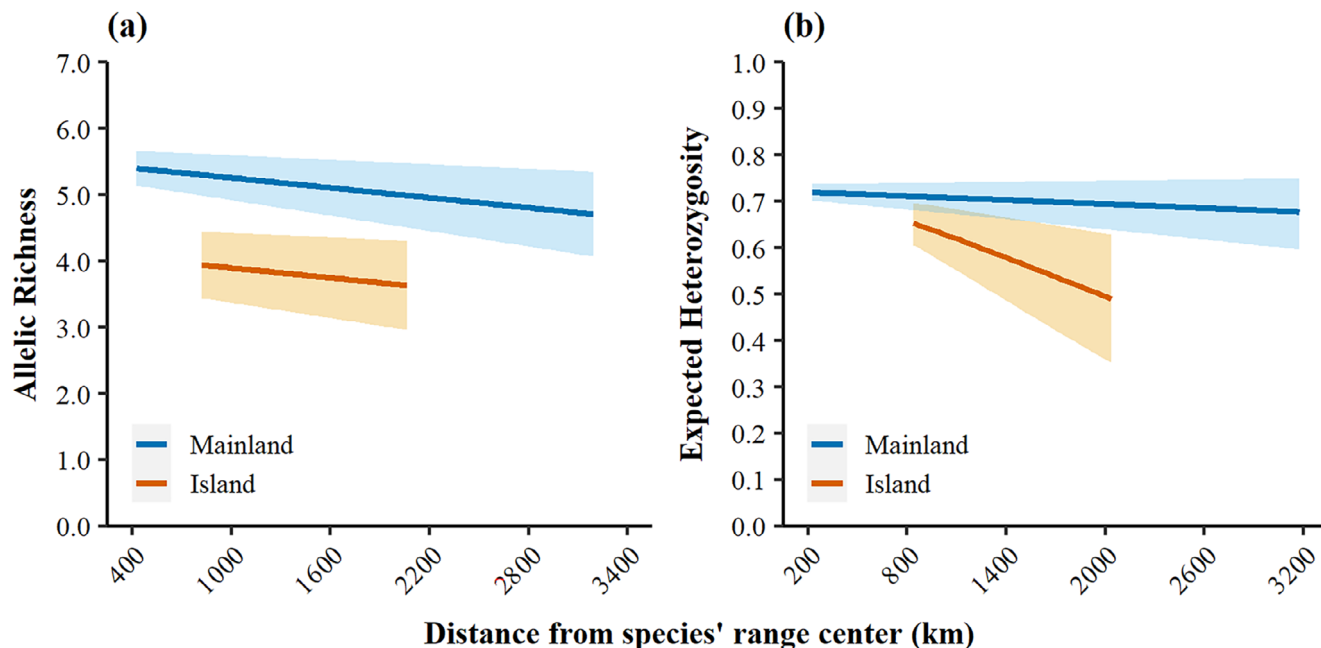
FIGURE 3 Effects of geographic isolation (distance to species' sampled range center in kilometers and island habitation) on the allelic richness (AR) (a) and expected heterozygosity (H_e) (b) of 2421 wolves from 24 groups across northern North America. Lines are population-averaged fitted values with 95% CIs (shaded areas) from the best fit models of AR (Table 3a) and H_e (Table 5). Differences in the range of the x-axes in (a) and (b) reflect minor differences in the spatial extent of the AR and H_e datasets. Due to the geography of North America, island groups with centroids <800 km of the centroid of wolf distribution are nonexistent and were not fitted; likewise, no islands were sampled beyond 2100 km of the centroid of wolf distribution.

Expected heterozygosity

The model describing an interactive effect of distance from the sampled range center and mainland–island position on H_e (Distance × Location) outperformed all other models, which performed poorly ($\Delta AIC_c > 18$; Table 4). The null model also fits the data poorly ($\Delta AIC_c = 141.09$), which indicates an overall strong influence of edge and island effects on H_e.

The best model for H_e describes a reduction of genetic diversity on islands compared with the mainland with a 95% CI for the Distance × Location interaction that excluded zero, indicating strong support for synergistic edge and island effects. The negative effect of distance on H_e was measurably stronger for island groups than it was for mainland groups (Table 5; Figure 3b).

