ARTICLE

Density and genetic diversity of grizzly bears at the northern edge of their distribution

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Abstract

Species at the periphery of their range are typically limited in density by poor habitat quality. As a result, the central–marginal hypothesis (CMH) predicts a decline in genetic diversity of populations toward the periphery of a species' range. Grizzly bears (*Ursus arctos*) once ranged throughout most of North America but have been extirpated from nearly half of their former range, mainly in the south. They are considered a species at risk even in Canada's remote North, where they occupy the northernmost edge of the species' continental distribution in a low-productivity tundra environment. With climate change, one of their main prey species in the tundra (caribou), which has always shown yearly fluctuations, is declining, but simultaneously, grizzlies appear to be expanding their range northward in the same tundra environment. Yet, a lack of population density estimates across the North is hindering effective conservation action. The CMH has implications for the viability of peripheral populations, and the links between population fluctuations, potential bottlenecks, and genetic diversity need to be determined to contribute to species' conservation. Using noninvasive genetic sampling from 2012 to 2014 and autosomal DNA genotyping (via microsatellites), we estimated bear density using a spatial capture–recapture framework and analyzed genetic diversity using observed heterozygosity (Ho), allelic richness (AR), and expected heterozygosity (He). We compared our findings to other studies that used comparable methodologies on grizzly bears and a related species (black bears; *Ursus americanus*). We found densities of grizzly bears that were low for the species but characteristic for the region (5.9 ± 0.4 bears/1000 km^2), but with high Ho (0.81 ± 0.05), AR (7 ± 0.78), and He (0.71 ± 0.03), despite a signal of recent bottlenecks. In both species, peripherality was not correlated with Ho but was negatively correlated with density. We suggest that the apparent growth of this expanding population of grizzlies offsets the negative impacts of recent bottlenecks on Ho. Indigenous knowledge provides historical context (on the order of centuries, e.g., arctic large mammal fluctuations, grizzly bear

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bottlenecks) for the current bear population dynamics (on the order of decades, e.g., climate change, northern grizzly bear expansion).

INTRODUCTION

Compared to a species' core populations, peripheral populations are typically limited in density by poorer habitat quality, which can result in lower genetic diversity and greater impacts from genetic drift (Antonovics, 1976; Brussard, 1984; Eckert et al., 2008; Sagarin & Gaines, 2002). In addition, peripheral populations may be at greater risk of inbreeding depression (Bijlsma et al., 2000; O'Grady et al., 2006). These characteristics can compromise evolutionary potential of peripheral populations, making them less resilient to variations in environmental conditions (Hoffmann & Sgró, 2011; Hughes et al., 2008). The central–marginal hypothesis (CMH) provides a theoretical framework for interpreting such spatial variation in genetic diversity and accordingly predicts a decline in the genetic diversity of populations at the periphery of a species range (Eckert et al., 2008).

High-latitude regions may be experiencing range expansions for some species in relation to climate change (Gibson et al., 2009). However, populations at high latitudes are also subject to extreme environmental fluctuations, which might prompt similar fluctuations in density and genetic diversity (Carnaval et al., 2009; Yannic et al., 2014). Northern populations might therefore undergo periods at very low numbers (bottlenecks) that are known to contribute to genetic drift (Campos et al., 2010). Yet, obtaining the much-needed sampling and count data to study these changes is challenging at high latitudes due to extreme weather conditions and the difficulty of human access owing to a lack of infrastructure (International Expert Panel on Science Priorities for the Canadian Arctic Research Initiative, 2008). Similar challenges are typically experienced while attempting to conduct research on sensitive wildlife species, including bears at high latitudes (Evans et al., 2003).

Continental North America is inhabited by two bear species: black bears (*Ursus americanus*), and grizzlies. In the past, grizzlies had been largely extirpated in the southern part of North America (Figure 1) (Kellert et al., 1996; Laliberte & Ripple, 2004; Miller, 1990). Then, the species became largely protected, but even in the North, they are still designated as a species of "Special Concern" under Canada's Species at Risk Act in 2018 (SARA

Species at Risk Act, 2018). In the Northwest Territories (NT), Canada, barren-ground grizzly bears occupy the northernmost edge of the species' continental distribution, a low-productivity tundra environment characterized by a short growing season (Dumond et al., 2015; McLoughlin et al., 2003). Barren-ground grizzly bears appear to occur at lower densities in the NT than more southerly populations of grizzlies (Dumond et al., 2015), with individual home ranges among the largest in North America (Gau et al., 2004; McLoughlin et al., 1999). The primary threats to grizzly bears here include overhunting and other human-caused mortality, as well as a reduction in the availability of barren-ground caribou (*Rangifer tarandus*) as a fundamental prey resource (Gau et al., 2002; McLoughlin et al., 2002, 2003; Vors & Boyce, 2009). Somewhat in contrast to these ongoing conservation concerns, grizzly bears may also be currently expanding northward and westward in regions including the NT (Clark, 2007; Clark et al., 2019; Doupé et al., 2007; Pongracz et al., 2017; Rockwell et al., 2008). If the species is indeed expanding its range, genetic signals of population expansion (Zenger et al., 2003) are likely.

Overall, estimates of grizzly bear density and genetic diversity in the NT are lacking as in other northern reaches of the species' distribution, in part due to the typical logistical constraints of field studies in the northern tundra (Banci et al., 1994; Dumond et al., 2015; McLoughlin et al., 2003). This lack of population data hinders effective species management. Bear studies on such matters can provide information (e.g., lower than expected density or genetic diversity) to be incorporated in recommendations to management authorities for action and policy development, which are crucial for the species survival (Baciu et al., 2022).

