Sex-specific differences in familial networks, dispersal and reproductive success are driven by heterogeneity in density

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Author contribution statement

MM and GP conceived and designed the study. SM implemented the analysis and wrote the manuscript with help from MM and TJ. PW coordinated DNA extraction and analysis. DP coordinated and analyzed the spatial density covariate data. GM coordinated hormone extraction and analysis. All authors contributed to subsequent drafts and gave final approval for publication.

Keywords

density dependence, Dispersal, Familial networks, Individual fitness, pedigree, Rangifer tarandus

Abstract

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Density is an important demographic parameter that is commonly overlooked in studies of wild populations. We examined a range of spatially explicit demographic parameters in a wild population of a cryptic ungulate, boreal woodland caribou (Rangifer tarandus caribou). Using noninvasive genetic sampling, we applied spatial capture-recapture methods with covariates to estimate density of boreal woodland caribou across a 108 806 km2 study area. We then created a familial network from reconstructed parent-offspring relationships and determined whether spatial density influenced sex-specific dispersal distance, individual reproductive success, and female pregnancy status. We find that density varied greatly, leading to variation in dispersal distances, with offspring moving shorter distances when parents were found in higher density areas. Familial networks showed lower closeness centrality and lower degree centrality for males in higher density areas, indicating that females found in higher density areas tend to be less broadly associated to animals across the range. Density significantly affected both male and female reproductive success, with males showing positive density dependence, and females showing negative density dependence. No differences were found in female pregnancy rates occurring in high- and low-density areas. Although high density areas do reflect good quality caribou habitat, the observed decreased closeness and degree centrality measures, dispersal rates and lower female recruitment rates suggest that remnant habitat patches may trigger positive feedbacks.

Contribution to the field

Habitat quality and disturbance can strongly influence a species' distribution, population dynamics and spatial population density. It is therefore critical to understand how density can lead to variability in demographic responses, but measuring these parameters in wide-ranging populations is extremely difficult. To overcome this, we used a highly comprehensive genetic dataset in new and inventive ways, outside the realm of how they are typically applied. We used this genetic dataset along with spatial capture-recapture (SCR) modelling and spatial network analyses to better understand how density influences population dynamics. We estimated spatial density of boreal caribou, then reconstructed parent-offspring relationships to create a familial network, and determined whether spatial density influenced sex-specific network centrality, dispersal distance, individual reproductive success, and pregnancy status. We show that caribou density varied greatly, primarily affected by landscape composition and fragmentation, and had sex-specific influences on dispersal distance, reproductive success, and network centrality. High-density areas reflected good-quality caribou habitat, and the decreased dispersal rates and female reproductive output suggest that these remnant habitat patches may be influencing demographic responses of caribou. These results are groundbreaking and transformative, greatly advancing our understanding of the species ecology and conservation, and introduce new analytical methods to the research field.

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Keywords: density dependence, dispersal, familial networks, individual fitness, pedigree, *Rangifer tarandus*

Abstract

Density is an important demographic parameter that is commonly overlooked in studies of wild populations. We examined a range of spatially explicit demographic parameters in a wild population of a cryptic ungulate, boreal woodland caribou (*Rangifer tarandus caribou*). Using noninvasive genetic sampling, we applied spatial capture-recapture methods with covariates to estimate density of boreal woodland caribou across a 108 806 km^2 study area. We then created a familial network from reconstructed parent-offspring relationships and determined whether spatial density influenced sex-specific dispersal distance, individual reproductive success, and female pregnancy status. We find that density varied greatly in response to land cover types and disturbance, leading to variation in dispersal distances, with offspring moving shorter distances when parents were found in higher density areas. Familial networks showed lower closeness centrality and lower degree centrality for males in higher density areas, indicating that females found in higher density areas tend to be less broadly associated to animals across the range. Density significantly affected both male and female reproductive success, with males showing positive density dependence, and females showing negative density dependence. No differences were found in female pregnancy rates occurring in high- and low-density areas. Although high density areas do reflect good quality caribou habitat, the observed decreased closeness and degree centrality measures, dispersal rates and lower female recruitment rates suggest that remnant habitat patches may trigger positive feedbacks.

1 Introduction

Demographic parameters of wild populations, including dispersal (Travis et al., 1999; Matthysen, 2005), kinship (De Bona et al., 2019), and reproductive success (e.g. McLoughlin et al., 2006; Hamel et al., 2009) vary with population density. While this has been shown using population-based metrics

(Fowler, 1987), individual heterogeneity in demographic rates in response to population density is less well documented. Predicting population-level response to habitat change, for instance, will benefit from knowing how individual demographic rates vary as populations change. As part of a study to explore the spatial structure of familial networks in boreal woodland caribou (McFarlane et al., 2021), we measured individual recruitment and dispersal rates across a population density gradient driven by changes in habitat quality and quantity. This enabled us to address the question of whether boreal woodland caribou recruitment and dispersal are density-dependent.

In most species, density is heterogeneous across their range, reflecting patterns resulting from an individual's selective use of habitat resources to maximize fitness (Morris, 2003), and responses to habitat disturbance (Tischendorf et al., 2005). Variation in habitat quality can strongly influence a species' distribution, affecting population density by altering resource abundance and habitat structure, and influencing movement or landscape connectivity (Łomnicki, 1980; Smith et al., 2016). Habitat fragmentation can increase or decrease local population density in remnant habitat patches, shifting the balance between emigration and immigration (Bowers and Matter, 1997; Tischendorf et al., 2005).