DISCUSSION

Despite the logical appeal of the CMH, its applicability may vary according to a species' ecology and the physical properties that shape its range (Dai & Fu, 2011; Eckert et al., 2008). We sought to determine if the CMH's central prediction—that genetic diversity decreases in edge populations—applies to a terrestrial vertebrate species

with exceptional dispersal ability, such as the gray wolf. To do so, we compiled and analyzed microsatellite data for 2421 wolves in a study area spanning >7.3 million km^2 of northern North America, comparable in size to a few other studies that also focused on wolf genetics at a continental scale (Geffen et al., 2004; Schweizer et al., 2016; Vonholdt et al., 2011).

Consistent with the CMH's central prediction, we found that genetic diversity of wolf groups decreased with distance from the sampled range center irrespective of the wolf's long-range dispersal ability. Models accounting for distance from the range center and mainland–island position, as well as the interaction between the two variables, best explain patterns of wolf genetic diversity with respect to AR and H_e.

Our results are also consistent with an island effect. Wolves can swim across open water (Stronen et al., 2014) and travel long distances across frozen water bodies (Anderson et al., 2018; Mech & Dean Cluff, 2011). Nevertheless, we found that island groups exhibited less genetic diversity than did mainland groups, consistent with previous studies of wolves (Adams et al., 2011; Carmichael et al., 2008; Hedrick et al., 2014; Räikkönen et al., 2009; Robinson et al., 2019) and other species (see review by Frankham, 1997). Our results add to this body of knowledge by demonstrating how the detrimental

TABLE 4 Model selection results for beta regression models describing the effects of geographic isolation on expected heterozygosity of wolves in northern North America.

Model	LL	K	AIC$_c$	ΔAIC$_c$	W
Distance × Location	**355.06**	**5**	**−699.98**	**0.00**	**1.00**
Distance + Location	344.95	4	−681.81	18.17	0.00
Latitude × Location	345.62	5	−681.10	18.88	0.00
Latitude + Location	341.74	4	−675.39	24.59	0.00
Location	338.91	3	−671.76	28.22	0.00
Latitude	309.75	3	−613.44	86.54	0.00
Distance	295.60	3	−585.14	114.84	0.00
Null	281.46	2	−558.89	141.09	0.00

Note: Log-likelihood (LL), number of parameters (K), corrected Akaike information criterion (AIC$_c$), differences in AIC$_c$ compared to the best scoring model (ΔAIC$_c$), and AIC$_c$ weights (W) are given for each model. The best model is in bold.

TABLE 5 Best fit beta regression model for the effects of geographic isolation on expected heterozygosity of wolf groups in northern North America.

Parameter	β	SE	Z	95% CI
Intercept	0.88	0.09	9.99	0.71, 1.05
Distance	−0.04	0.03	−1.49	−0.10, 0.01
Location:island	−0.43	0.07	−6.48	−0.57, −0.30
Distance × Location:island	−0.32	0.07	−4.50	−0.46, −0.18

Note: Model coefficient (β), SE, and Z value (Z) are given for each model variable. The reference location is mainland.

effect of island habitation on genetic diversity increases with distance to the species' range center, which is especially evident in our analysis of H$_e$. The stronger effect of distance on island groups found with H$_e$ compared with AR may stem from heightened sensitivity of H$_e$ to loss of genetic diversity due to reduced gene flow in smaller populations (Barrandeguy & García, 2021). Overall, we provide rare empirical support for the patterns of genetic diversity predicted by the CMH when "edge" is defined by distance from the range center.

Contrary to expectations, we found little support for the hypothesis that genetic diversity of wolf groups decreased with increasing latitude, despite the generally severe environmental conditions at high latitudes. This result contrasts with empirical studies of other mammals (Castellanos-Morales et al., 2014; Jenkins et al., 2018; Rodríguez-Rodríguez et al., 2015), but it is consistent with studies demonstrating wolf adaptations to the extreme climatic conditions found in northern and Arctic regions (Carmichael et al., 2008; Dalerum et al., 2018; Hendricks et al., 2019), as well as previous findings that low-latitude coastal islands were not on the whole more genetically diverse than higher latitude Arctic islands (Carmichael et al., 2007).

Although the genetic markers used in this study reflect recent conditions more than long-term conditions,

our results provide some potential insight about the role of historical climate during the Last-Glacial Maximum on genetic diversity of wolves (see the methodological approach in Yannic et al., 2014, which also used autosomal microsatellites as markers). The absence of an effect of latitude on genetic diversity in the samples we analyzed suggests a relatively weak influence of historical climate factors on contemporary geographic patterns of genetic diversity of wolves in northern North America. This could be related to the presence of higher latitude ice-free refugia in Greenland and Alaska that, like the low-latitude refugia in Southern United States and Mexico, may have been continuously inhabited by wolves during glacial periods (Nowak, 2003).

