

Social network analysis of mating patterns in American black bears (*Ursus americanus*)

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Abstract

Nonrandom mating can structure populations and has important implications for population-level processes. Investigating how and why mating deviates from random is important for understanding evolutionary processes as well as informing conservation and management. Prior to the implementation of parentage analyses, understanding mating patterns in solitary, elusive species like bears was virtually impossible. Here, we capitalize on a long-term genetic data set collected from black bears (*Ursus americanus*) ($N = 2422$) in the Northern Lower Peninsula (NLP) of Michigan, USA. We identified mated pairs using parentage analysis and applied logistic regression (selection) models that controlled for features of the social network, to quantify the effects of individual characteristics, and spatial and population demographic factors on mating dynamics. Logistic regression models revealed that black bear mating was associated with spatial proximity of mates, male age, the time a pair had coexisted, local population density and relatedness. Mated pairs were more likely to contain older males. On average, bears tended to mate with nearby individuals to whom they were related, which does not support the existence of kin recognition in black bears. Pairwise relatedness was especially high for mated pairs containing young males. Restricted dispersal and high male turnover from intensive harvest mortality of NLP black bears are probably the underlying factors associated with younger male bears mating more often with female relatives. Our findings illustrate how harvest has the potential to disrupt the social structure of game species, which warrants further attention for conservation and management.

Keywords: bear, mating system, parentage, reproduction, social network

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Introduction

The question of who mates with whom, and why, is an important and fundamental focus in evolutionary and conservation biology (Greenwood 1980). Answering this question provides direct insights into population dynamics and responses to evolutionary processes and can provide critical information on inbreeding levels to aid conservation and management. A male and female's

ability and decisions about whether or not to mate are affected by many factors that are both internal and external to the individuals.

Thus, mating patterns are context specific and can vary considerably depending on an animal's phenotype, dispersal patterns, spatial structure and the surrounding social, demographic and environmental conditions (Greenwood 1980; Clobert *et al.* 2009).

Age and body size are two variables that are often associated with reproductive success, especially for males (Mathis 1991; Zedrosser *et al.* 2007; Moore *et al.* 2009). Large or older males usually have a higher

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probability of dispersal and are more successful in resource acquisition and conspecific competition (Gaines & McClenaghan 1980; Greenwood 1980; Clobert *et al.* 2009; Moore *et al.* 2014). However, whether a pair mates is ultimately dependent upon the male and female's encounters with one another, which can be a function of spatial structure and proximity (Nakamichi *et al.* 1997), operational sex ratio (Kvarnemo & Ahnesjö 1996), population age or size structure, and population density (Kokko & Rankin 2006). Thus, extrinsic anthropogenic factors (e.g. harvest, habitat fragmentation) that affect the aforementioned parameters will ultimately affect mating patterns and could lead to undesirable consequences like elevated levels of inbreeding (Allendorf *et al.* 2008).

Social network analysis is a powerful tool for understanding ecological and evolutionary processes in animal populations (Pinter-Wollman *et al.* 2013). Social network analysis has been widely used by social scientists to investigate human social interactions, using behavioural data. The foundation of social network theory is that individuals differ in their interactions and relationships with other individuals and that this network of interactions can in turn affect the individual and the network. In other words, the social environment that an animal experiences can impact decisions made in future social encounters (Kurvers *et al.* 2014). For example, Sih *et al.* (2009) illustrate how a female's choosiness can depend upon the number of males with which she interacts; within a network, females are expected to be choosier if they are better connected within the network and thus have more regular interactions with high-quality males. The strength of sexual selection (i.e. a female's choosiness or a male's competitiveness) is therefore affected by connectedness of the average individual (Sih *et al.* 2009). Social network analysis provides a means to quantify an individual's position in a network, and the network's potential influence on that individual. For example, an individual's connectedness within the network, or *degree*, is a central parameter in social network analyses (Kurvers *et al.* 2014). From a mating standpoint, *degree* equates to the average number of mates per individual, which affects an individual's reproductive success (Clutton-Brock 1989).