Density dependence occurs when a population parameter (most often population dynamics such as population growth rate, vital rates, and reproduction) varies as a result of density (Hixon and Johnson, 2009). Density-dependent demographic parameters have been observed in numerous large mammal species, with reproduction and growth rate typically decreasing with increased density (Fowler, 1987). In cases where density influences mean vital rates, absolute and relative reproductive success of individuals in the population can change with population size or density, with absolute reproductive success and population growth rate decreasing with increasing population size (Sæther and Engen, 2015). For example, McLoughlin et al. (2006) found that lifetime reproductive success of female red deer (*Cervus elaphus*) was inversely associated with local density, and reproductive benefits from selecting good-quality habitat decreased as density increased.

Understanding and accounting for individual heterogeneity in reproductive success is fundamental to make inferences about ecological patterns and processes, bearing in mind that inherent reproductive differences among individuals can lead to incorrect interpretations (Weladji et al., 2008; Badger et al., 2020). Genetic parentage data can provide detailed information on individual-based reproductive success of wild populations, allowing for a wider look at reproduction, and can include measures of reproductive success and recruitment for individuals who are not directly sampled (McFarlane et al., 2018). Individual differences in reproductive success are especially pronounced in long-lived species (Clutton-Brock and Sheldon, 2010), and this variation can have important consequences for population dynamics and demography (Clutton-Brock, 1988; Newton, 1989; Clutton-Brock and Sheldon, 2010). Accurately assessing and accounting for individual variation in reproductive success and recruitment is critical for improving our understanding of mating systems and sexual selection (Bowler and Benton, 2005).

There is growing evidence that dispersal is a highly heterogeneous process (Bowler and Benton, 2005; Fronhofer et al., 2018), dependent on multiple factors such as resource availability (Aguillon and Duckworth, 2015), predation risk (Bestion et al., 2014), or density (Matthysen, 2005; Bitume et al., 2013). Density-dependent dispersal is common across many taxa and can be positive or negative depending on the driving mechanism (Matthysen,2005). Positive density-dependent dispersal can be a result of local competition increasing the likelihood of individuals dispersing to improve fitness prospects by leaving high-density areas (Travis et al., 1999; Matthysen, 2005), while negative density-dependent dispersal can result from high densities reducing dispersal probability due to increased likelihood of aggressive encounters (Matthysen, 2005). Most studies of density-dependent dispersal predict that high patch density should result in increased dispersal (positive density dependence; Travis, 1999; Poethke and Hovestadt, 2002; Leturque and Rousset, 2003), with few studies predicting that high patch density will result in decreased dispersal rates (negative density dependence; Matthysen, 2005).

Boreal woodland caribou (*Rangifer tarandus caribou*, hereafter referred to as boreal caribou) in Saskatchewan, Canada provide an ideal system for testing demographic density responses hypotheses as they exhibit relatively small-scale movements and occur over large areas with no discrete populations (Ball et al., 2010; Priadka et al., 2019; McFarlane et al., 2021). They select large tracks of mature to old-growth coniferous forests that provide abundant lichens, or wetlands mixed with upland areas, and avoid early-stage, successional deciduous forests (Stuart-Smith et al., 1997; Environment Canada, 2012). Habitat alteration through anthropogenic disturbance generates indirect habitat loss for boreal caribou through the conversion of old-growth coniferous forests to early-stage deciduous forests (Polfus et al., 2011; Rudolph et al., 2017). Roads and linear features facilitate predator movement, affecting calf and adult survival (Dussault et al., 2012; Leblond et al., 2013). To investigate these factors on density dependence, we first used noninvasive genetic sampling and spatial capture-recapture (SCR) modeling to generate a spatially-explicit density raster layer. We constructed familial networks and calculated individual recruitment and dispersal rates along with a range of networks metrics to assess the contribution of individual boreal caribou to the population (McFarlane et al., 2021, Jones and Manseau 2022). We have previously shown spatial variation in individual measures of network centrality across Saskatchewan, with animals in the southern part of their range presenting higher numbers of parent-offspring relationships, along with connections to other highly connected individuals (McFarlane et al., 2021). We extend these analyses to examine the relationship between familial network metrics and density, a novel approach to testing the effects of density variation on population demographics.

Our hypothesis is that boreal caribou exhibit density dependence, with the spatial variation in density leading to significant heterogeneity in demographic responses (Figure 1). In ungulate populations, density dependence is observed through changes in vital rates, such that increased population density results in decreased female reproductive success through decreased survival of young, reduced pregnancy rate, and increased age of first reproduction (Gaillard et al., 2000; Bowyer et al., 2014). However, increased density can lead to increased reproductive success for males due to the greater number of available females, leading to greater individual variation in male reproductive success (McCullough, 1999). We predicted female reproductive success and pregnancy status would be negatively correlated with density, and male reproductive success would be positively correlated with density. Boreal caribou pregnancy rate was also measured from each sampled female to assess whether the lower reproductive success predicted in higher density areas corresponds to lower pregnancy rates, suggesting females were not in good body condition (Gerhart et al., 1996; Stewart et al., 2005) or a larger proportion of non-reproductive females (younger/older) in these areas.

We predicted that dispersal would be negatively correlated with density for both sexes, with a stronger influence on dispersal in females, as female ungulates typically disperse less than males. Little is known about sex-specific dispersal in boreal caribou; radio-telemetry collaring is the most commonly used method of estimating movement of caribou and males are seldom collared (e.g. van Oort et al., 2011). These predictions have seldom been tested in wild populations of long-lived mammal species, but the increasing availability of genetic data and advanced analytical methods are providing a unique opportunity to uncover fine scale population demographic responses to landscape conditions.

