



Contents lists available at ScienceDirect

Global Ecology and Conservation

journal homepage: www.elsevier.com/locate/gecco

Novel multilayer network analysis to assess variation in the spatial co-occurrences of close kin in wild caribou populations

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ARTICLE INFO

Keywords:

Spatial network

Connectivity

Familial pedigree

Demographic parameters

Population status

ABSTRACT

Understanding how individuals within populations are connected genetically and through shared space-use is critical to understanding the demographic patterns of at-risk populations. In recent years, non-invasive genetic sampling methods have allowed us to begin addressing these questions. Using a network analysis framework, we examined the spatial co-occurrence and genetic relatedness of boreal and central mountain caribou (*Rangifer tarandus*) in populations varying in sizes and trend from across western Canada. Using 15 microsatellites loci and a sex-specific marker, we developed pedigree networks for each population, including first to third order relationships. We constructed networks of individual spatial co-occurrence, and using multilayer network analysis, we determined the degree to which caribou that co-occurred spatially were related. Caribou populations varied in the extent and classes of familial relationships which co-occurred in space. In most populations, spatial co-occurrences were greater than expected only for parent-offspring relationships. A sex-specific analysis of the longest sampled population revealed that this was driven by a significant overlap between mothers and their offspring. Whereas in populations where very few parent-offspring relationships were detected, no significant overlap was found between any relationship categories. The lack of overlap in these populations may be an indication of poor calf survival. On the other hand, the higher degree of overlap with more distant relations (i.e., grandparents) seen in some populations may indicate a population that lacks mobility. Our research presents a new approach to explore both spatial and genetic overlap at the individual level in support of the conservation of threatened populations.

1. Introduction

Within a population, individual space use can influence social associations (Spiegel et al., 2016; Genoves et al., 2018; Evans et al., 2020b) as well as disease and predation risk (Schauber et al., 2007; Albery et al., 2021). Even when the home ranges of two individuals overlap, different levels of social association are possible based on their temporal overlap within the space. Individuals can share space

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<https://doi.org/10.1016/j.gecco.2023.e02688>

Received 23 August 2023; Received in revised form 16 October 2023; Accepted 16 October 2023

Available online 17 October 2023

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at the same time to access clumped resources (i.e. Evans and Morand-Ferron, 2019; Peignier et al., 2019) or for the protective benefits obtained from foraging in groups (Krause and Ruxton, 2005). Not all individuals will interact or co-occur equally, especially in fission-fusion societies where groups form and split over time (Aureli et al., 2008). In some species spatial-temporal overlap and associated social interactions may be linked to genetic relationships between individuals (i.e. King et al., 2011; Carter et al., 2013; Diaz-Aguirre et al., 2018; Evans et al., 2020a).

In some mammal groups or populations the level of relatedness between individuals can vary depending on factors such as breeding system and sex-biased dispersal (Chesser, 1991; Storz, 1999), habitat fragmentation and inbreeding (Frankham, 2006), and the typical age at which individuals disperse which for longer-lived species may not occur until individuals are some years old or approaching sexual maturity (i.e. Linklater and Cameron, 2009; Killeen et al., 2014). For species living in groups, there can be potential costs to associating with relatives, such as competition for resources (Perrin and Mazalov, 2000) and risk of negative impacts of inbreeding (Keller and Waller, 2002). Alternatively, living with close kin can increase the benefits provided by group living, such as co-operative behaviours benefitting close relatives and through inclusive fitness effects (Krause and Ruxton, 2005). Additionally in species with delayed dispersal, offspring closely sharing space with parents, such as by remaining in the same social group, is expected to be an indicator of offspring recruitment (Dane, 2002; Bowyer et al., 2020). Species may adopt a group size and composition to balance these costs and benefits as seen in boreal caribou that have been found to winter in mixed-sexed groups of around 8 individuals, which may balance group protection benefits while avoiding easier predator detection of larger group sizes (Jung et al., 2019).

Understanding how populations are genetically and spatially structured is a component of population demographics and dynamics that can be critical for monitoring and managing declining species and species at risk such as understanding contemporary barriers to movement (Escoda et al., 2017) or understanding sex-specific spatial behaviour (such as sex-biased dispersal) (Mysterud et al., 2002). As genetic research findings and associated methodologies become more available it is increasingly possible to examine connectivity not only between populations, but also within populations (DeSalle and Amato, 2004; Foroughirad et al., 2019). In particular, genetic sampling combined with pedigree reconstruction methods (Cowell, 2009; Riester et al., 2009; Jones and Wang, 2010) enables estimation of detailed pedigrees, and is especially beneficial when parentage is impossible to assess through other means (McFarlane et al., 2018).

Network analysis allows the study of various types of connections to be examined within a common framework (Newman, 2010). In particular, network analysis can be used to examine both individual-level and population-level genetic relationships (Jones and Manseau, 2022). Recent studies have demonstrated the use of network analysis for pedigree-based analysis (Escoda et al., 2017, 2019; McFarlane et al., 2021). Network analysis has also become a common tool to quantify and study spatial and social relationships between individuals (Croft et al., 2008; Farine, 2015; Farine and Whitehead, 2015; Albery et al., 2021). Multilayer networks, a term used to describe any multidimensional network, combine multiple linked networks and provide tools to examine multiple association types, such as spatial and genetic relationships, or antagonistic and co-operative behaviours, together within the same set of individuals (Pilosof et al., 2017; Silk et al., 2018; Finn et al., 2019; Mello et al., 2019). For example, social patterns between close relatives were found to vary seasonally in house mice (*Mus musculus domesticus*), with less association between close kin observed in the breeding season (Evans et al., 2020a).