In the last two decades, social network analysis has been increasingly applied to animal species (Lusseau 2003; Hamede *et al.* 2009; Godfrey *et al.* 2010; Holekamp *et al.* 2012), especially nonhuman primates (Berman *et al.* 1997; McCowan *et al.* 2008; Kasper & Voelkl 2009), but few studies have focused on solitary or harvested animals. In this context, relationships (i.e. mating events) are identified using genetic techniques, like parentage, rather than behavioural observations. Prior to the implementation of genetic parentage analysis,

studying the mating patterns of solitary animals was difficult. Wide-ranging, solitary animals (like bears) only come into contact with one another for brief periods of time as mated pairs, mother and offspring, or while foraging at concentrated food resources, which makes behavioural observations of mating extremely difficult (Barber & Lindzey 1986; Rogers 1987; Schenk & Kovacs 1995). Parentage analysis, based on samples collected over multiple years and generations, enables researchers to investigate mating patterns even for elusive, nonsocial animals like bears. Long-term genetic monitoring (Schwartz *et al.* 2007) can provide the samples that are necessary to conduct a network analysis of mating for an elusive species.

We used genetic parentage reconstruction to identify mated pairs of American black bears (*Ursus americanus*) from a data set spanning 9 years (approximately three generations in this population, Etter *et al.* 2002). We applied social network analysis with the overall objective of understanding the internal and external factors that affect mating dynamics of the black bear population inhabiting the Northern Lower Peninsula of Michigan, USA. We modelled mated and unmated pairs and tested the following hypotheses:

- 1 Black bear mating is dependent upon spatial proximity and the number of years that a pair of bears was alive together (coexisted) (Clutton-Brock 1989).
- 2 Mated pairs are not more closely related than unmated pairs. Male-biased dispersal is common in mammals (Greenwood 1980; Handley & Perrin 2007) and is present in the NLP black bear population (Moore *et al.* 2014). If male-biased dispersal serves as an inbreeding avoidance mechanism (Pusey 1987) for this population, we would expect mated pairs to be no more or less related (on average) than unmated pairs.
- 3 The likelihood of a pair mating increases with increasing age of the male. Age and body size are closely correlated for many large mammals (Hogg & Forbes 1997; McElligott *et al.* 2002; Zedrosser *et al.* 2007). Kovach & Powell (2003) found that larger body size does not equate to larger home range size for black bears, but it does increase encounter rates with breeding females. Body size and age are often important for male–male competition, as they equate to increased fighting ability, experience, dominance and increased access to females (Coltman *et al.* 2002; Kovach & Powell 2003; Zedrosser *et al.* 2007).
- 4 Black bears exhibit age-assortative mating. That is, males and females of mated pairs are closer in age than unmated pairs. Age-assortative mating can result from males preferentially competing for old (large) high-quality females that may convey high

reproductive success to males through more numerous or higher quality offspring (Webster *et al.* 1995; McGuire *et al.* 2014) or because older animals can preferentially acquire and retain occupancy of high-quality territories and therefore are more likely to come into contact with one another (e.g. Ferrer & Penteriani 2003).

- 5 Mated pairs are more likely to occur in areas of high bear population density. Zedrosser *et al.* (2007) found that reproductive success was higher in areas with higher population density, which is likely attributed to higher mate encounter rates in these areas (Kokko & Rankin 2006).

Materials and methods

Study area

Our study area covered the northern two-thirds of the Lower Peninsula of Michigan (~47 739 km²). Bears in

this area constitute a closed, isolated population, as they are bounded on three sides by the Great Lakes, and to the south by an uninhabitable landscape composed of intensive agricultural and expansive urban areas. The northern Lower Peninsula (NLP) landscape is a forested mix of northern and mixed hardwoods, conifers, forested and nonforested wetlands, and some agriculture (Fig. 1).

Field sampling

A bear hunting season occurs annually during September and October in the NLP, during which approximately 13–29% of the population is harvested annually [D. Etter, unpublished, Michigan Department of Natural Resources (MDNR)]. The NLP black bear population has fluctuated between an estimated 1500–1900 bears over the study period (D. Etter, unpublished, MDNR). All hunted bears must be registered at check stations that are facilitated by the MDNR. At check stations, hunters report the bear's sex and harvest location (to a