Our study therefore had the following objectives: to estimate the (1) genetically assessed effective population size (Nei & Tajima, 1981); (2) signatures of past bottlenecks or of population expansion; (3) genetic diversity in a grizzly bear population inhabiting the margins of its continental distribution in North America; and (4) population density. As an additional objective, we evaluated our study's estimates for density and genetic diversity (using the common metric of observed heterozygosity, Ho, as a proxy) in view of other studies on black and
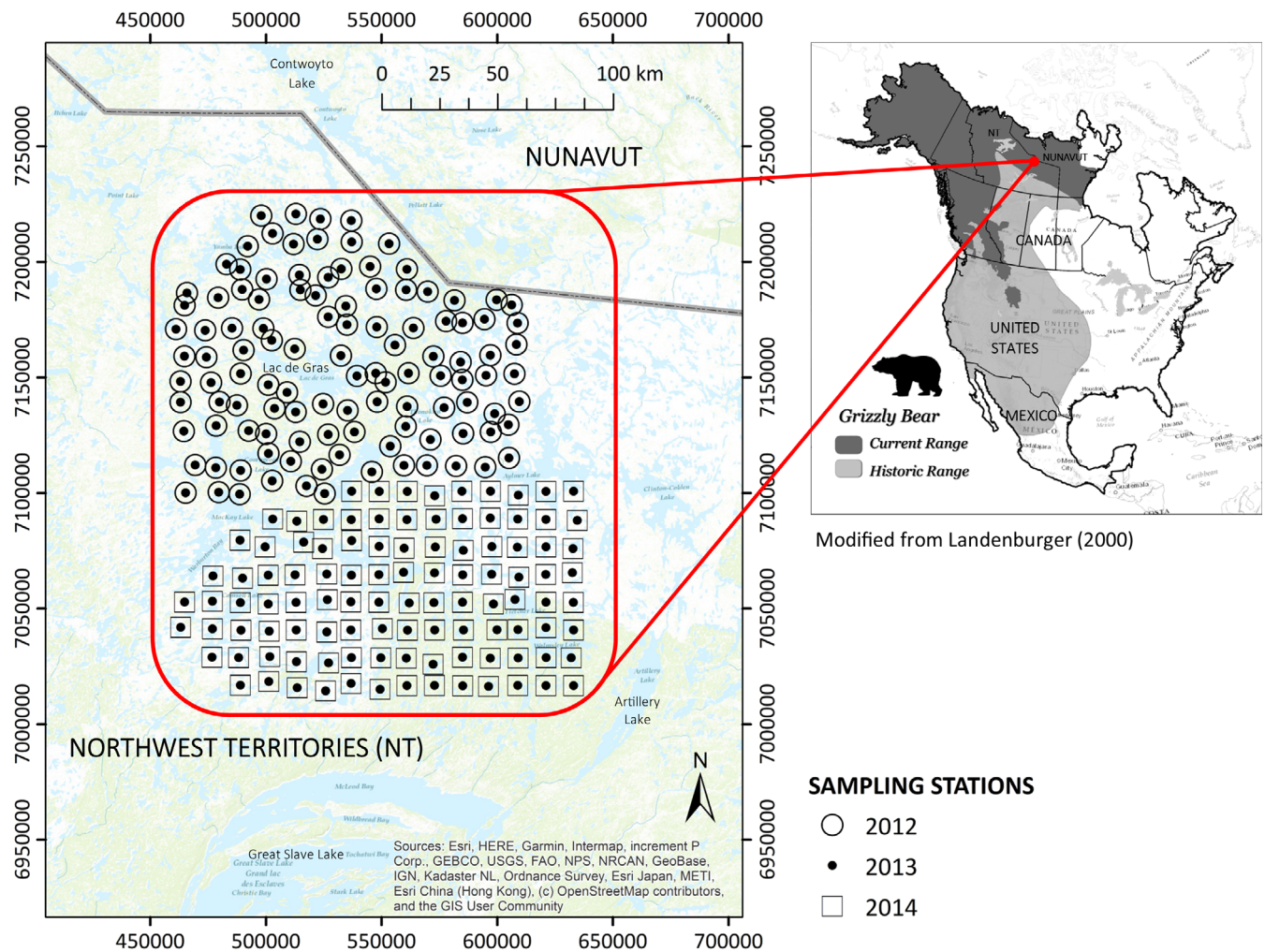
FIGURE 1 Grizzly bear (*Ursus arctos horribilis*) study area in the Northwest Territories of Canada, and distribution of the 218 hair snare sampling stations that were deployed for this study. Historic and current range of the species in North America, with reference to this study's area.

grizzly bears that were comparable in methodological approach. We predicted that, in accordance with the CMH, density would be low compared to other more central bear populations, and effective population size would also be low, reflecting a similar proportion of reproductive individuals as in other studies. We also predicted that past bottlenecks that are due to the fluctuations of northern environments would be detected and that, as a result, genetic diversity would be lower than in more central populations.