Woodland caribou (*Rangifer tarandus*) of the boreal and southern mountain - central group Designatable Units in Canada are respectively listed as threatened and endangered under the Species at Risk Act (SARA) (Government of Canada, 2020). This species is experiencing significant habitat change and loss (e.g. Nagy-Reis et al., 2021), and associated habitat-mediated competition (Environment Canada, 2011). Along with other demographic parameters relevant to woodland caribou conservation and recovery, it is valuable to understand how populations are spatially and genetically structured in winter, including how patterns of social cohesion or dispersal vary across populations of different sizes and trend. However, for many long-lived and wide-ranging species it has been difficult to simultaneously obtain spatial data and familial relationships to examine these factors together within a single framework. In this study we use genetic sampling and combine pedigree reconstruction of wild caribou populations with multilayer network analysis. Our goal is to assess the degree to which animals of different sex and familial relations co-occur in space. While it is possible to disentangle shared use of space from social preferences in some cases (Evans et al., 2020b), for the purposes of our study we consider our measure of shared space in terms of spatial overlap, although it can also be seen as an indication of potential social associations. We collected data from 14 caribou populations distributed across western Canada in mountain (4) and boreal (10) ecozones. Woodland caribou in mountainous areas are typically migratory, with distinct seasonal ranges, while boreal caribou move short distances throughout the year and do not migrate between seasonal ranges (Theoret et al., 2022). Mountain caribou migrate to higher elevations in the spring for calving, they aggregate during the fall rut and disperse in small groups to lower elevation forested ranges over winter (Edmonds, 1988). Boreal caribou tend to be solitary from pre-calving to late summer and form small mixed sex and age groups in winter (Metsaranta and Mallory, 2007), with group size possibly associated with population and environmental factors (Jung et al., 2019). Adult females (≥ 3 years) can have up to one calf per year, resulting in a lower reproductive rate than other similar deer species (COSEWIC, 2014). Calf predation rates are highest in the first 12 weeks (Lewis and Mahoney, 2014) and no significant difference between male and female calf survival (Mahoney and Weir, 2009) is observed.

We examine how shared space use by close kin varies across populations of different sizes, experiencing different population trends, and from habitats presenting different levels of natural and anthropogenic disturbances. We measure the proportion of mother-offspring dyads per female sampled as a proxy measure of recruitment, though this is not a direct reflection of annual recruitment rate. We predict that populations experiencing stable or positive population trends will have higher numbers of mother-offspring dyads, and higher social cohesion in these dyads (as measured by significant overlap in space-use between parents and offspring). However, due to constraints in sampling size, we examine parent-offspring relationships as in most populations we did not have the statistical power to implement sex-specific analyses. We also predict that many third-order kin relationships, in particular grandparent-

grandoffspring could reflect either a high level of survival and calf recruitment within the population or a lack of ability to disperse, though it is difficult to entirely disentangle these factors.

2. Methods

2.1. Study populations

We collected data from 14 populations of caribou from two ecozones (4 central mountain and 10 boreal ranges) across western Canada (Alberta, Saskatchewan, and Manitoba; Fig. 1). In each population, systematic surveys to collect fecal pellet genetic samples were conducted two to four times per year during winter (Oct–March). In Jasper, surveys were timed to coincide with the first snow falls and before the animals moved below the treeline, while in all other populations samples were collected during winter after fresh snowfall. In each population, fecal pellet samples were collected for a minimum of 1 year (range 1–11 years; see Table 1). Feeding sites (cratering through snow to access ground lichen) were located along aerial transects systematically flown at 3-km intervals using rotary- or fixed-wing aircrafts following the protocol of [Hettinga et al. \(2012\)](#). Rotary-wing aircraft visited identified feeding sites and team members collected fecal pellets from the immediate vicinity. Collection sites were generally spaced at least a kilometer apart. Surveys were conducted approximately 1 month apart to enable capture-mark-recapture (CMR) and spatial capture-recapture analyses (SCR) ([Hettinga et al., 2012](#); [McFarlane et al., 2018](#); [McFarlane et al., 2020](#)), and to construct spatial co-occurrence networks.

Briefly, fecal pellets were placed in sterile bags and kept frozen at -20°C prior to DNA extraction. We followed the DNA extraction protocol of [Ball et al., \(2007, 2010\)](#) and generated individual-specific genetic profiles from fifteen polymorphic microsatellite loci (BM848, BM888, Map2C, [Bishop et al., 1994](#); FCB193, [Buchanan and Crawford, 1993](#); NVHRT16, [Røed and Midtthjell, 1998](#); OHEQ, [Jones et al., 2000](#); RT1, RT5, RT6, RT7, RT9, RT13, RT24, RT27, RT30, [Wilson et al., 1997](#)) along with caribou-specific Zfx/Zfy primers for sex identification. DNA was extracted using a Qiagen DNeasy tissue extraction kit following manufacturer's instructions. DNA profiles of microsatellite loci were done using PCR amplification and fragment analysis via capillary electrophoresis. Alleles were