Conservation applications

The level of neutral genetic diversity found in edge populations, including islands, relative to core populations provides conservationists with information on evolutionary processes outside of selection, most significantly on the relative effects of gene flow and drift in populations of interest (Moritz, 2002). This study therefore has practical applications for conservation planning in wolves and other species.

Our results support previous research indicating that island wolf populations are vulnerable to reduced gene flow that may diminish genetic diversity and population viability. Island wolves in the Arctic and west coast of Canada do not currently exhibit any deleterious effects of decreased genetic diversity comparable to those observed in Isle Royale wolves prior to genetic rescue (Adams et al., 2011; Hedrick et al., 2014; Räikkönen et al., 2009; Robinson et al., 2019). Nevertheless, wildlife managers might consider monitoring the genetic diversity of island populations, especially those located at the edge of the species' distribution. There, they face the combined effect of distance from the range center and island isolation.

Historical factors that were not directly accounted for in this study may also contribute to shaping current patterns of genetic diversity of wolf populations, for example, island populations may be more susceptible to the past and present effects of human activity as population and genetic rescue by immigration to these populations is more limited. This further emphasizes the need to monitor these populations for loss in genetic diversity and the effects of human activity.

Artificial islands resulting from historical processes are also worth considering when assessing conservation needs. Wolf populations in the contiguous United States and Mexico, which form the southern edge of the North American range, were eliminated nearly entirely in the early to mid-1900s (U.S. Fish and Wildlife Service, 2020a). Following reintroduction efforts and successful dispersal, some of the past range has been recolonized, though some southern and western populations remain partially isolated in a metapopulation structure similar to European wolves (Boitani et al., 2018; U.S. Fish and Wildlife Service, 2020a). Knowledge about the genetic diversity of these lower 48 wolf populations is important because diminished genetic diversity is one of several potential threats considered in decision-making about the classification of the gray wolf under the Endangered Species Act (U.S. Fish and Wildlife Service, 2009, 2020b). Our results suggest the potential for reduced genetic diversity in some of these population due to their island-like isolation and relatively long distance from the species' North American range center.

Our findings are also applicable to other terrestrial vertebrates characterized by excellent dispersal ability and expansive historical ranges. Bengal tigers (*Panthera tigris tigris*) have the highest genetic diversity of the extant tiger subspecies and, like gray wolves, are capable of long-range dispersal through a variety of habitat types (Mondol et al., 2009). However, they occupy highly fragmented habitat islands (Goodrich et al., 2015), where genetic erosion might be a conservation problem (Bay et al., 2014). Our results suggest that terrestrial vertebrate populations located in habitats that are both geographically isolated and near the distribution edge may host less genetic diversity, and thus be more prone to declines if subject to environmental or human impacts (Bijlsma et al., 1999; Sgrò et al., 2011; Spielman et al., 2004).

CONCLUSION

Broadly, there is value in evaluating how well ecological theories such as the CMH explain observed ecological patterns in species regardless of conservation concern, especially since it has not been universally supported (Eckert et al., 2008). We found some support for the CMH in a species with ecological traits that could counteract the predicted loss of genetic diversity at the range edge. Knowing this provides important information for the successful long-term management of the species, as wolves are still endangered in many regions (Boitani et al., 2018; Fritts et al., 2003). Our study emphasizes the need to target monitoring and conservation efforts of highly mobile terrestrial species to islands that are peripheral to their distributions, as geographic isolation remains a threat to the genetic diversity and viability of terrestrial vertebrate populations among species capable of long-range dispersal.

AUTHOR CONTRIBUTIONS

All authors contributed to the study conception and design. Material preparation and data collection for the Ellesmere data were performed by Daniel R. MacNulty, Morgan Anderson, H. Dean Cluff, and L. Dave Mech. Data analysis was performed by Salomé A. Frévol and Daniel R. MacNulty. The first draft of the manuscript was written by Salomé A. Frévol, and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

ORCID

Salomé A. Frévol https://orcid.org/0000-0002-3336-4148

H. Dean Cluff https://orcid.org/0000-0002-9233-1450

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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