2 Methods

2.1 Study area

Data were collected from boreal caribou across the boreal plains ecozone in Saskatchewan, Canada (Figure S1.1). The boreal plains are characterized by mixed-wood forests, lakes, and large areas of low-lying peatlands (Saskatchewan Ministry of Environment, 2019). Boreal caribou are part of the boreal caribou Designatable Unit (DU6) (COSEWIC, 2011) and are listed as *Threatened* under the Canadian *Species at Risk Act* (SARA) and are listed as *Vulnerable* in Saskatchewan (SKCDC, 2020). Due to relatively high levels of anthropogenic disturbance, boreal caribou populations in Saskatchewan's boreal plains are at a higher risk of decline and potential extirpation due to range retraction at the southern margin of the boreal caribou range (Arsenault, 2003). See Appendix 1 for more details on the study area.

2.2 Data collection and analysis

Two surveys per year were conducted to collect fecal pellets for spatial capture-recapture analysis, with sampling occasions spaced approximately one month apart. Following the aerial survey protocol outlined in Hettinga *et al.* (2012), aerial transects were systematically flown at 3 km intervals across each survey area using rotary- or fixed-wing aircraft, or a combination of both, to locate boreal caribou feeding locations. Additional samples were collected across the boreal plains for population genetic surveys between 2013 and 2016 (Priadka et al., 2019). All samples were kept frozen at −20°C until DNA extraction was performed. We followed the DNA extraction protocol outlined by Ball et al. (2007) to generate individual-specific genetic profiles. To generate familial pedigree networks, we amplified DNA samples at 15 variable microsatellite loci (McFarlane et al., 2021).

2.3 Demographic data

2.3.1 Density

We used SCR models to estimate the spatial density of boreal caribou in the Saskatchewan boreal plain. We created a multi-session SCR model with one session for each survey area (SK West, SK Central, and SK East) to obtain density estimates across survey areas. We used a maximum likelihood approach implemented in the R package *secr* (Efford, 2018; R Core Team, 2019). The density model allows for the input of spatial covariates to create a heterogeneous density surface across the study area. We used three groups of spatial covariates to investigate the factors that affect population density and to obtain a spatially explicit density surface: habitat (good- and poor-quality), distance to anthropogenic disturbance (roads or linear features), and habitat potential (Appendix 1). Habitat data were extracted from the 2015 Land Cover of Canada dataset at 30 m resolution (Natural Resources Canada, 2020). Based on results from resource selection analyses (Boyce and McDonald, 1999; Manly et al., 2002), we considered needleleaf forests as good-quality habitat, deciduous and mixed-wood forests (hereafter referred to as deciduous) and grasses and shrubs as poor-quality habitat. The linear feature layer included roads, railways, trails, seismic lines, protection structures (dike, levees, etc.), pipelines, and power lines. We tested the effects of linear features by creating a distance to roads variable and a distance to all linear features variable. Finally, we used ranked boreal caribou habitat potential data to account for an ecosite's potential to provide forage, refuge and calving habitat. Ecosites were ranked by a panel of biologists with expertise on boreal caribou habitat use in Saskatchewan (Saskatchewan Ministry of Environment, 2019). We resampled all spatial covariates to 1 km^2 spatial resolution, with each grid cell representing the fraction of the original 30 m for the selected class or classes. We then calculated the median proportion of each land cover type and habitat potential within a 12 km radius of each detection location, based on the larger of the estimated home range radii for females (~12 km) and males (~6 km) calculated from the SK Central population density estimation without any covariates (S. McFarlane, unpublished data). See Appendix 2 for more information on density modeling and R code.

We used the relationships between density and covariates from the top-ranked density model to create a density surface for each of the survey areas and applied these density-covariate relationships across the boreal plains. We constrained this to just outside of the boreal plains ecozone as an ecological unit with distinct biotic and abiotic features (Marshall et al., 1999). We calculated the median population density (per ha) within a 12 km radius of each sampling location using the same method as mentioned above for the spatial covariates. The resulting density surface was used to estimate the influence of density on sex-specific network metrics, dispersal distance, individual reproductive success, and female pregnancy status.

2.3.2 Reconstruction of familial relationships

We identified boreal caribou families by reconstructing parent-offspring relationships using COLONY v2.0.6.5 (Jones and Wang, 2010). COLONY uses a full-likelihood method for sibship inference and parentage assignment, assigning all sampled offspring to hypothetical maternal and paternal families (Wang, 2004). Input parameters were set to allow for female and male polygynous mating systems without inbreeding avoidance, and the probability of mothers or fathers being present in the sampled data set was set to 50% in the absence of other prior information. COLONY infers parental genotypes for missing parents; inferred parents are genotypes that are not included in the candidate parent samples, either because that individual was not captured during sampling, or that parent was no longer alive when sampling occurred, resulting in a family network with more individuals than were sampled. We used Cytoscape v3.7.2 (Shannon et al., 2003) to create a familial network from the reconstructed parent-offspring relationships identified by COLONY. Each individual has their parents and offspring identified by COLONY enabling a network to be created from the multigenerational relationships among individuals. As boreal caribou mating systems are polygamous, a dense and complicated network is created; node-based measures of network centrality allow for easier identification of patterns and trends within the network. We confirmed the direction of all parent-offspring dyads by comparing them to the full sibling and parent pair outputs provided by COLONY.

2.3.3 Network centrality

We used the protocol outlined by McFarlane et al. (2021) to identify individuals that are central to the network, with the R package *CINNA* (Ashtiani et al., 2018) to determine individual node-based network centrality. Nodes represent individuals while edges represent parent to offspring relationships. We quantified distinct aspects of network centrality using three node-based centrality measures: alpha, closeness, and degree centrality. Alpha centrality identifies individuals that are connected to other highly connected individuals, indicating indirect reproductive success, even for those with few direct connections (McFarlane et al., 2021). Reproductive output can be highly variable and asymmetrical (McFarlane et al., 2018) and alpha centrality can indicate if an individual is part of a large extended family and if they are connected to highly connected individuals. Degree centrality represents the number of edges connected to a node; in familial networks, the in-degree represents the parents of an individual and the out-degree is the number of offspring associated with that individual (Harary, 1969; McFarlane et al., 2021). Closeness centrality has commonly been used to measure how fast information can spread from a given node to all other reachable nodes in a network (Latora and Marchiori, 2001). In familial networks, individuals with higher closeness centrality come either from more connected families, or larger families with more generations captured during sampling.