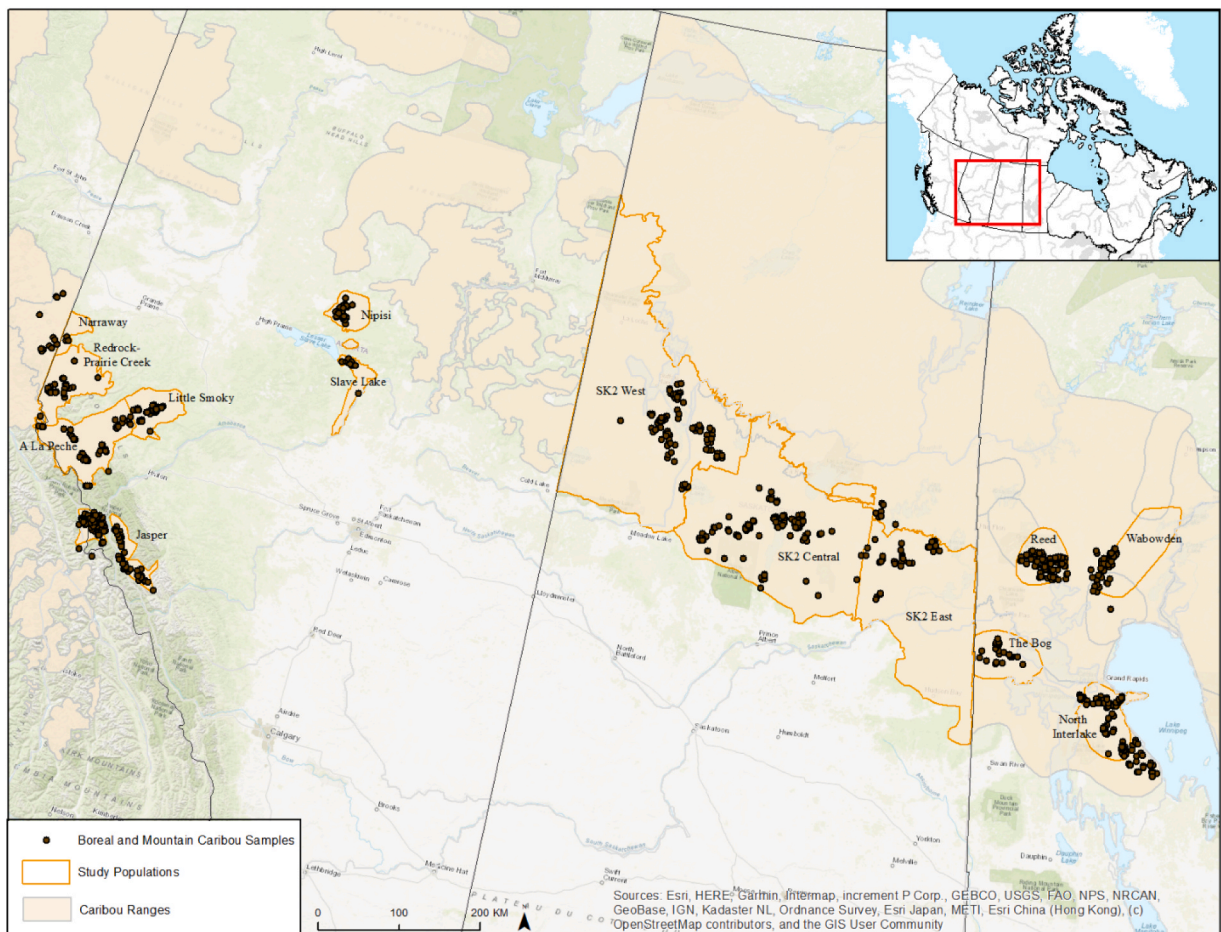


Fig. 1. Map of studied caribou populations across Alberta, Saskatchewan, and Manitoba in western Canada. Populations are delineated with orange borders and sampling locations are indicated with black circles.

Table 1

Summary of populations studied, number of years surveyed, number of unique individuals genotyped and composition, and estimated proportion of the total population sampled as determined from population estimates calculated using CMR methods.

Population	Trend and Risk Assessment	Years sampled	Number of collections per year	Unique number of individuals sampled	Male: Female	Mother-Offspring dyads	Father-Offspring dyads	Range of estimated annual population sizes	Average Proportion of Population Sampled (%)
Central Mountain caribou									
A la Pêche ^b	Increasing; NSS	1 (2018)	3	134	68:65	52	25	162	83
Jasper	Declining; NSS	11 (2006–16)	2–3	250	101:123	138	131	69–98	89
Redrock Prairie Creek ^b	Declining; NSS	1 (2019)	4	174	63:110	43	12	153	79
Narraway ^b	Declining; NSS	1 (2019)	3	45	14:31	7	3	57	80
Boreal caribou									
Little Smoky ^b	Stable; NSS/SS	1 (2015)	3	108	35:73	34	8	119	91
Nipisi ^b	Declining; NSS	1 (2018)	3	65	22:38	7	3	71	91
Slave Lake ^b	Declining; NSS	1 (2018)	3	38	12:26	2	5	50	76
SK2Central	Declining; NSS/SS ^d	3 (2017–19)	2	214	79:130	33	23	125–181	73
SK2 West	Not available; NSS/SS ^d	2 (2020–21)	2	275	98:176	96	24	112–224	39
SK2 East	Not available; NSS/SS ^d	2 (2020–21)	2	121	61:60	16	8	67–77	49
Bog	Declining; NSS/SS	3 (2015/17/19)	2	125	41:84	30	20	81–209	49
North Interlake	Declining; NSS/SS	7 (2003–10)	2	199	68:97	65	51	105–165	51
Naosap-Reed	Declining; NSS/SS	3 (2015/17/19)	2	265	112:153	41	54	175–365	41
Wabowden	Stable; SS	3 (2015/17/19)	2	173	76:97	43	35	105–147	65

^a Risk Assessment is the status of self-sustainability of the local populations where SS=self-sustaining; NSS = not self-sustaining; NSS/SS = as likely as not self-sustaining. Sources: [Environment Canada \(2014\)](#), [Environment and Climate Change Canada \(2020\)](#). Sources for trend results: Alberta Government. 2017; Government of Saskatchewan. 2019, 2021; [Hettinga et al. \(2012\)](#), Trend results for SK2 Central, Bog, Naosap-Reed and Wabowden available at [Ecogenomicscanada.ca/publications/#3](#).

^b A wolf reduction program has been ongoing in west-central Alberta since 2005/2006.

^c Population size estimates produced from capture-mark-recapture analysis. [Hettinga et al. \(2012\)](#), [McFarlane et al., \(2018, 2020\)](#); Unpublished results available at [www.EcogenomicsCanada.ca](#).

^d Risk assessment done on SK2 - Boreal Plains which includes SK2 east, SK2 west and SK2 central as used in the surveys and for the analysis.

scored using GeneMarker® (SoftGenetics, State College, PA).