METHODS

Study area

The 30,000-km² study area, centered at 64.2° N, 110.0° W, was located in the Southern Arctic (Coppermine River Upland [CRU] ecoregion) and Taiga Shield (Takijuq Lake Upland [TLU] ecoregion) Ecozones (Figure 1) (Ecological Stratification Working Group Canada, 1995). Its northern limit extended to the border of NT and Nunavut, and its southern limit extended to the tree line. The mean annual temperature of the CRU ecoregion was −7.5°C, and −10.5°C for the TLU ecoregion (Ecological Stratification Working Group Canada, 1995). Average temperatures at the time of the study were likely higher than those cited above due to a changing climate (Post et al., 2009). The tundra area is considered semi-arid, with mean annual precipitation ranging from 200 to 300 mm and mostly continuous permafrost characterized by a rolling landscape of uplands, lowlands, and plateaus (Ecological Stratification Working Group Canada, 1995). Eskers, created through glaciation and composed of stratified sand and gravel, are found throughout the landscape and form most of the relief in this area. Lowlands are generally a mosaic of

sedge-dominated wetlands composed of fens and bogs as well as lakes and rivers. Vegetative cover is typically dominated by heath and shrub species such as Labrador tea (*Rhododendron* spp.), dwarf birch (*Betula nana*), and willow (*Salix herbacea*). Mammals inhabiting the area include barren-ground caribou, moose (*Alces alces*), but at very low densities, grizzly bears, wolves (*Canis* spp.), red and arctic foxes (*Vulpes* spp.), and small rodents.

Grizzly bear sampling approach

Noninvasive genetic sampling of bears can be conducted using natural rub sites (e.g., trees), or human-made objects usually placed within predetermined grid cells delineated prior to detector deployment (Boulanger et al., 2018; Dumond et al., 2015; Karamanlidis et al., 2010; Woods et al., 1999). The spatial organization of a detector array for use in capture–recapture studies depends on the movement ecology of species (Royle et al., 2014; Sollmann et al., 2012). We divided the study area into 221 square grid cells of 144 km^2 each. This area was based on a rough approximation of the 14-day home ranges of barren-ground female grizzly bears, which was based on previous studies (McLoughlin et al., 1999) (Figure 1). Owing to the lack of natural rub sites in the tundra, we constructed hair snare posts from wooden boards wrapped in barbed wire and fastened together into a tripod shape so that posts could be transported by helicopter and deployed in the field (Dumond et al., 2015) (Figure 2). Hair snares were deployed near the center of each grid cell while avoiding locations on lakes or waterbodies, which also influenced logistics of access. They were baited with a nonreward scent lure corresponding to the seasonal availability of food sources to attract grizzly bears, as identified during a Traditional Ecological Knowledge (TEK) workshop held in the community of Lutsel K'e, NT, in 2015 (Jessen, 2017) and based on previous studies (Gau et al., 2002). In early and late summer, rotten cow's blood and fish oil were used, while bergamot, raspberry, and cranberry oils were used in the mid-summer (Appendix S1: Table S1).

We conducted six sampling occasions (rounds of site visits) per session (year), each lasting 10–14 days to minimize hair sample degradation from weather exposure, which increases with time (Dumond et al., 2015) (Appendix S1: Methods, Table S1). Hair samples, that is, clumps of hair captured by a single barb, were collected during each visit and placed in labeled paper envelopes, which were stored in a cool, dry place. Sampling of the northern half of the study area was carried out from mid-June to mid-September of 2012 and 2013, and sampling of the southern half of the study area was identically conducted from mid-June to mid-September of 2013 and 2014 (Figure 1).

FIGURE 2 A grizzly bear (*Ursus arctos horribilis*) interacting with a hair snare post during the 2013 field season near Aylmer Lake, Northwest Territories, Canada. The barbed wire wrapped around wooden posts collected small tufts of hair suitable for genetic analysis (autosomal microsatellites). Photo credit: Tyler Jessen.

Laboratory and statistical analyses of genetic data

A high-quality set of hair (either ≥30 underfur or ≥2 guard hair roots) was chosen from each hair sample and analyzed for species confirmation, sex, and genotype using established techniques, including established genotyping error-checking protocols (Paetkau, 2003). We used a ZFX/ZFY gender marker, plus eight microsatellite markers (G10B, CXX110, G1D, G10H, G10J, G10M, G10P, and MU59) (Paetkau et al., 1999). Using 5 loci is considered sufficient for accurately detecting individuals in brown bears (Waits et al., 2001), and typically 7–8 loci are used in studies of brown bear populations (Boulanger et al., 2001; Dumond et al., 2015). All genetic analyses were conducted by Wildlife Genetics International (WGI) in Nelson, British Columbia.

Scoring errors and the presence of null alleles were detected using MICROCHECKER version 2.2.3 (Van Oosterhout et al., 2004). We also tested markers for deviations from Hardy–Weinberg equilibrium (HWE) and for linkage disequilibrium (LD), using the exact probability test in Genepop version 4.2 (Rousset, 2008) (Appendix S1: Supplemental Methods). Allelic richness (AR), Ho, and Nei's unbiased expected heterozygosity (He; Nei & Roychoudhury, 1974) were used as measures of genetic diversity. Both were used 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, while He accounts for both the number of alleles and the evenness of allele frequencies. AR was calculated using the rarefaction method implemented in FSTAT version 2.9.4 (Goudet, 2003), and He was obtained using Genetix version 4.05.2 (Belkhir et al., 2004).

We used the program NeEstimator to estimate effective population size (Ne) with its LD single-sample estimator without the lowest allele frequency restriction (Do et al., 2014). We also tested for heterozygosity excesses and signs of a genetic bottleneck using the program Bottleneck (Cornuet & Luikart, 1996; Cristescu et al., 2010). Its infinite allele model (IAM), two-phase model (TPM), and stepwise mutation model (SMM) were all applied. It should be noted that all are legitimate, although imperfect models of mutations, and simulation results are inconclusive on which is the most appropriate for autosomal microsatellite data (i.e., our data) in particular (Shriver et al., 1993). Ultimately, these models, for which no consensus currently exists on which is best, allow assessing genetic signatures of population bottlenecks or of population expansions; however, these cannot be distinguished from genetic signatures resulting from natural fluctuations in density.