2.4 Analyses

2.4.1 Familial network and density

We ran sex-specific generalized linear models (GLMs) to determine the influence of density on the three individual network centrality measures using a Gaussian error structure. Each centrality measure was standardized between 0 and 1. To validate the familial network centrality measures used in these models (due to the lack of independence of data points present in network data), 10,000 random familial networks with a burn-in of 1,000 networks were generated using permutations (Jones and Manseau, 2022). Each network was created by swapping mothers or fathers and swapping offspring. As with the real data, each individual's network metrics were recalculated using these permuted networks. All global models were recalculated for each of the 10,000 permuted networks. The sizes of the coefficients were then compared to the size of the global models based on the original data. A *p*-value was calculated as the proportion of times the observed value was more extreme than the permutated values (Farine, 2013). A network centrality measure effect was considered significant if this *p*-value was < 0.05 and the coefficients' confidence interval did not include zero.

2.4.2 Dispersal and density

To test for density-dependent dispersal, we ran sex-specific GLMs with a Gaussian error distribution to determine the influence of density at the parental site on offspring dispersal. Dispersal events can be inferred when parents and offspring relationships, reconstructed through sibship assignment, are found in different locations (e.g. Norman and Spong, 2015; Fountain et al., 2017). Although the actual dispersal route cannot be determined, recent gene flow and movement among locations can be inferred, and applying this method to many pairs of relationships, the population's dispersal patterns can be estimated (Escoda et al., 2017). We defined dispersal as the movement of offspring away from their natal source (Nathan, 2005), defining the natal source as the location of the parent. We calculated Euclidean dispersal distances in the R package *geosphere* (Hijmans, 2019) for all parent-offspring dyads and calculated the difference between the minimum and maximum dispersal distances of parent-offspring dyads (Figure S2.1). As we calculated the median population density within the estimated home range (12 km), and most dyads (93%; Figure S2.1) had a range of dispersal distances within 0-20 km, we used the maximum dispersal distance between the parent-offspring dyads to represent offspring dispersal.

2.4.3 Recruitment, pregnancy and density

We ran sex-specific binomial GLMs to determine the influence of density on the probability of female and male boreal caribou having offspring using a binary classification of individual reproductive success (did or did not have offspring) calculated from the reconstructed parent-offspring relationships. Following the protocol outlined by Flasko *et al.* (2017), 460 samples were measured for fecal pregnane concentrations to determine yearly female pregnancy status of 363 female caribou, using a threshold of 700 ng/g dry mass (Table S5.1). We ran binomial GLMs to determine the influence of density on female pregnancy status.

3 Results

A total of 2616 samples were collected and 2331 were successfully scored (average success rate of 92.1%), resulting in the identification of 762 unique individuals (Table 1). 455 females, 298 males, and 9 individuals of unknown sex were identified. Overall, the average allele dropout rate was 0.0027% and the average false allele rate was 0.01%.

3.1 Density estimation

Recaptures, including within-occasion recaptures, were sufficient in all three study areas (Table 2). Using a multi-session SCR model allowed us to increase the number of captures and recaptures used in the overall density model (Table 2). 282 individual caribou were included in the multi-session SCR model with a total of 404 detections at 96 unique locations (Table 2). Median spatial recapture distances varied from 3.4 km in SK Central to 7.6 km in SK East (Figure S2.2).

Our results suggest that boreal caribou densities are low overall and animals are spatially clustered, with error below the 20% relative standard error threshold in all study areas (RSE = 11.5–13.9%), suggesting reasonably precise estimates. The top density model included good-quality habitat, a negative effect of poor-quality habitat, and a positive effect with greater distance to roads (Table S2.1, Figure 2). Although density was low overall (maximum density of 270 boreal caribou per 1,000 km^2), there was substantial variation in the distribution of lower- and higher-density areas (Figure 3). Distance to roads was a large contributor to the high variation in spatial density; large undisturbed areas far away from roads had the highest boreal caribou densities (Figures 2, 3). Poor-quality habitat was also a large driver of boreal caribou density, with density dropping to 0 in areas with >20% poor quality (deciduous) cover.

3.2 Familial network analysis

Pedigree reconstruction inferred an additional 227 females and 231 males, for a total familial network of 1220 individuals (Figure S3.1). 305 females and 270 males were identified as parents (47% of all individuals). Comparison of the observed network to the 10,000 permuted networks indicated that females from lower density areas have a higher closeness centrality and higher degree centrality than expected compared to a null of random familial relationships (Figure S4.1, Table 3), indicating that females found in lower density areas tend to be more broadly associated to animals across the range. Conversely, we observed no pattern in degree and closeness centrality in response to density for males, and no pattern in alpha centrality in response to density for either males or females. This highlights that males network position is not influenced by density, and alpha centrality is not influenced by density for either sex.

3.3 Dispersal and density

In cases where an offspring was assigned a sampled mother or father, it was possible to infer effective offspring dispersal distance. Boreal caribou offspring disperse primarily within short distances of their parents; 86% of offspring dispersal events were < 40 km (Figure 4a). The largest dispersal distances were between fathers and their offspring (Figure 4b). The maximum dispersal distance between fathers and their offspring was 232 km with a mean of 22 km (± 32 SD), while the maximum dispersal distance between mothers and their offspring was 152 km with a mean of 20 km (± 25 SD). There were 35 parent-offspring pairs where both the parent and offspring were only located together, with 49% of these being mother-daughter pairs.