2.2. Pedigree reconstruction and network

For quality control, we retained only samples which were successfully genotyped at ≥ 12 of the 15 loci. For each population, we used the ALLELEMATCH package version 2.5.1 (Galpern et al., 2012) in R version 4.0.5 (R Core Team, 2016) to identify which samples belonged to the same individual, retaining a single sample for each unique individual. Across the 15 loci for all samples, there was an average of 8.8 alleles per locus, an average observed heterozygosity of 0.72, and an average of 3.9% of samples contained missing alleles across all loci (Tables S1-S3). We then used COLONY version 2.0.6.8 (Jones and Wang, 2010) to infer parentage for the set of unique individuals, with parentage for each individual assigned to sampled individuals, inferred individuals (i.e., unsampled individuals with an inferred genotype), or both (i.e., one sampled parent and one inferred parent). We retained all parent-offspring pairs assigned by COLONY, including both sampled and inferred individuals. Pedigrees were constructed and visualized using the visPedigree package version 0.2.6 (Sheng, 2018). We determined pairwise first, second, and third-order relationships from the pedigrees. Relationship categories considered include parent, offspring, sibling, grandparent, grandoffspring, cousin, aunt or uncle, and niece or nephew. We made no distinction between full and half relationships (i.e., full- vs. half- sibling, cousin, etc.). In cases where an individual had multiple pairwise relationships to the same individual due to inbreeding, we assigned it to the closest-order relationship. For example, an individual that was both another individual's sibling and niece or nephew was assigned to the sibling class.

To construct a pedigree network for each population we first removed all inferred individuals from the COLONY output, while retaining any subsequently identified relationships (i.e., siblings identified through a shared inferred parent). We then built a weighted network in R by converting the categorical relationship to a numerical weight ordered from the highest order (parent-offspring) to the lowest order (cousin) relationships. For each population, a single undirected weighted network was built representing the pedigree data.

2.3. Spatial co-occurrence network

Genetic samples were grouped spatiotemporally by feeding site and date of collection. As samples were collected during the late fall or winter season after fresh snow, we treated all samples that were collected from the same feeding site on the same day as co-occurring in time and space (i.e., individuals were deemed to be part of the same group within the collected samples). We used the R package CMRnet (Silk et al., 2021) to construct spatial co-occurrence networks, with data from all studied years included to give a single network for each population sampled. Thus, these networks reflect which individuals ever co-occurred together at any point in time during our study, and which did not. These data can also be considered as reflecting the social network of the individuals under the common assumptions of a 'gambit-of-the-group' approach in which all individuals within a single group are deemed as socially associating (Franks et al., 2010), however, here we chose to use the term 'spatial co-occurrence network' to highlight that spatial nature of these associations in our context.

2.4. Multilayer network and edge overlap

We combined the two network types (pedigree and spatial co-occurrence) into a multilayer network. Multilayer networks are made up of layers of single networks that are also connected to one another through interlayer edges. In this case the same individuals are present in both network layers but in different contexts (spatial co-occurrence, and familial relationship), thus the interlayer edge connects each individual to itself in the other layer forming a multi-relational multiplex network (Finn et al., 2019). The use of multilayer analysis allows us to assess how the connections in one context (genetic relatedness) relate to the connections in another (spatial co-occurrence) in a single framework (Silk et al., 2018; Finn et al., 2019).

Edge overlap is a multilayer network metric that quantifies the proportion of edges shared between all layers (Bianconi, 2013; De Domenico et al., 2015). As we were interested in the overlap of specific categorical relationships, instead of calculating the global overlap of each multilayer network, we identified all edges that were shared between the genetic and the spatial network layers at a dyad level.

2.5. Sex-specific overlap

For the population with the longest sampling period (Jasper; 11 years sampled) we performed an additional sex-specific analysis assessing the multilayer edge overlap for a network subset which included only the parent-offspring relationships divided into sex-specific categories (father-daughter, father-son, mother-daughter, and mother-son). This analysis followed the same procedures as the full network analysis.

2.6. Statistical analysis

To assess the relationship between level of familial relationship on the spatial co-occurrence of individuals we coded all dyads that shared a familial relationship but no spatial co-occurrence as 0 and all dyads that had both a familial and a spatial connection as 1. We omitted all dyads that shared only a spatial connection from the analysis as we could not assess a lack of familial relationship with the same degree of confidence as an identified familial connection, and the high number of dyads with no identified familial relationship

produced a highly 0 skewed distribution.

The binary overlap value for each dyad was used as the response variable in a binominal linear mixed model using the package lme4 (Bates et al., 2015). The familial relationship category and a sex category (identifying the dyad as male-male, female-female or male-female) were fitted as explanatory variables with individuals' ids fitted as random effects. To account for the lack of independence inherent in network data, we assessed statistical significance by comparing the observed model coefficients to those obtained from running the model on 1500 permutations of the multilayer network (Farine and Whitehead, 2015; Farine, 2017). For each permutation we performed swaps of the relationship category of dyads to create a null model against which to test the effect of relationship category on the overlap between the two network layers, by preserving the same proportion of relationships and overlaps observed and allowing us to determine if overlap is driven by specific relationship categories. P-values were obtained as the proportion of times the values obtained from the observed coefficients were more extreme than the coefficients from the permuted data (Farine, 2017).

3. Results

Studied populations ranged in size from 50 to over 300 animals (Table 1). In general, there was an equal or larger number of females sampled in each population, with the ratio varying between 1:1 and 2:1. When three surveys were completed within a year the proportion of animals sampled was higher than when only two surveys were done (76–91% vs. 39–73%). The proportion of mother: offspring dyads (a proxy of recruitment rate) showed large variation (ranging from 0.08 to 0.8), with highest rate in A La Peche which is subject to a wolf population reduction program, and lowest rates in Nipisi and Slave Lake, the two smallest and declining populations (Table 1).