Estimating density using spatial capture–recapture

We developed spatial capture–recapture (SCR) encounter histories of individual bears based on the hair samples (Boulanger et al., 2018; Mowat & Strobeck, 2000; Woods et al., 1999). We used SCR models to estimate density. SCR models join an observation model that describes the decreasing probability of detecting an individual as a function of the distance between a detector location and an animal's home range center, to a spatial point process model that describes the distribution of animal home range centers on a landscape (Efford, 2004; Efford & Fewster, 2013; Royle & Young, 2008).

We estimated bear density in the study area for the years 2012, 2013, and 2014 separately, using the secr package version 4.5.5 (Efford, 2022) in the program R, version 4.1.3 (R Core Team, 2022). To account for peripheral individuals with home range centers outside the detector array, we applied a 48-km buffer zone, approximately double the greatest root pooled spatial variance for males or females for 2012, 2013, and 2014 (Efford, 2004, 2019). We used the mask.check command in secr to ensure that the buffer size was appropriate. The study area and the buffer zone, summed together, made up an area of approximately 85,000 km². Models were fitted using the secr.fit command, which maximizes model likelihood through integration over the unknown locations of individuals' home range centers. We used a halfnormal Gaussian encounter probability function in all density estimates. We classified the hair snares as "proximity" detectors that allow for multiple, independent animal detections at a single detector on each sampling occasion, but only one detection per individual per sampling occasion. SCR models explicitly account for the distance and spatial layout of the sampling stations, even if they are not fully evenly spaced (Efford & Fewster, 2013, Royle & Young, 2008). We excluded water bodies from usable habitat using the polygon "inland lakes and rivers" from the Canadian 2011 Census boundary files (Open Canada, 2022) and the habitat mask feature from the secr package.

For each year, we conducted model selection using the Akaike information criterion corrected for small samples (AIC$_c$), to find the most parsimonious fitting model (Anderson & Burnham, 2004). Densities of grizzly bears might differ by sex, and SCR models can account for sex either by conducting analyses separately for females and males or by conducting analyses for all animals pooled but including sex-specific covariates. To determine the best model structure for density estimation, we proceeded in three steps.

1. To determine which parameters should be sex-specific, we first compared eight "sex-specific"

models with all combinations of the following covariates: no sex covariates, sex-specific densities, sex-specific baseline detection probabilities, and sex-specific sigmas (Appendix S1: Table S2). Sigma is the spatial scale parameter (also called the movement parameter) in SCR models, and in terrestrial wildlife species, it is related to the radius (r) of 95% home range estimates (e.g., from telemetry studies) through the equation sigma = $r/2.45$ (Sun et al., 2014).

2. We then compared 12 "pooled" models without sex-specific covariates with combinations of the following detection probability covariates: null model (no covariates), individual local behavioral response (bk), individual global behavioral response (Bk), linear time (T), factorial time (t), and lure type (lure). We tested for behavioral responses because grizzly bears tend to revisit rub trees and other hair snag sites that they previously visited (Lamb et al., 2018; Morehouse & Boyce, 2016). We did not fit models that included both lure type and time covariates because lure type was partly correlated with time (Appendix S1: Table S3).

3. To determine the model to be used for density estimation, we combined the best sex-specific models ($dAIC_c < 2$) with the best pooled models ($dAIC_c < 2$), also including interactions of detection covariates with sex, to arrive at a suite of competing "combined" models. We then used the best combined model for parameter estimation.

Literature search methods

To compare our results, we conducted a literature search for studies on brown and black bears (*Ursus* spp.) that used similar methodologies to ours, including both DNA fingerprinting, based on autosomal microsatellite analyses, and SCR methods, and that reported population density estimates and measures of genetic diversity from the same data. The choice of microsatellite loci depends on a study's objectives and methodological steps. SCR studies typically aim at estimating densities of valued species, and a key methodological step is that of choosing microsatellites that are known for the species and variable enough to allow individual recognition (Waits & Paetkau, 2005). Obviously, this choice has implications for values of genetic diversity that can be extrapolated from the same microsatellites. We therefore did not include in our comparative analysis studies that only estimated genetic diversity, as they might have used other less variable markers.

We searched for research papers using both Web of Science and Google Scholar as of June 1, 2022. We used keyword searches with common bear names and the terms "secr," "scr," "recapture," "heterozygosity," "ursus," "genetic diversity," "density," and "spatial capture recapture." We did not include academic theses as it was difficult to find unequivocal estimates, and some numbers were repeated and slightly changed in related publications. We established the latitude for the study areas by either using the reported coordinates or, where no coordinates were reported, by contacting the respective study authors. We included studies on brown bears of Eurasia with those of North America to increase the number of studies. We used Pearson's product–moment correlation (two-sided) to test for an association of density with latitude.

RESULTS

Between 2012 and 2014, we detected 205 individual bears (120 females and 85 males) (Table 1). Of the individuals, 53 females and 42 males were detected in one, 61 and 38 in two, and 5 and 5 in all three years, respectively. DNA extraction success rates are in Appendix S1: Results.

Genetic estimates of population diversity, effective population size, and bottlenecks

For our study, AR was 7.00 (SE = 0.78), He was 0.710 (SE = 0.026), and Ho was 0.81 (SE = 0.05) (Figure 3). LD methods indicated an effective population size (Ne) of 83 bears (95% CIs 68–102). Our findings indicated the possibility of recent bottlenecks in the grizzly bear population. The sign test, standardized differences test, and Wilcoxon test all showed a significant heterozygosity excess under the IAM ($p = 0.011$, $p < 0.001$, and $p = 0.004$, respectively), whereas the SMM results for all three tests were not significant. In addition, the population also exhibited a significant heterozygosity excess consistent with a recent genetic bottleneck, as detected using a TPM (standardized differences test, $p = 0.022$). Furthermore, the Wilcoxon test, which is known to be the most appropriate for the potential occurrence of recent bottlenecks, also showed significant signatures of a population bottleneck under both the IAM and TPM models ($p = 0.004$ and $p = 0.008$, respectively).