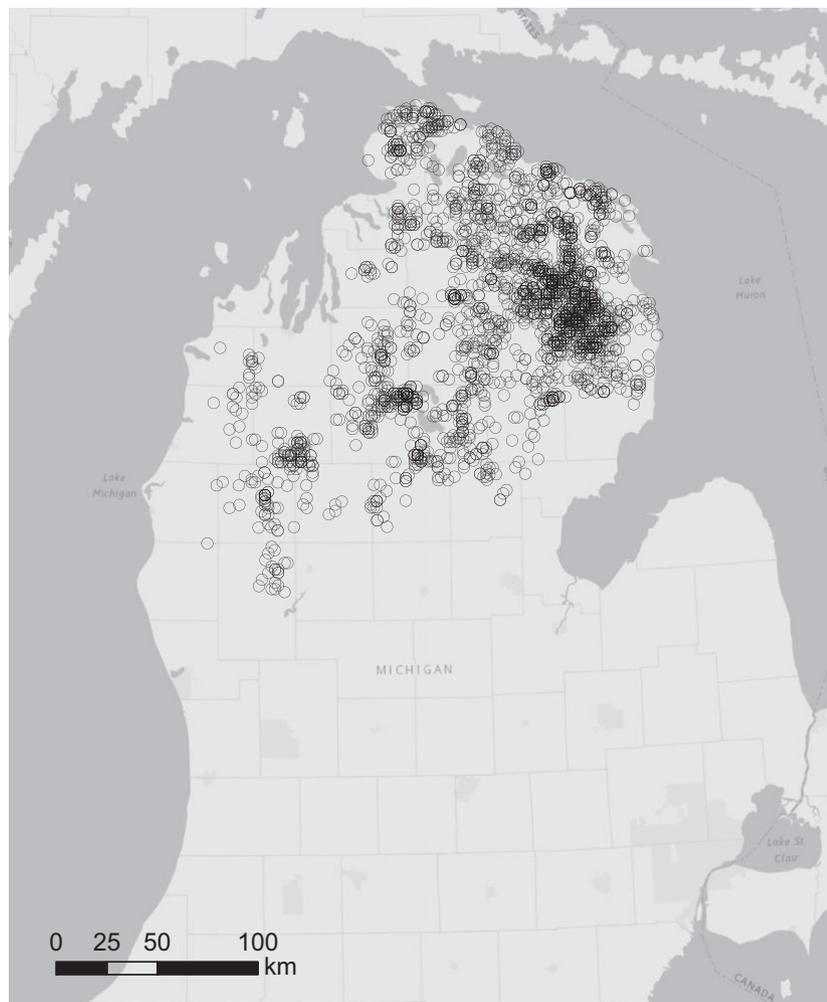


Fig. 1 Harvest locations, within the state of Michigan, for all black bears included in the parentage analysis, including county boundaries.

township, range and section; 2.6 km²), and a premolar tooth is extracted for ageing and DNA extraction. Bears are aged by the MDNR using the cementum annuli method (Willey 1974). In 7 years (2002, 2003 and 2006–2010), MDNR personnel collected data and tooth samples from 2580 bears. Bears were assigned UTM coordinates based on the centroids of their reported harvest sections, from which Euclidean (straight-line) distances were calculated between all pairs. All samples were collected from bears that were legally harvested under bear hunting licenses issued by the MDNR to individual hunters, and tooth samples were provided to us by MDNR cooperators.

Laboratory analysis

We extracted DNA from bear teeth using Qiagen DNEasy Tissue Kits following manufacturer protocols (Qiagen Inc., Valencia, CA, USA). DNA was quantified using a Nanodrop spectrophotometer (Thermo Scientific, Waltham, MA, USA) and diluted to a 20 ng/μL working concentration. Using polymerase chain reaction (PCR), we amplified 12 microsatellite loci including *G10X*, *G10L*, *G10D*, *G10M*, *G10B* (Paetkau *et al.* 1995), *UarMU59*, *UarMU50* (Taberlet *et al.* 1997), *UT29*, *UT35*, *UT38* (Shih *et al.* 2009), *ABB1* and *ABB4* (Wu *et al.* 2010) following the conditions described in Moore *et al.* (2014). We used 6.5% denaturing acrylamide gels for electrophoresis visualized on a LI-COR 4200 Global IR2 System (LI-COR Inc., Lincoln, NE, USA). We included molecular weight standards and individual bears with known genotypes on each gel. Alleles were scored independently by two experienced laboratory personnel using SAGA GENOTYPING software (LI-COR Inc., Lincoln, NE, USA), and 10% of samples were randomly selected and genotyped twice to provide an average genotyping error rate of 2% for all loci. We checked our loci for the presence of null alleles using the program MICROCHECKER (Van Oosterhout *et al.* 2004) and found no significant evidence of null alleles.