Density at the parent location had no significant effect on dispersal when accounting for parental sex; however, a negative trend was identified for mothers and their offspring ($p = 0.068$, Table 3). When accounting for the sex of the dispersing offspring, dispersal distance of male offspring was significantly and inversely related to parental density (Table S3.1, Figure 4b), while dispersal of female offspring from their parents was not significantly related to parental density (Table S3.1). Further investigation into sex differences in dispersal indicated that dispersal distance between mothers and male offspring was also significant (Table S3.2), corresponding to the significant results for male offspring and the trend identified for mothers.

3.4 Recruitment, pregnancy and density

We identified large reproductive skew in both sexes, with 87% of sampled males and 83% of sampled females not successfully producing calves that survived until fall. Pregnancy rates were substantially higher than the proportion of individuals who successfully reproduced; yearly female pregnancy rate ranged from 0.71 to 0.87, with an overall pregnancy rate of 0.78 (Table S5.1).

Density significantly affected the reproductive success of both females and males (female $p = 0.043$, male $p = 0.038$; Table 3) but affected the sexes differently. For females, the predicted probability of successfully having offspring was highest at lower densities, while for males it was highest at high densities (Figure S3.2). Density did not significantly affect the pregnancy status of females (Table 3).

4 Discussion

We used network analyses to measure density-dependent demographic responses in a large mammal population. As predicted, we detected density-dependent demographic responses in female and male boreal caribou and the use of familial networks allowed us to measure how density influences both direct and indirect reproductive success within a population. We found that boreal caribou density at the natal site affected male, but not female, offspring dispersal distance and reproductive success of both males and females. Our results demonstrate that the influence of density varies between sexes and by the association between animals, i.e. centrality, within the entire population (Table 3). The significantly higher network centrality observed for females from low density areas indicates that not only is the direct reproductive success of females in low density areas higher, but that they are also connected to family lines (i.e. parents or offspring) who also have higher reproductive success compounding this effect.

Integrating familial network metrics allowed us to better capture complex demographic processes that may vary with density. By building a familial network from parent-offspring relationships, we were able to account for the contribution of non-reproducing individuals in the overall demographic structure of the population and assess how density dependence affects reproductive success. Boreal caribou mate polygynously, with mating occurring in loose harems (Thomas and Kiliaan, 1989), and males defending access to mates such that reproductive success of males is dominated by larger and older individuals (Hirotani, 1994). Familial network analyses indicated that only 13% of sampled males successfully sired a calf that survived until fall. Because the males with the highest reproductive success were found in higher-density areas, reproductive output was dominated by relatively few males. It may be beneficial for subordinate males to remain within these higher-density areas, remaining with a female group and waiting for the sexual activity of dominant males to wane, or for the possibility of gaining the dominant position and the associated reproductive benefits (Røed et al., 2002). At low densities, males may be more efficient at defending harems due to less competition from other males, leading to lower overall reproductive success in lower-density areas.

The reproductive success observed for females was low and varied with density. Our pregnancy results indicated that the overall pregnancy rate was 81%, yet our familial network analysis found that only 17% of sampled females successfully reproduced a calf that survived until fall, indicating that calf mortality is high and is a contributing factor in the low successful reproduction rate. Although some of the non-reproducing females may be subadults not yet capable of breeding, this likely would not account for a large proportion of the population. Calf survival in caribou is low, with calf loss to predation highest during the first month of life (Stuart-Smith et al., 1997, Pinard et al., 2012); predation by black bears (*Ursus americanus*) and wolves (*Canis lupus*) can account for more than half of calf mortalities (Pinard et al., 2012). In our study, recruitment was inversely density-dependent, as calf survival was greater in lower density populations, similar to what has been observed in a few other studies (Toïgo et al., 2002; McLoughlin et al., 2006). Alpine ibex (*Capra ibex*) show greater variance of female reproductive success in a density-dependent population than a population with no density dependence (Toïgo et al., 2002), and the lifetime reproductive success of female red deer was inversely density-dependent (McLoughlin et al., 2006).

There may be marked differences in individual reproductive quality among females (Byers, 1997; Weladji et al., 2006; Weladji et al., 2008; Hamel et al., 2009), which may be exacerbated by population density (Bonenfant et al., 2009). Weladji et al. (2008) showed that female reindeer (*Rangifer tarandus*) that were successful breeders had higher subsequent reproductive success than non-breeders and unsuccessful breeders, and Weladji et al. (2006) showed that larger and older reindeer had higher lifetime reproductive success, possibly due to a higher social rank or ability to minimize high mortality risks. In pronghorns (*Antilocapra americana*), experienced breeding females had lower calf losses to predation (Byers, 1997), and in a longitudinal study of mountain goats (*Oreamnos americanus*), bighorn sheep (*Ovis canadensis*) and roe deer (*Capreolus capreolus*), higher quality females all had a higher probability of reproduction in all three species (Hamel et al., 2009). Network analysis can help identify both density-dependent and independent factors that affect female reproductive success leading to an overall better understanding of population dynamics. Our study is the first to assess how centrality within the familial network vary with density in a wild population.