A single spatial co-occurrence network was constructed for each of the 14 caribou populations, spanning all sampling years (Fig. 2a&c). Pedigree reconstruction for each population produced a pedigree of up to three generations with inferred individuals, with

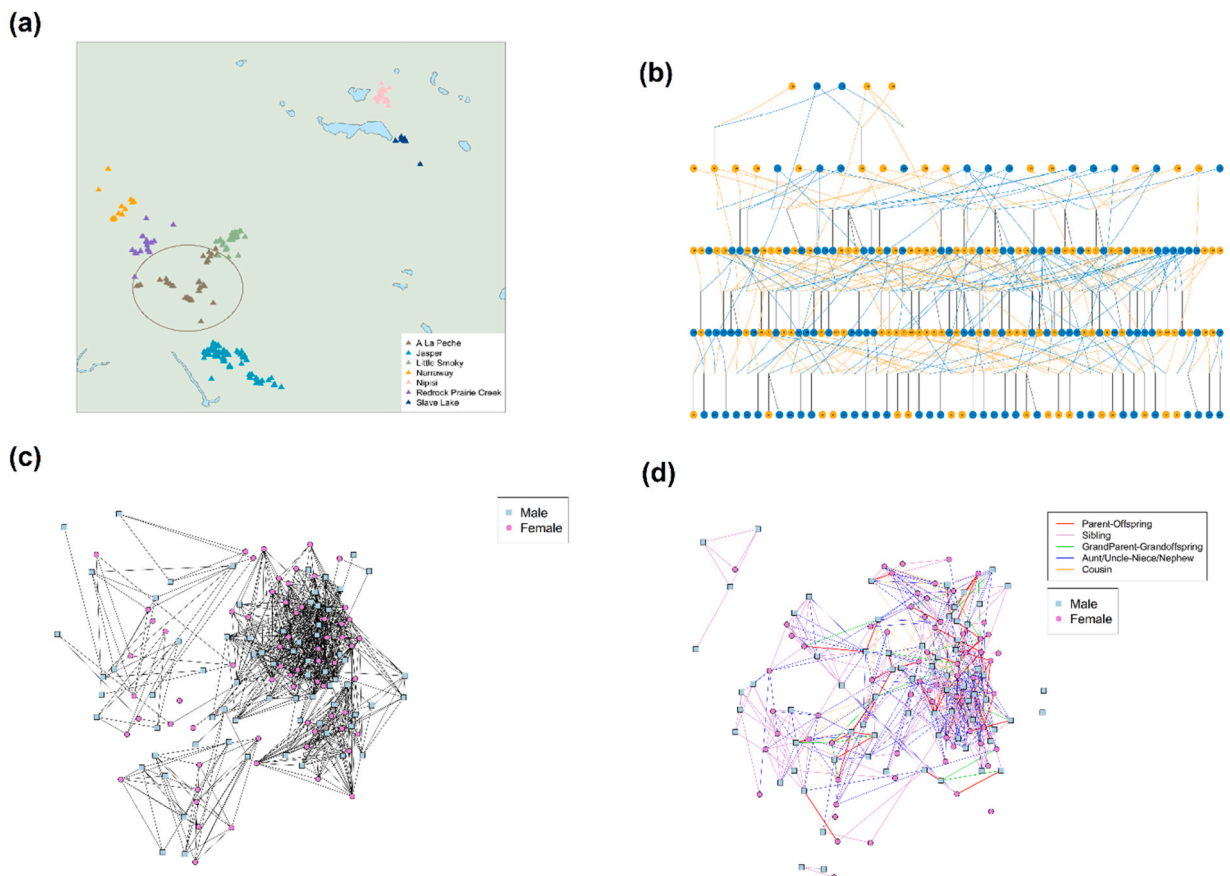


Fig. 2. Example networks from Alberta population A La Peche. (a) Sampling locations of Alberta populations with A La Peche samples indicated by a circle. (b) A La Peche pedigree output showing all sampled individuals and inferred individuals added through COLONY, each row represents a generation (c) Spatial co-occurrence network in which edges represent individuals that were sampled together from the same sampling day and location using the CMRnet package in R. (d) Pedigree network constructed from the estimated pedigree (b) after inferred individuals have been removed. Each edge represents a specific familial relationship as indicated by edge colour. In (c) and (d) individual node positions are preserved for comparison, and together these network layers form the multilayer network.

more comprehensive pedigrees obtained from longer sampled populations. Relationships of all studied categories were identified from each pedigree, apart from Slave Lake in which no grandparent-grandoffspring relationships were detected (Table 2). Each pedigree was converted into a weighted undirected network (Fig. 2b&d). The overlap between the spatial co-occurrence network and pedigree network layers were identified and the number of close relatives that were found to have a spatial relationship was determined for each relationship category (Fig. 3, Table 2).

3.1. Multilayer network and edge overlap

Six of the 14 populations were found to have very low numbers of relatives which also exhibited spatial co-occurrence (Table 2). These populations were generally very small, often with population estimates < 100 (Table 2) and are considered to be non-self-sustaining or unlikely to be self-sustaining populations based on landscape condition (Table 1, Environment Canada, 2011). Due to the extremely low levels of spatial co-occurrence and genetic overlap found in these populations we were unable to statistically assess the impact of relationship category on overlap in these populations as the models failed to converge in all cases, even when excluding the sparsest relationship categories (grandparent-grandoffspring and cousins).

For the remaining eight populations we examined the effect of closeness of familial relationship on the likelihood of a dyad also sharing a spatial co-occurrence relationship using a binominal linear mixed model and network-based permutations to create a null model for assessing significance. In most populations (5/8) parent-offspring dyads were observed to overlap spatially more often than would be expected by chance. Siblings were found to co-occur spatially greater than expected in four of the eight populations. While grandparent-grandoffspring overlapped more often than expected compared to the null models in only two populations (Jasper and Reed). In no populations was aunt/uncle-niece/nephew overlap found to occur at a rate differing from the expected by our null model. Cousin relationships were found to spatially overlap less often than expected by chance in four populations. Three populations (SK2 Central, North Interlake, and Redrock Prairie Creek) had no relationship types that spatially co-occurred greater or less than expected in the given null model (Table 3).