Parentage analysis

We conducted parentage analysis using the program FRANZ (Riester *et al.* 2009) to identify the parents of offspring (Moore *et al.* 2014) and thus determine which bears had mated. For each male parent–female parent–offspring triad identified, FRANZ estimates a posterior probability of the identified parent being the true parent (Meagher & Thompson 1986; Riester *et al.* 2009; Moore *et al.* 2014). To assess the accuracy of parentage assignment and to set the threshold posterior probability for accepting true parentage assignments, we first performed a simulation by assigning parentages to

known (simulated) offspring (see Appendix S1, Supporting Information for detailed methodology). In the simulation, FRANZ identified the correct parents for 98.5% of the simulated offspring with posterior probabilities ranging from 0.41 to 1 (mean = 0.96). We then performed a parentage analysis in FRANZ using the real bear genotypes, with sex, birth year and death year as priors. To better reflect the conditions in our data set and population, we changed the following parameter settings from the FRANZ defaults: maximum number of candidate fathers (N_{\max}) = 800, our empirical estimate of genotyping error = 0.02, the increment in steady-state distribution variational distance (δ) = 0.01 and the convergence tolerance (ϵ) = 0.1. We identified mated pairs as parents of offspring with posterior probabilities ≥ 0.8 (based on simulation results, a threshold posterior probability of 0.8 would have caused us to reject 6.3% of true parentages (type I error) while retaining only 0.9% of false parentages (type II error), (Appendix S1, Supporting Information).

Spatial analysis

We used localized harvest density, based on bear harvest locations, as a proxy for local bear population density, as in Moore *et al.* (2014). Briefly, we used the harvest locations for each year from 2002 to 2010 to create annual kernel density function grids (Silverman 1986) in ARCGIS 10.0 and reclassified grids into categories ranging from 1 to 10 (low to high harvest density). We then created a median harvest density grid by calculating the median values over the nine annual harvest density grids. A 1.61-km-diameter circular buffer (representing the approximate length of a square section) was created around each female mate's harvest location, and we extracted harvest density and grid cell values falling within each circular buffer. The value that constituted the majority of grid cells within a buffer was assigned for the female's location. We assumed that mating occurred within the female's home range, so local harvest density was assigned as a female attribute for each pair of bears.

Statistical analysis

For each pair of bears, we estimated pairwise relatedness (r_{XY}), or the probability that two individuals share alleles identical by descent, compared to the average probability of pairs in the population. We first performed a simulation in the program COANCESTRY (Wang 2011) to identify the most appropriate relatedness estimator based on our loci and allele frequencies from the NLP bear population. We simulated 3000 genotypes of individuals with predefined relationships using the

NLP bear loci and allele frequencies and calculated seven different pairwise relatedness estimators (Wang 2011). We ran multiple simulations with different proportions of pairs related at different levels. Regardless of the distribution of relationships in the simulation, the maximum-likelihood (ML) estimator of Milligan (2003) always had the highest correlation with the true relatedness values (correlation coefficients between ML relatedness estimates and true relatedness ranged from 0.79 to 0.99 depending on the distribution of simulated relationships). Therefore, we used Coancestry to estimate the pairwise ML relatedness for all pairs of bears in our data set. The pairwise ML relatedness values range from 0 to 1, with values of 0.5 consistent with full-sibling, and 0.25 consistent with half-sibling relationships.

We defined mated pairs as any male–female pair that shared offspring, and unmated pairs as any male–female pair that was alive at the same time, but did not share offspring. We recognize there is a possibility some of the unmated pairs may have mated, but if we did not sample their offspring, they were not identified as a mated pair. For instance, the likelihood of sampling a bear's offspring may be higher for older parents (who probably had more mating opportunities), while the likelihood of identifying a bear's parents may be lower for offspring harvested in earlier years of sampling (because the parents may have been harvested prior to our sampling). However, as the mortality rate is so high, few NLP bears live to old age, these potential biases may cancel one another out and we expect minimal impact on our results. We defined the following parameters for all individuals (1), mated males only (2) and all pairs (3, 4):