No other studies have assessed ecological and demographic drivers of dispersal in boreal caribou. Measuring dispersal in ungulate populations can be difficult due to long dispersal distances, sex-biased behaviours, differences in detection probability of dispersers and non-dispersers, and the multiple interactions (Moore et al., 2014). Here we successfully used network analyses to better understand what drives sex-specific dispersal. SCR modeling and the construction of familial networks from noninvasive genetic sampling allowed us to overcome some of these challenges. We found that male offspring stayed closer to their mothers when the mother was located in a high-density area (Table S3.2, Figure S3.2). Because boreal caribou are dispersing shorter distances at higher densities, and boreal caribou density was positively related to high-quality habitat availability and negatively correlated with distance to roads, individuals may become trapped within remnant patches of suitable habitat that can support higher densities. This suggests that anthropogenic disturbance can disrupt natal dispersal patterns, turning source populations into fragmented sinks (Fattebert et al., 2015). These results further emphasize the impact of landscape fragmentation on population demography and the importance for some species to maintain low population densities with high spatial connectivity throughout their range. Variation in natal dispersal has been linked to population density and group characteristics in several species, including feral horses (*Equus ferus caballus*, Marjamäki et al., 2013)] and African lions (*Panthera* leo, VanderWaal et al., 2009). In most polygynous mammal species, males are the dispersing sex while females are philopatric (Greenwood, 1980; Wolff, 1997).

Boreal caribou density is influenced by landscape composition and fragmentation, resulting in patches of higher density that lead to individual heterogeneity in demographic responses. Driven, in part, by anthropogenic disturbances, density-dependent variation in demographic traits may be triggering positive feedback loops as both the reproductive success of females and the dispersal distances of male offspring were lower in higher density areas. Network centrality metrics allowed us to improve the resolution of broad measures of demographic parameters to gain a better understanding of the density-dependent demographic processes of boreal caribou populations. Demographic processes, such as reproductive success, calf survival and dispersal, can alter the network structure among individuals in a population by adding or removing an individual and its connections (Shizuka and Johnson, 2020). To our knowledge, this is the first study looking at the effects of variable density across the range of a wild ungulate population on individual-level measures of reproductive success and dispersal rates.

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6 Authors' contributions

MM and GP conceived and designed the study. SM implemented the analysis and wrote the manuscript with help from MM and TJ. PW coordinated DNA extraction and analysis. DP coordinated and analyzed the spatial density covariate data. GM coordinated hormone extraction and analysis. All authors contributed to subsequent drafts and gave final approval for publication.

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8 Figure titles

Figure 1. The effects of variable spatial density on demographic parameters.

Figure 2. Predicted responses of the top density model showing the relationships between (A) good-quality habitat and caribou density, (B) poor-quality habitat and caribou density and (C) distance to linear features and caribou density.

Figure 3. Spatially-explicit boreal caribou density across the Saskatchewan Boreal Plains caribou range. Boreal caribou density was associated with good- and poor-quality habitat and linear

disturbances. Densities are low overall and spatially clustered, greatest away from linear features and poor-quality habitat.

Figure 4. Frequency of maximum dispersal distances between parents and offspring by parent sex (a). Distribution of maximum dispersal distances versus density at the parent location by (b) parent sex and (c) offspring sex.

9 Tables

Table 1. Sampling data

Survey Area	Survey Year	Number of Samples Collected	Number of Samples Successfully Scored	Number of Unique Genotypes	Genotyping Success (%)
Fin Flon	2014	336	320	119	95.2
La Ronge	2013 & 2015	497	403	140	81.1
SK Boreal Plains West	2016	242	233	117	96.3
SK Central	2017-2019	1,184	1,030	214	87
SK East	2020	159	152	63	95.6
SK West	2020	198	193	109	97.5
Total	-	**2,616**	**2,331**	**762**	-

Table 2. Summary of spatial capture-recapture data used in the multi-spatial session model for estimating density.

	SK Central			SK East			SK West			
Within-year occasions	1	2	**Total**	1	2	**Total**	1	2	**Total**	**Grand Total**
Number of individuals detected on each occasion	69	78	**147**	47	26	**73**	62	53	**115**	**335**
Number of individuals detected for the first time on each occasion	69	36	**105**	47	19	**66**	62	49	**111**	**282**
Number of individuals detected exactly f times	63	42	**105**	59	7	**66**	107	4	**111**	**282**

Cumulative number of individuals detected	69	105	**105**	47	66	**66**	62	111	**111**	**282**
Number of detections (including within-occasion 'recaptures')	89	113	**202**	52	26	**78**	68	56	**124**	**404**
Traps visited (number of detectors at which at least one detection was recorded	21	26	**47**	13	6	**19**	19	11	**30**	**96**

Table 3. Generalized linear model results for effect of density on several demographic parameters. P-values for centrality measures are obtained from permutations. *** indicates significant model results.

Parameter	Females	estimate	p-value	Males	estimate	p-value
Alpha centrality	None	−0.0003	0.51	None	0.0003	0.260
Closeness centrality	Negative	−0.0018	0.0007***	Negative trend	−0.00093	0.097
Degree centrality	Negative	−0.00044	0.034***	None	0.00036	0.790
Dispersal (parent sex)	Negative trend	−211.28	0.068	None	−221.24	0.230
Dispersal (offspring sex)	None	−112.11	0.47	Negative	−307.62	0.009***
Recruitment	Negative	−0.012	0.043***	Positive	0.019	0.038***
Pregnancy	None	−0.0024	0.69	-	-	-

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11 Data availability statement

The datasets generated and analyzed for this study can be found in the FigShare repository (https://doi.org/10.6084/m9.figshare.19905142).

12 Supplementary Material

The Supplementary Material for this article can be found online at: [LINK].