By comparison, information we gathered from 11 published studies (Appendix S1: Table S4) that used similar methodologies to ours, including both DNA fingerprinting based on autosomal microsatellite analyses and SCR methods for density estimation, indicated that AR ranged from 3.3 to 13.2 for black bears (mean = 6.2;

TABLE 1 Grizzly bear (*Ursus arctos horribilis*) hair samples collected from 2012 to 2014 in the Northwest Territories of Canada by year (year), which also corresponds to the portion of study area sampled (area), and summary statistics of recaptures.

Characteristic	2012	2013	2014	Total
Area	North	North + South	South	
No. samples	1902	4983	1108	7993
No. females	70	96	24	120
No. males	42	69	22	85
Mean recaptures females	1.94	2.81	2.21	3.86[a]
Mean recaptures males	2.02	2.51	2.23	3.61[a]
Mean occasions females	1.67	2.30	1.83	2.79[a]
Mean occasions males	1.64	2.09	1.91	2.64[a]
Mean sites females	1.69	2.11	1.67	2.76[a]
Mean sites males	1.79	2.03	1.73	2.78[a]

Note: Displayed are number (*N*) of samples and number of individuals of each sex identified with genetic analysis, the mean number of recaptures per individual, and the mean number of occasions and the mean number of sites at which an individual was detected.
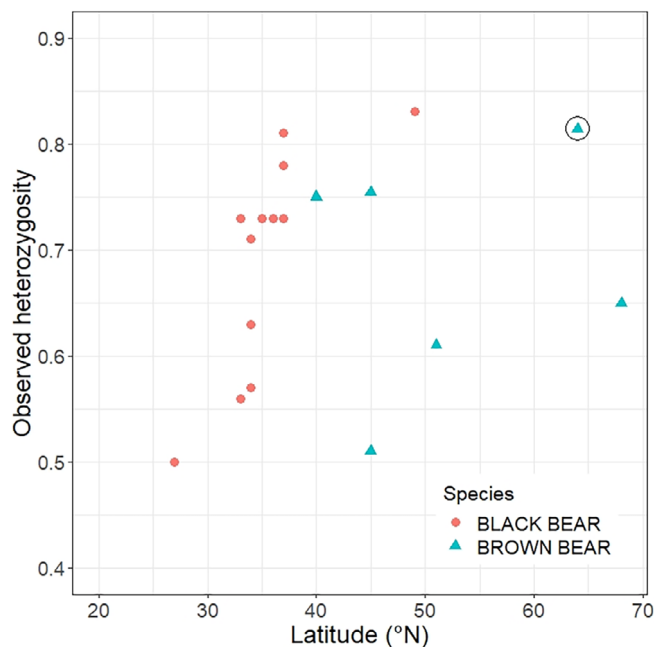[a]Means calculated across all three years of data.

FIGURE 3 Observed heterozygosity and latitude of study area (°N) from seven published studies on black bears (*Ursus americanus*) (red circles; including *n* = 12 distinct estimates, as some studies had multiple estimates), four studies on brown bears (blue triangles; including Eurasian brown bears and North American grizzly bears, and including *n* = 5 distinct estimates), plus this study on grizzly bears (circled in black). All studies used methodologies comparable to this study's, including both DNA fingerprinting (based on autosomal microsatellites) and spatial capture–recapture methods.

SD = 3.3; *n* = 8) and from 6.5 to 7 for grizzly bears (mean = 6.75; SD = 0.35; *n* = 2). In these studies, Ho for black bears ranged from 0.5 to 0.83 (mean = 0.68; SD = 0.12) and did not decrease with latitude but actually increased (two-sided alternative: $r(11) = 0.75$, $p = 0.003$; Figure 3). For brown bears, including our estimate, Ho (mean = 0.68; SD = 0.11) ranged from 0.51 to 0.81 and did not decrease with latitude ($r(4) = 0.16$, $p = 0.76$; Figure 3).

Density and encounter probability estimates

After initial data exploration, we decided not to test for sex effects on local trap response because of a general lack of such sex effects. The best combined models differed between the three years, but all had detection probability covariates for local trap responses, lure type, and sex (Appendix S1: Table S5). The best models for 2012 and 2013, but not 2014, also included sex-specific density and sigma. Density estimates from the best models were equivalent to estimates derived from model-averaging of all combined models, and thus only results from the best models are presented.

For 2012, the highest ranking sex-specific model had sex covariates for density, detection probability, and sigma (Appendix S1: Table S2). The highest ranking pooled model included a local trap response and a linear time effect (Appendix S1: Table S3). The best combined model was one with detection probability parameters for a local trap response and sex-specific lure type effect, sex effects for sigma and density, but a combined model with the same parameters but without sex-specific density had virtually the same support from the data (Appendix S1: Table S5). For 2013, the highest ranking sex-specific

model was one with sex covariates for density, detection probability, and sigma (Appendix S1: Table S2). The highest pooled model included a detection probability covariate for a local trap response and lure type (Appendix S1: Table S3). The best combined model was one with detection probability parameters for a local trap response and lure type, and sex covariates for density, detection probability, and sigma (Appendix S1: Table S5). For 2014, the highest ranking sex-specific model was one without sex covariates (Appendix S1: Table S2). The highest ranking pooled model included a detection probability covariate for a local trap response and lure type, but models with linear or factorial time, or no additional covariate, were nearly equally well supported by the data (Appendix S1: Table S3). The combination of the best sex-specific and pooled models therefore did not include sex effects, but other models with a sex-specific sigma had some support from the data (Appendix S1: Table S5).