- (1) Birth year = Harvest year – Age at harvest
- (2) Male age at mating = Offspring birth year – Father birth year
- (3) Distance = Euclidean distance between individuals
- (4) Birth difference = Female birth year – male birth year

For each pair, we also determined coexistence time by subtracting the birth year of whichever individual in the pair was born last from the death year of whichever individual died first. For the unmated pairs, we defined the equivalent to male age at mating as the average age of the male during the time it coexisted with the female. For instance, if a male bear was 1 year old when the female was born and 3 years old when the female died, then the male's average age during his coexistence with that female was two. If mated pairs were found to have mated more than once, we only included the first instance of mating in analyses.

Ageing teeth via the cementum annuli method can be prone to error, which occurs most commonly for old bears and 1-year-olds (McLaughlin *et al.* 1990). Identifying the first-year annulus can be difficult due to the degree of separation of the cementum layer from the dentine layer (Willey 1974), which is dependent upon food abundance, condition and denning dates (Rogers 1978). Therefore, any individuals whose age at mating (for mated pairs) or average age during coexistence (for unmated pairs) was determined to be <2 were binned into a category as 2-year-olds. We thus assumed that the identification of any 0- and 1-year-old parents was due to ageing error associated with identifying the first growth annulus.

Social network analysis

We first qualitatively plotted networks of all bears and defined the network ties based on mating derived from inferred parent–offspring relationships. We used non-metric multidimensional scaling to locate bears in two-dimensional space (Frank 1996) and identified bear family trees as components (Frank 1995; Krause *et al.* 2003). A component is a group of nodes (individuals) who have access (through a network path) to each other. Networks were generated using the freely available software program NETDRAW 2.119 (Borgatti 2002).

To statistically analyse mating patterns, we primarily used logistic regression modelling that controlled for degree, which is a type of social network selection model. Selection models are termed as such because an individual's selection of a partner depends upon the attributes of the individuals in that network (Robins *et al.* 2001). Importantly, attributes of the nodes (individuals) influence the formation or strength of ties between individuals, and the network structure itself can influence individual characteristics through the particular network ties of an individual. The independent variables we used were the nodal or dyadic attributes, and the dependent variable is the association matrix (i.e. the pairs of bears; Lazega & van Duijn 1997). One of the primary assumptions of the model is that there are no third party influences (i.e. neighbourhood effects) that affect the dyads, which we felt was a reasonable assumption for black bears.

Pairs of bears were coded depending on whether they mated (1; $n = 172$ pairs) or did not mate (0; $n = 749$ 149 pairs). We used all possible pairs of bears and unmated pairs were generated for any male and female pair that coexisted in time, and whose harvest locations were <150 km from one another (distance threshold based on the maximum distance between two known mated bears). To address uncertainty in the 150 km distance threshold defining unmated pairs, we

reran our top three best-supported models (based on AIC values, below) using unmated pairs that were <100, <50, <30 and <18.24 km apart. These pairwise distances, respectively, encompass 95%, 82%, 64% and 50% of the mated pairs. To examine effects of other variables while controlling for distance, we also generated an unmated pair data set using stratified sampling that mimicked the frequency distribution of pairwise distances from the mated pairs (for 150, 100, 50, 30 and 18.24-km thresholds). We used 1000 bootstrap replicates of the best-supported model to assess significance of model parameters other than distance (Appendix S3, Supporting Information).

Independent variables included pairwise relatedness, male age at the time of mating (or average male age during coexistence with the female, as defined above, for unmated pairs), female age at the time of harvest, pairwise Euclidean distance, male–female birth year difference, number of years the pair coexisted in time, harvest density (measured at the female’s location, as we assumed that mating would have occurred within the female’s home range) and degree. An example model equation takes the following form:

$$\log \left[\frac{p(\text{mate}_{i'})}{1 - p(\text{mate}_{i'})} \right] = \gamma_0 + \gamma_1 \log(\text{distance}_{i'}) + \gamma_2 \text{Relatedness}_{i'} + \gamma_3 \text{Male Age At Mating}_{i'} + \gamma_4 \text{Relatedness}_{i'} * \text{Male Age At Mating}_{i'} + \gamma_5 \text{density}_{i'} + \text{degree}_{i'}$$