Figure 1.JPEG

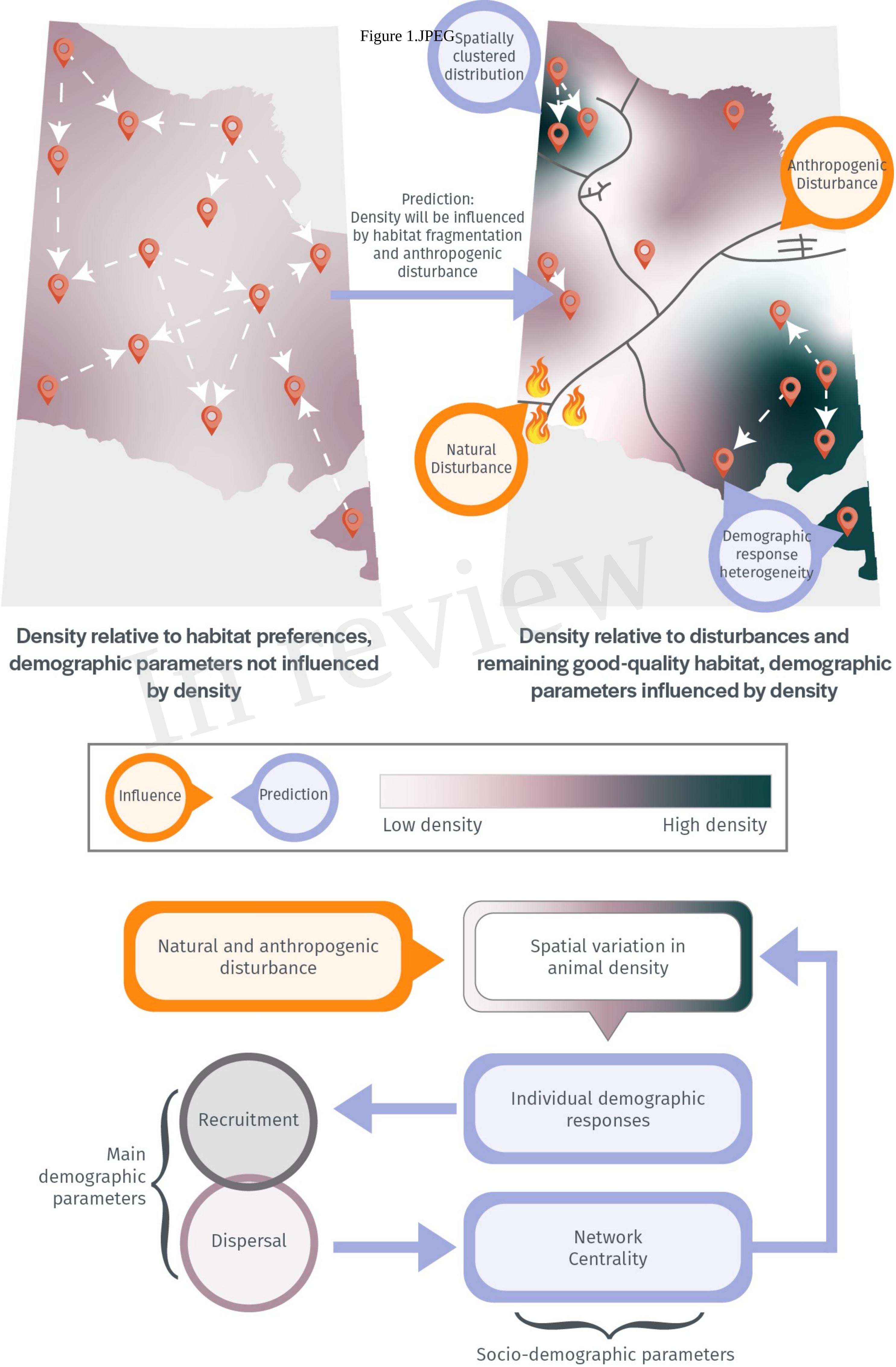

Figure 2.JPEG