3.2. Sex-specific overlap

As parent-offspring relationships were the most commonly identified category that shared space-use, we performed a sex-specific analysis using the largest dataset from the 11-year monitoring of the Jasper population. We found that both mother-daughter and mother-son dyads also co-occurred in space significantly more than expected given the null model. While father-daughter dyads co-occurred in space significantly less than expected and father-son dyads did not share space at a rate that differed from the null model expectations (Table 4). Thus, the high rate of observed overlap in space use between parent-offspring dyads appears to be driven exclusively by mother-offspring relationships.

4. Discussion

Using multilayer network analysis based on non-invasive genetic sampling, we were able to examine the spatial co-occurrence and familial relationships between individual caribou within a single framework. We applied this analysis to 14 caribou populations across western Canada and examined how familial spatial overlap varied between populations experiencing different population sizes and trends: providing new insights into the population status. We found that the proportion of mother-offspring dyads per female sampled

Table 2

Summary of multilayer network overlaps from each population studied. The number of dyads in each relationship category which were found to spatially overlap are compared with the number of dyads from that relationship type which shared no spatial overlap. Populations highlighted in grey had insufficient overlap between the pedigree network layer and the spatial network layer for further statistical analysis.

Spatial Overlap: Non-overlap by relationship categories					
Population	Parent-offspring	Sibling	Grandparent-Grandoffspring	Aunt/Uncle-Niece/Nephew	Cousin
Central mountain caribou					
A la Peche	34:43	54:210	3:21	48:198	8:55
Jasper	129:140	154:547	31:158	179:1140	82:669
Redrock Prairie Creek	18:37	28:159	1:13	17:125	3:26
Narraway*	4:6	319:32	0:1	8:17	0:0
Boreal caribou					
Little Smoky*	11:31	18:203	0:9	11:153	2:20
Nipisi*	4:6	52:83	1:2	16:17	2:0
Slave Lake*	5:2	37:29	0:0	19:4	4:0
SK2 Central	25:31	96:291	3:9	29:144	3:13
SK2 West	66:54	220:380	10:21	161:392	35:109
SK2 East*	6:18	71:147	1:3	14:70	1:2
The Bog	6:40	25:169	0:11	6:163	1:25
North Interlake	15:98	49:318	7:63	36:425	19:143
Naosap-Reed	19:75	32:446	3:31	11:352	1:76
Wabowden	15:59	35:316	0:15	28:335	5:91

* Analysis was also attempted after excluding Grandparent-Grandoffspring and Cousin categories.

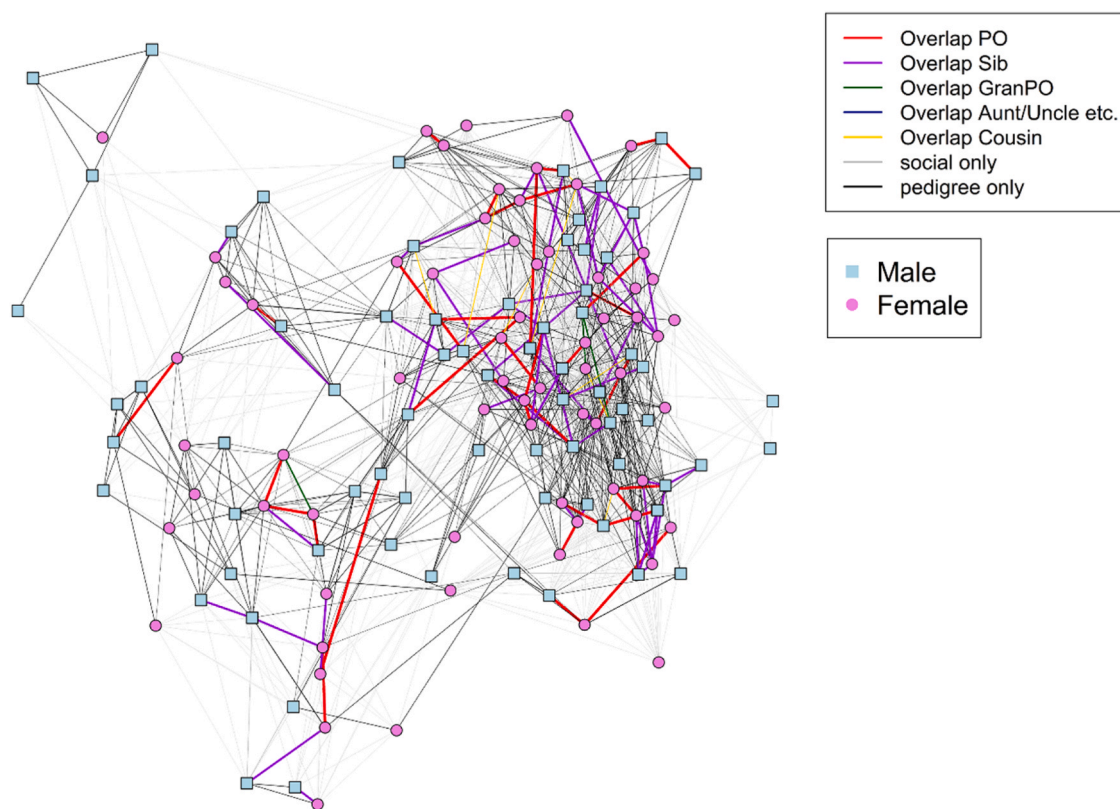


Fig. 3. A 2-dimensional representation of the overlap found between the two layers (spatial co-occurrence and familial) of our multilayer network for the Alberta population A La Peche, in which the coloured edges show the overlap between the two network layers, while edges shown in black, and grey indicate edges found in only the pedigree network and spatial co-occurrence network respectively.

Table 3

Observed model estimates for each of the seven populations with sufficient multilayer overlap data and significance values obtained by compared the observed estimate to the null model estimates obtained from 1500 network-based permutations. Values in bold are significant at a two-tailed $p = 0.05$, thus values are considered significant if < 0.025 or > 0.975 .