In this example, the probability of a male bear i mating with a female bear i' is a function of pair-level variables including the geographic distance between the two bears, γ_1 , the pairwise genetic relatedness between the two bears, γ_2 , the male age at the time of mating, γ_3 , the interaction between genetic relatedness and male age at the time of mating, γ_4 , and female i' ’s attributes (such as harvest density, γ_5). We controlled for the effects of degree (number of mates) using geometrically weighted degree counts (Snijders *et al.* 2006), which assigns geometrically decreasing weights to degree counts so that high degrees have lower weights. We therefore controlled for degree distribution with this single term. We also verified our results by controlling for degree using a random effects model (also known as a p2 model, van Duijn *et al.* 2004). For details of this model, see Appendix S4 (Supporting Information).

We tested all variables for normality, and non-normal variables (e.g. pairwise distance) were log-transformed. We examined descriptive tables and box-and-whisker plots to detect outliers. We removed one mated pair due to a pairwise distance outlier, and removal of this

pair did not affect our overall results. We constructed 70 hypothetical models based on combinations of only independent variables that were not highly correlated. Examination of variance inflation factors (VIFs) of variables in the full model (that included all main variables) showed collinearity among the age-related variables (VIFs > 16). Therefore, no models included both birth difference and coexistence years. We recalculated VIFs for our best-supported model and found no evidence of collinear variables (VIF range = 1.09–1.44). Models also included interaction terms (see Appendix S2, Supporting Information for full list of models). We used Akaike’s information criterion values, delta AIC values and Akaike weights (w_i) to assess model support (Burnham & Anderson 2002). Models with ΔAIC values <2 are considered to be substantially supported within the candidate model set. All statistical analyses were performed in R using the *glm* function or the *lme4* package (for random effects models). R codes are available from the authors upon request.

Results

We identified 172 mated pairs, which were parents of offspring that were assigned with high probability (posterior probability >0.8), from the parentage analysis of 2422 genotyped and georeferenced black bears (1351 males, 1071 females, Fig. 1). Mated pairs consisted of 152 female bears and 141 male bears. The number of mated bears we identified may be somewhat lower than the true number, which probably reflects our conservative threshold for accepting ‘true’ parentages as we wanted to avoid classifying unmated pairs as mated. Average pairwise relatedness of mated pairs was 0.11 ± 0.16 SD, compared to the overall population mean of 0.06 ± 0.087 SD (Table 1). Among mated pairs, 66 pairs (38%) had pairwise relatedness ≥ 0.1 , 25 pairs (14.5%) were ≥ 0.25 , and 12 pairs (7%) were ≥ 0.5 . Among unmated pairs, 182 134 pairs (24.3%) had pairwise relatedness ≥ 0.1 , 33 869 pairs (4.5%) were ≥ 0.25 , and 1992 pairs (0.27%) were ≥ 0.5 . Euclidean distances between mated pairs, measured from harvest locations, averaged 29.82 km (vs. an average of 69.9 km for unmated pairs). The average age for mated males was 4.89 years (Table 1). The average number of mates (degree) was 0.18 for females and 0.14 for males.

Networks revealed variability in the size of bear family groups (components that are linked by shared ties between mated pairs or parents and offspring) (Fig. 2a). Examination of the two largest components (Fig. 2b) shows the unique nature of our data, which has provided the ability to identify multiple mating partners and generations of parents and offspring (‘strings’ of nodes linked by black ties). We identified males with

Table 1 Descriptive data summarizing attributes of all mated pairs ($n = 172$) (identified through parentage analysis) and unmated pairs ($n = 749$ 149) (pairs of male and female bears who were alive at the same time and were within 150 km of one another) of black bears ($n = 2422$) in the Northern Lower Peninsula, Michigan

Parameter	Unmated pairs	Mated pairs
Pairwise relatedness ($r_{x,y}$)	0.06 (0.087)	0.11 (0.16)
Male age (years)	2.52 (1.53)	4.89 (2.99)
Euclidean distance (km)	69.93 (37.34)	29.82 (30.91)
Log Euclidean distance	10.95 (0.73)	9.77 (1.10)
Harvest density (1–10, low to high)	2.94 (1.97)	3.13 (2.09)

Data are presented as means (1 SD).

up to five different mating partners and females with up to three different mating partners (illustrated in Fig. 3). The network of mated pairs (Fig. 3) qualitatively illustrates that the pairs with the highest relatedness (thickest ties) contain the youngest males (≤ 2 years old at the time of mating; solid ties) and that pairs with lower relatedness (thinnest ties) tend to contain older males (≥ 5 years old at the time of mating; dotted ties).