The best combined models (Appendix S1: Table S5) yielded a density of 3.0, 2.4, and 1.9 male bears/1000 km^2 in 2012 (northern part of study area), 2013 (northern and southern part), and 2014 (southern part), respectively. For females, the respective densities were 4.4, 3.5, and 1.9 bears/1000 km^2 (Table 2). The mean density of males was lower than that of females in 2012 and 2013, at approximately 68% and 69% of that of female bears, respectively (Table 2). In 2014, density of males and females was the same.

Sigma, the spatial scale parameter of the detection function, which represents the extent of individual movements, was different between sexes in 2012 (larger female sigma) and 2013 (larger male sigma), but 95% CIs slightly overlapped (Table 2). Bear encounter probability varied between years and sex and was affected by lure type, with berry scent being associated with the highest detection probabilities with the exception of male bears in 2012 (Table 2). The local trap response was positive in all years and models: Detection probability at a site that had been previously visited by an individual was on average 6.2 (females) and 6.3 (males) times higher for subsequent visits by the same individual (Table 2).

In the same collection of comparable studies that also used both DNA fingerprinting and SCR methods, black bear densities ranged from 46 to 339 bears/1000 km^2 (mean = 183.2 bears/1000 km^2) and did not decrease with latitude ($r(10) = -0.02$, $p = 0.475$; Figure 4A). For grizzly bears, densities ranged from 5 to 59 bears/1000 km^2 (mean = 18.9 bears/1000 km^2) and decreased with latitude ($r(7) = -0.77$, $p = 0.007$; Figure 4B).

TABLE 2 Grizzly bear predicted density estimates using the best combined model of each year for females (F) and males (M), for each part, North (N), South (S), or combined (N + S), of the study area in the Northwest Territories of Canada.

| | | | | | | | Detection probability g(0) | | | | | |
| | Density (bears/1000 km^2) | | | Sigma (km) | | | Berry | | Blood | | Berg | |
Sex	Mean	SE	95% CI	Mean	SE	bk[a]	Mean	SE	Mean	SE	Mean	SE
2012 (N)												
F	4.4	0.7	3.3–5.9	22.4	2.1	bk = 0	0.019	0.004	0.015	0.003	0.010	0.003
						bk = 1	0.113	0.027	0.091	0.022	0.060	0.020
M	3.0	0.5	2.1–4.2	15.4	1.6	bk = 0	0.034	0.009	0.020	0.005	0.049	0.014
						bk = 1	0.190	0.044	0.118	0.032	0.256	0.065
2013 (N + S)												
F	3.5	0.4	2.8–4.3	13.0	0.6	bk = 0	0.057	0.008	0.048	0.006	0.040	0.007
						bk = 1	0.270	0.030	0.235	0.028	0.204	0.031
M	2.4	0.3	1.8–3.1	16.1	1.0	bk = 0	0.038	0.006	0.032	0.005	0.027	0.005
						bk = 1	0.195	0.027	0.167	0.025	0.143	0.026
2014 (S)												
F	1.9	0.3	1.3–2.7	13.9	1.4	bk = 0	0.041	0.011	0.025	0.007	0.039	0.012
						bk = 1	0.322	0.066	0.222	0.053	0.312	0.082
M	1.9	0.3	1.3–2.7	13.9	1.4	bk = 0	0.041	0.011	0.025	0.007	0.039	0.012
						bk = 1	0.322	0.066	0.222	0.053	0.312	0.082

Note: Included are also the spatial scale parameters sigma and detection probabilities g(0) by lure type (berry, cow blood, or bergamot scent). For 2014, the best combined model did not include sex covariates for density or for sigma.

[a]bk = 0 (i.e., detection probability for the first visit at a trap for an individual bear); bk = 1 (subsequent visits at a trap by the same individual).
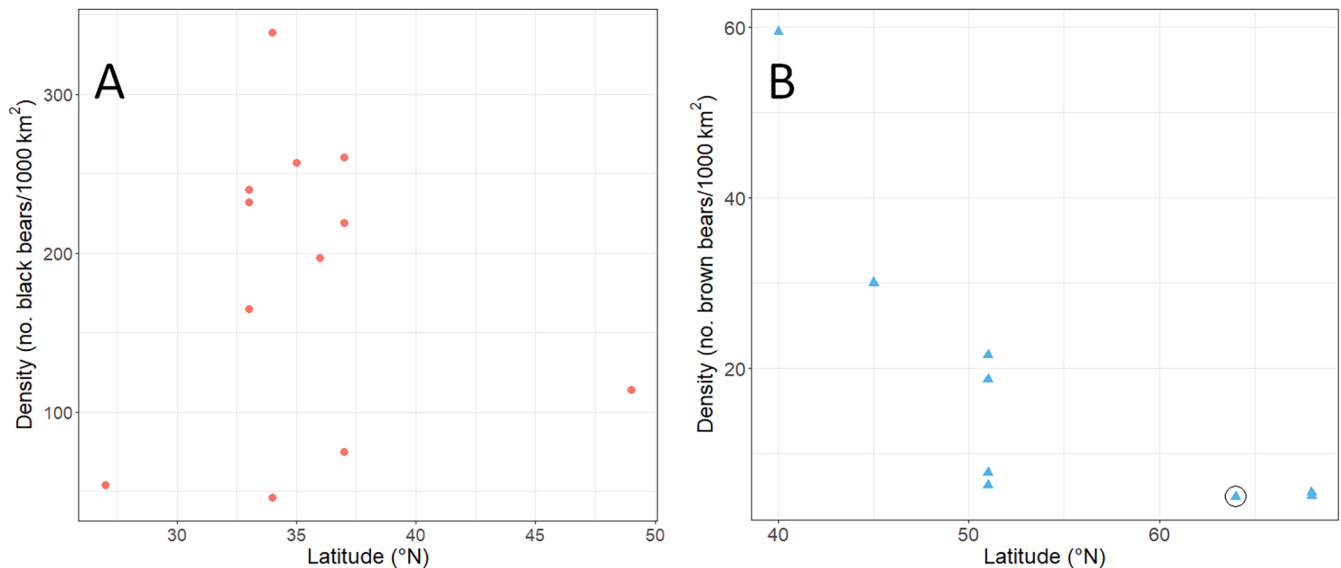
FIGURE 4 (A) Density estimates (number of bears/1000 km^2) by latitude of study area (°N) from seven published studies on black bears (*Ursus americanus*; including $n = 12$ distinct estimates, as some studies had multiple estimates). (B) Density estimates by latitude from four published studies on brown bears (*Ursus arctos*; including Eurasian brown bears and North American grizzlies, and including $n = 8$ distinct estimates), plus the density estimate of grizzly bears from this study (circled in black). All studies used methodologies comparable to this study's, including both DNA fingerprinting (based on autosomal microsatellites) and spatial capture–recapture methods.