Population	Parent-offspring		Sibling		Grandparent-Grandoffspring		Aunt/Uncle-Niece/Nephew		Cousin (Intercept)	
	Observed Estimate	p*	Observed Estimate	p	Observed Estimate	p	Observed Estimate	p	Observed Estimate	p
Central mountain caribou										
A la Peche	2.03	< 0.01	0.59	0.09	0.01	0.49	0.60	0.09	-1.90	0.98
Jasper	2.30	< 0.01	0.81	< 0.01	0.43	0.02	0.16	0.31	-1.95	0.99
Redrock Prairie Creek	1.57	0.04	0.20	0.39	-0.39	0.63	0.04	0.50	-1.72	0.69
Boreal caribou										
SK2Central	1.47	0.09	0.23	0.44	0.58	0.34	-0.32	0.71	-1.59	0.57
SK2 West	1.96	< 0.01	0.65	< 0.01	0.02	0.39	0.14	0.26	-1.19	0.99
North Interlake	0.12	0.39	0.26	0.28	0.02	0.40	-0.55	0.95	-2.26	0.38
Reed	3.18	< 0.01	1.80	0.01	2.25	0.01	0.98	0.07	-4.37	0.99
Wabowden	2.12	< 0.01	0.96	0.02	-12.57	0.86	0.47	0.19	-3.26	0.97

* P-values were obtained as the proportion of times the values obtained from the observed coefficients were more extreme than the coefficients from the permuted data

tended to be higher in populations of larger sizes and stable trends. Additionally, mother-offspring dyads were higher in populations with delivery of annual wolf population reduction programs (Table 5). Small proportions of mother-offspring dyads may suggest low recruitment rate, and low effective population sizes (Hoban et al., 2014). For roughly half of our studied populations (6/14) there was insufficient co-occurrences between close kin observed to be assessed statistically, as the models failed to run when too few close kin relationships occurred. For the remaining 8 populations we observed that most populations had significant spatial overlap between

Table 4

Overlap between the spatial co-occurrence network and the sex-specific parent-offspring for Jasper. Model observed estimates are given along with significance values obtained by comparing the observed estimate to the null model estimates obtained from 1500 network-based permutations. Values in bold are significant at a two-tailed $p = 0.05$, thus values are considered significant if < 0.025 or > 0.975 .

Parent-Offspring Relationship	Spatial Overlap: Non-Overlap	Observed Estimate	p
Mother-Daughter	50:23	2.67	< 0.01
Mother-Son	47:18	2.84	< 0.01
Father-Daughter	18:45	-1.32	0.99
Father-Son	14:54	-0.69	0.85

Table 5

Summary of the results grouped by the number of years populations were sampled and proportion of mother:offspring dyads per female sampled. Wolf reduction indicates if the specified population range is subject to annual wolf-reduction program delivery, and Risk is the status of self-sustainability of the local populations where SS=self-sustaining; NSS = not self-sustaining; NSS/SS = as likely as not self-sustaining (from Table 1). The number of parent-offspring dyads overlapping is presented as a proportion of all parent-offspring dyads along the multilayer network overlap results from Table 2.

Populations	Trend	Wolf reduction program	Risk	Proportion of mother:offspring dyads per female sampled	Overlap Parent-offspring (%)	Significant spatial overlap			
						Parent-offspring	Sibling	Grandparent-Grandoffspring	Cousin
1–3 years of sampling									
A la Pêche	Increasing	Yes	NSS	High	0.44	Yes	No (p=0.09)	No	Yes
SK2 West	Unknown stable		NSS/SS	High	0.55	Yes	Yes	No	Yes
Little Smoky	Stable	Yes	NSS/SS	High	0.26				
Wabowden	Stable		SS	High	0.20	Yes	Yes	No	No
Redrock	Declining or more recently stable	Yes	NSS	High	0.33	Yes	No	No	No
Prairie Creek									
Bog	Unknown stable		NSS/SS	Med	0.13	-	-	-	-
Naosap-Reed	Unknown stable		NSS/SS	Med	0.20	Yes	Yes	Yes	Yes
SK2Central	Unknown declining		NSS/SS	Med	0.47	No (p=0.09)	No	No	No
SK2 East	Unknown declining		NSS/SS	Med	0.25	-	-	-	-
Narraway	Declining - stable	Yes	NSS	Med	0.40	-	-	-	-
Nipisi	Declining	Yes	NSS	Low	0.40	-	-	-	-
Slave Lake	Declining	Yes	NSS	Low	0.71	-	-	-	-
7–11 years sampling									
Jasper	Declining		NSS		0.48	Yes	Yes	Yes	Yes
North Interlake	Declining		NSS/SS		0.13	No	No	No	No

parent-offspring dyads, and in some populations significant levels of spatial co-occurrences were also found in siblings and grandparent-grandoffspring dyads. When accounting for the sex of the parent (using the largest.

available dataset) we were able to show that mother-offspring dyads drive this pattern, thus accounting for the sex of the parent when assessing parent-offspring dyads is necessary. Conversely, in several populations cousins were found to overlap spatially significantly less often than expected in our null models.