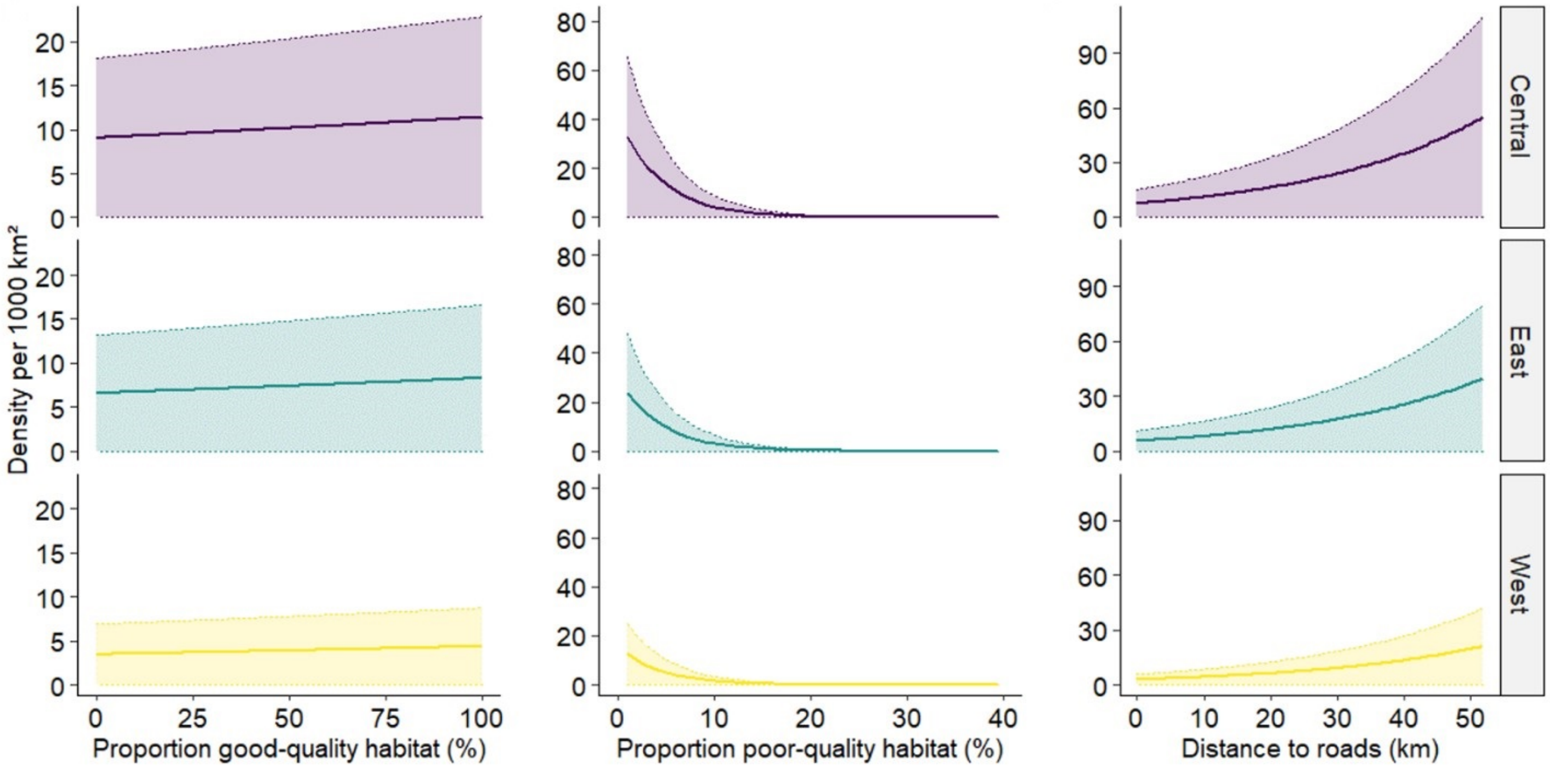

Figure 3.JPEG

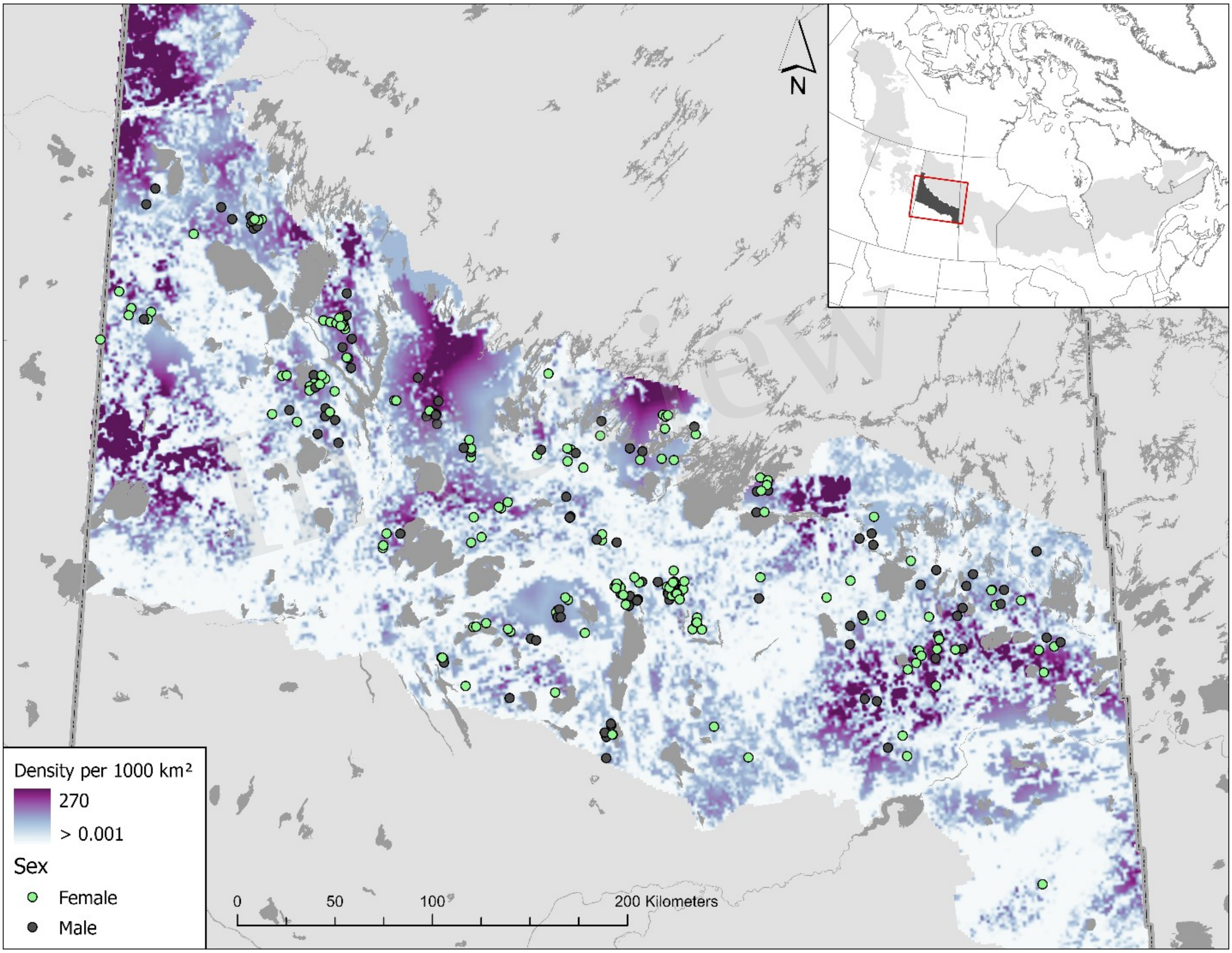

Figure 4.JPEG