DISCUSSION

Our findings suggested that grizzly bears inhabiting the margins of the species' current continental distribution in North America live at low population densities compared to other more central bear populations. Our study area was located at the northern edge of bears' historical distribution, and our finding of lower density was similar to a previous study (Dumond et al., 2015) and to other terrestrial organisms also living at high latitudes (Cook, 1969; Kiester, 1971; Simpson, 1964). These results were consistent with the CMH when interpreted in relation to lower habitat quality at the periphery of a species distribution (Eckert et al., 2008). Accordingly, our genetically assessed effective population size was also low for the area assessed, reflecting a similar proportion of reproductive individuals as in other bear studies and as rationalized in view of the species mating system (Kamath et al., 2015).

The test for a genetic bottleneck that we used examines whether population-wide estimates of heterozygosity are larger than expected by chance (i.e., excess in heterozygosity). The indication of a bottleneck that we report on is only observable for a few generations (2Ne–4Ne) (Cornuet & Luikart, 1996), during which time the surviving population has allele frequencies and heterozygosity characteristics of its formerly larger Ne (Luikart et al., 1998). Taking this into consideration, the generation time of brown bears of about 10 years (Miller & Waits, 2003),

and the effective population size we determined (Ne = 68–102), our findings suggest a bottleneck occurrence during a period between 1360 and 4080 years ago. We therefore detected signatures of a "recent" (in evolutionary terms) bottleneck, which is consistent with likely fluctuations of northern bear populations, as their plant food and prey items are both known to also dramatically fluctuate in numbers across years (Diepstraten, 2017; Gunn, 2020; Parlee & Caine, 2018). However, our expectation that genetic diversity of bears would be lower than in other more central studies was not met, and we propose that density increases in relation to species range expansions (in relation, for example, to climate change; see below), and bottlenecks might interplay in affecting diversity in peripheral populations in general.

The total grizzly bear density across the study area (30,000 km^2) in 2013 was 5.9 bears/1000 km^2. This was comparable to estimates of 5 bears/1000 km^2 in similar tundra habitat 460 km to the northwest, which were obtained using sampling and estimation methods directly comparable to ours but, as far as we can tell, did not exclude waterbodies, which means their density estimates were inherently lower than ours (Dumond et al., 2015). Densities in the northern half of our study area (sampled in 2012) were approximately double those of the southern half (sampled in 2014) (Table 2). This spatial variation in density most likely reflected spatial variation in resource availability and/or mortality, not a

drastic decline in grizzly abundance between 2012 and 2014 (Apps et al., 2016). For example, caribou, which are a staple prey of grizzly bears, only occurred in the northern half of the study area (Jessen, 2017).

Our results provide qualified support to the hypothesis that grizzly bear populations are increasing in size in the NT (Dumond et al., 2015). The average annual rate of increase has been estimated at 3% (McLoughlin et al., 2003). Our density estimates for 2013, when the entire study area was sampled, were consistent with an annual rate of population increase of that magnitude since the 1990s, when density estimates of 3.6 bears/1000 km^2 and minimum estimates of 3.5 grizzly bears/1000 km^2 were made for the wider region (Banci et al., 1994; McLoughlin et al., 2003). However, these temporal trends are hypothetical only, as there were important methodological differences between ours and these two earlier studies: The former was largely based on expert opinion (Banci et al., 1994), and the latter was likely negatively biased and a relatively crude measure based on counts of collared and observed bears (McLoughlin & Messier, 2001). Finally, our analysis excludes water bodies as habitat, which previous studies did not do, an exclusion that could contribute to augmenting our estimates.