We found that in all populations with fewer than 15 observed parent-offspring spatial overlaps, there was insufficient overlap data to conduct statistical network-based analysis, and in three other populations with low overlap no significant relationships were found. Of these populations, many were small (< 100 individuals) and identified as not self-sustaining based on landscape conditions (Table 1, Table 2). For the populations where we sampled a significant portion of the population (76%+) it therefore seems likely that the low levels of observed spatial co-occurrences between parents and offspring reflect a true lack of relationships, and not a lack of collected data. This is further supported by the overall low numbers of parent-offspring pairs recorded, regardless of spatial distribution. These observations are undoubtedly related to high levels of anthropogenic habitat disturbance, which has been shown to be correlated with both calf recruitment and adult female survival in woodland caribou (Environment Canada, 2008, 2011; Johnson et al., 2020; Nagy-Reis et al., 2021). The lack of spatial overlap in parent-offspring reflects unfavourable caribou vital rates and, thereby, poor

population status. For The Bog and SK2East populations where low overlap was also observed, we collected data on a much lower percent of the population as determined from the CMR population estimates, during sampling (~50%) and thus, part of the absence of parent-offspring pairs could be accounted for by lack of data. However, other Manitoba and Saskatchewan populations with similar sampling effort and only slightly larger estimated populations were found to have sufficient data, suggesting that the observed lack of parent-offspring dyads recorded is reflective of a true lack of these relationships. Importantly, we observed no defining patterns between mountain and boreal caribou, despite their different ecology and seasonal range use patterns. This suggests that despite their seasonal migratory behaviour, mountain caribou may maintain similar patterns of spatial overlap with close kin as the boreal ecotype.

High spatial overlap between other close kin (sibling-sibling and grandparent-grandoffspring) was seen in several of the other populations and could be an indicator of a lack of connectivity of habitat preventing animal movement (Carroll and Gaggiotti, 2019; Escoda et al., 2019). In fact, an earlier study of boreal caribou in Saskatchewan has shown that offspring moved shorter distances when parents occupied higher quality habitats which may reflect caribou becoming trapped in remnant habitat patches (McFarlane et al., 2022) and dispersal lacking when populations become fragmented (van Oort et al., 2011). This is particularly notable in the Jasper population, which has declined sharply over the years studied, becoming fractured into three subpopulations over time with limited movement between them (COSEWIC, 2014, also see McFarlane et al., 2018 for more information). Thus, spatial overlap between parent-offspring dyads and other close kin dyads may provide a metric that complements other demographic measures, with high parent-offspring overlap being a marker of calf recruitment while high overlap with second- and third-order relatives provides an indicator of a lack of outward dispersal.

Our sex-specific analysis of the Jasper population highlights that spatial overlap between parent-offspring pairs is driven by mother-offspring pairs, with father-daughter pairs co-occurring in space less often than expected by our statistical model, a potential mechanism to avoid breeding with close kin, and father-son pairs not differing from the null. As calves and non-breeding young may disperse from their mothers at a later age (as in other ungulates; Linklater and Cameron, 2009; Killeen et al., 2014), an age-specific analysis of the spatial overlap between mother's and their offspring would be ideal as it would provide insight into the dispersal patterns of the population as well as enabling the metric of spatial overlap to further inform population status if older individuals are also found to share high overlap with their mothers. However, our data collection method of genetic sampling from fecal pellets did not allow us to examine age effects. It is also important to note that Jasper collections occurred in the late fall when animals were still at higher elevation and thus were present in larger (rutting and post-rutting mixed sex) group sizes than seen in other populations.

Spatial overlap between close-kin relatives is a potential metric to examine recent connectivity within and between populations that can't be examined with other genetic connectivity metrics which respond on slower timescales (Carroll and Gaggiotti, 2019) and adds a novel analysis to those used in spatio-temporal genetic analysis (such as those in Draheim et al., 2018). Here we were able to combine genetic sampling and pedigree reconstruction into a single multi-layer network framework to simultaneously examine individual level spatial co-occurrence and familial relationships for several caribou populations in western Canada. Our multilayer network analysis provides potential metrics with which to gauge population status based on close kin dynamics with a scalable framework that is ideal for any type of interaction-based data. As well we provide some indications of the percentage of population sampled and sampling periods required for network analysis. We found that for small populations very high sampling effort was needed, and for pedigree data longer sampling periods (>1 year data) were able to produce more extensive pedigrees. We also found that for statistical analysis of sex-specific relations (i.e. mother-daughter, mother-son) only the longest sampled dataset (11 years) provided sufficient resolution. In other systems this may not be the case, but in our small, at-risk populations only extending the sampling for a significant period allowed for these sex-based analyses. Overall, our analysis confirms important insight into caribou populations, and provides a method that is transferable to other species where direct observation of spatial and genetic relationships is complicated by large ranges, remote habitats, and polygynous or cryptic breeding systems.

Policies and ethics

All appropriate ethics and other approvals were obtained for the research.

Author contributions

TBJ and MM conceived and designed the study. TBJ and BM conducted the network and pedigree analysis respectively and TBJ wrote the manuscript with help from MM and BM. GP and DH coordinated fieldwork and samples collections. PJW coordinated lab analysis. All authors contributed to subsequent drafts and gave final approval for publication.

Funding

Funding from this research was provided by the Genomic Applications Partnership Program of Genome Canada (Round 17) and Environment and Climate Change Canada. Funding for the field surveys and genetic analyses was provided by the Government of Saskatchewan, Government of Alberta, Manitoba Hydro, Jasper National Park, Environment and Climate Change Canada, and NSERC [Collaborative Research & Development in partnership with Manitoba Hydro, Saskatchewan Power, and Weyerhaeuser].

Declaration of Competing Interest

The corresponding authors, on behalf of all the authors of a submission, is not benefitting from any financial and personal

relationships with other people or organizations that could inappropriately influence (bias) their work. The authors did not use generative AI and AI-assisted technologies in the writing process.

Data Availability

Data/codes can be found on GitHub (https://GitHub/EcoGenomicsCanada/CloseKinNetwork_Analyses).

Acknowledgments

We would like to thank Bridget Redquest and Austin Thompson at Trent University for DNA extraction and analysis, Julia Geue at Trent University for editorial comments and Sonesinh Keobouasone at Environment and Climate Change Canada for data management and mapping. Additionally, we are grateful to staff from the Government of Alberta, Government of Saskatchewan, Jasper National Park, Manitoba Hydro and AMEC Earth and Environmental Ltd. for planning and conducting the extensive field surveys and handling the samples.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.gecco.2023.e02688](https://doi.org/10.1016/j.gecco.2023.e02688).

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