Our estimates of the mean movement parameter sigma, ranging from 13.0 to 22.4 km, reflected the larger home ranges of barren-ground grizzly bears relative to more southern populations of grizzlies (Apps et al., 2016; McLoughlin et al., 1999; Morehouse & Boyce, 2016). There was an unexpected finding: in 2012, female grizzly bears had larger sigma values than males (see also Appendix S1: Results). Multiple females had traveled distances of up to 145 km between detections, which was not consistent with their usually more restricted home ranges and movement distances compared to males in the region (McLoughlin et al., 1999). That said, previous studies have documented even longer linear directional movements of several hundred kilometers by subadult males in the region (Gau et al., 2004) and by females at the southern edge of their range (Kendall et al., 2019), demonstrating high vagility in both sexes. The long-range movements that we documented for female bears occurred only in the part of the study area within caribou range (Jessen, 2017). Tracking of the caribou spring migration was considered a possible explanation for the long directional movements of subadult males (see previous paragraph), and it could also explain this study's movements by females, but for both sexes, dispersal behavior or even avoidance of conspecifics could also be factors (Gau et al., 2004). To conclude, it is possible that in 2012 our sampling grid extent (~16,000 km^2) was too small to capture the largest movements of male bears, which may have led to an underestimation of male

movement parameters sigma compared to that of females in that year. If we underestimated male sigma, this would have resulted in an overestimated male density, a possibility that should be considered when density comparisons are made across time or space, or our results are used by wildlife managers.

There were no clear or consistent patterns in sex-specific detection probability in this study: in 2012, male detection probability was higher, in 2013 that of females, and in 2014 there was no sex effect (Table 2), a finding that probably reflected individual behavioral variation or even personality of bears (Myers & Young, 2018). As expected, the local trap response was consistently strong, despite using a nonreward scent lure, and therefore should be included in similar studies to avoid biasing density estimates low (Royle et al., 2011). The best models for each year included a lure effect, but as the type of lure used on each occasion had a temporal component, we could not distinguish whether the increase in detection probability was mainly due to the scent used or also due to a time effect (Appendix S1: Table S1). The results for 2014, when models with either lure or a temporal covariate had virtually the same support from the data, suggest that there was some temporal effect (Appendix S1: Table S3).

Finally, in our study, 40% of the population (i.e., its genetically determined effective population size) was reproducing, which is considered a natural level for grizzly bears (Kamath et al., 2015). However, this population of bears may have increased uninterruptedly only recently, but not in the past. The bottleneck signals that we detected refer to a window of likely contractions of bear populations ranging from 4000 years ago to present (Cristescu et al., 2010). Northern climates are known to vary dramatically over time in terms of productivity, and increasingly so after the Industrial Revolution in relation to global warming (Post et al., 2009). Consequently, resources that are fundamental for grizzly bears might also have fluctuated significantly in the north during that time. For example, caribou, which in our study area are grizzly bears' staple prey item, are known to experience large fluctuations in numbers in relation to natural variation of northern climates and, more recently, to climate change (Brotton & Wall, 1997; Yannic et al., 2014). As caribou disappear, bear numbers may also come under increasing scrutiny as caribou predators (Dumond et al., 2015).

Our study was designed to estimate densities of bears. Like other studies, it adopted the most current methodological line of attack, which relied on sampling bear hairs and conducting analyses of autosomal microsatellites. Also similar to other studies, the microsatellite marker set was picked to be variable enough in terms of allele diversity to individually identify bears, that is, allowing DNA

fingerprinting (Chambers et al., 2014). We assessed genetic diversity with Ho, AR, and He, and those values should therefore only be evaluated relative to other studies that, as we did, also selected highly variable marker sets. Our findings on the latter two parameters (AR and He) were not readily comparable with other similar studies, as they were not reported consistently in these studies. We therefore only compared our Ho measure to those estimated in other grizzly populations in studies that also estimated bear density using SCR methods (Figure 3).

In this study of bears at the northern periphery of their range, genetic diversity values as represented by Ho were substantial, and our expectation that they were lower than those in more central studies was not met. In addition, genetic diversity, as reported in the literature for both black and brown bears, did not show a pattern of lower values at high latitudes (Figure 3). For black bears, this matched the patterns of AR and He, which both appear to increase with latitude, likely because of lower levels of habitat fragmentation and higher levels of gene flow toward the northern end of their range (Puckett & Davis, 2021). In grizzly bears, we found no apparent pattern in Ho with latitude, also matching lack of patterns in He and AR reported elsewhere (Puckett & Davis, 2021). Similar to black bears, in grizzly bears too heterozygosity might not decrease with latitude, mainly due to the shape of the North American continent (larger in the north) and the fragmentation of the species distribution in the south. These results on bears contrasted with empirical studies of other mammals that displayed lower genetic diversity further from the core of the range (Jenkins et al., 2018; Ratkiewicz et al., 2012; Rodríguez-Rodríguez et al., 2015). We also propose that species such as grizzly bears that are expanding in distribution in relation to climatic or other factors might experience increases in density in peripheral populations. Such increases, and likely immigration from more central populations, would contribute to genetic diversity, counteracting the diminishing effects of bottlenecks.

We evaluated our density estimates in view of other studies that were conducted decades ago and extrapolated a likely increase of bears. The timeframes implied by our bottleneck analyses, however, are one order of magnitude greater (up to several thousand years; see above): "recent" only if considered in evolutionary terms but not in human terms. Such timeframes should therefore be evaluated in terms of indigenous knowledge, as Europeans arrived in these northern areas only lately (Coates, 1985). TEK supports our findings in terms of a recent expansion of grizzly bears northward and also in terms of extreme fluctuations in numbers of large mammals in the arctic and subarctic in the last centuries, which includes bears' prey (Gunn, 2020; Parlee & Caine, 2018). More broadly, our study is transferable to other species and systems also characterized by range expansions and where peripheral populations live at low density, reproduce naturally, have reasonable levels of genetic diversity, but also experience fluctuations in numbers and periodic bottlenecks.

CONFLICT OF INTEREST STATEMENT
The authors declare no conflicts of interest.

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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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