Our best-supported model (AIC = 1967.6, $w_i = 0.94$) included six main effects predicting black bear mating and two interactions, including degree $\beta = -4.65$ (0.22 SE), log distance $\beta = -1.18$ (0.07 SE), male age at mating $\beta = 0.14$ (0.03 SE), relatedness $\beta = 7.92$ (1.03 SE), harvest density $\beta = -0.18$ (0.04 SE), coexistence time $\beta = 0.19$ (0.03 SE), and the male age*relatedness $\beta = -0.72$ (0.21 SE) and coexistence time*relatedness $\beta = -0.61$ (0.22 SE) interactions (Table 2). Our next best-supported model included all predictors in the top model except the coexistence time*relatedness interaction (degree $\beta = -4.64$ (0.22 SE), log distance $\beta = -1.18$ (0.06 SE), male age at mating $\beta = 0.15$ (0.02 SE), relatedness $\beta = 6.81$ (1.0 SE), harvest density $\beta = -0.18$ (0.04 SE), coexistence time $\beta = 0.14$ (0.02 SE), male age*relatedness $\beta = -0.92$ (0.22 SE)). Regression models revealed a number of noteworthy outcomes. First, pairwise relatedness had a positive main effect on the probability of mating (a 0.01 increase in pairwise relatedness equates to an 8% increase in the odds of two bears mating). Second, age of males at the time of mating had a positive effect on the probability of mating (a 1-year increase in male age at mating equates to a 15% increase in the odds of two bears mating). Third, harvest density had a negative effect on the probability of mating (a 1-unit decrease in harvest density equates to a 19% increase in the odds of two bears mating). Fourth, coexistence time had a positive effect on the probability of mating (a 1-year increase in coexistence time equates to a 21% increase in the odds of two bear mating). Lastly,

pairwise Euclidean distance at harvest had a negative effect on the probability of mating (a 1-unit decrease in log Euclidean distance equates to a 225% increase in the odds of two bears mating). Further, we found a significant interaction between pairwise genetic relatedness and male age at mating. Although mated pairs are more likely to contain older males, pairs composed of females and younger males had higher pairwise relatedness ($r_{x,y}$) values than pairs containing females and older males (Fig. 4). For mated pairs, $r_{x,y}$ decreases with increasing age of the male at the time of mating. Also, based on the coexistence time*relatedness interaction, the longer a mated pair has coexisted in time, the less likely the male and female are to be related to one another. We found no evidence for age-assortative mating as similarity in age (birth year difference) was not included in any of the best-supported models. Models were robust to the choice of distance threshold as the best-supported models and significant main effects and interactions remained consistent when unmated pairs were generated from within 100 km, 50 km, 30 km, 18.4 km, using all unmated pairs within those distances and using unmated pairs generated to mimic the frequency distribution of mated pairs (Appendix S3, Supporting Information).

Discussion

We applied parentage and social network analysis to three generations of black bears harvested in Michigan's Northern Lower Peninsula (NLP) and found that black bear mating is associated with spatial proximity of mates, male age, local harvest density, pairwise relatedness and the time a pair had coexisted. Black bear mates in the NLP are more closely related to one another than unmated pairs, and this finding is strongest for mated pairs containing young males. Young males in our system may be mating at or near their natal home ranges, prior to dispersal, which increases the likelihood of consanguineous mating (Moore *et al.* 2014).

Spatial proximity is a strong predictor of mating for many species, particularly those with well-defined spatial structures. Most male bears (with the exception of polar bears; Ramsay & Stirling 1986) have well-defined home ranges that can show considerable overlap with multiple females, depending on resource availability (Garshelis & Pelton 1981; Horner & Powell 1990; Schwartz & Franzmann 1992). Home ranges provide animals with access to resources, including mates, and male black bears are known to roam their large home ranges during breeding season to attempt mating with multiple females (Barber & Lindzey 1986; Schenk & Kovacs 1995; Costello *et al.* 2009). Therefore,

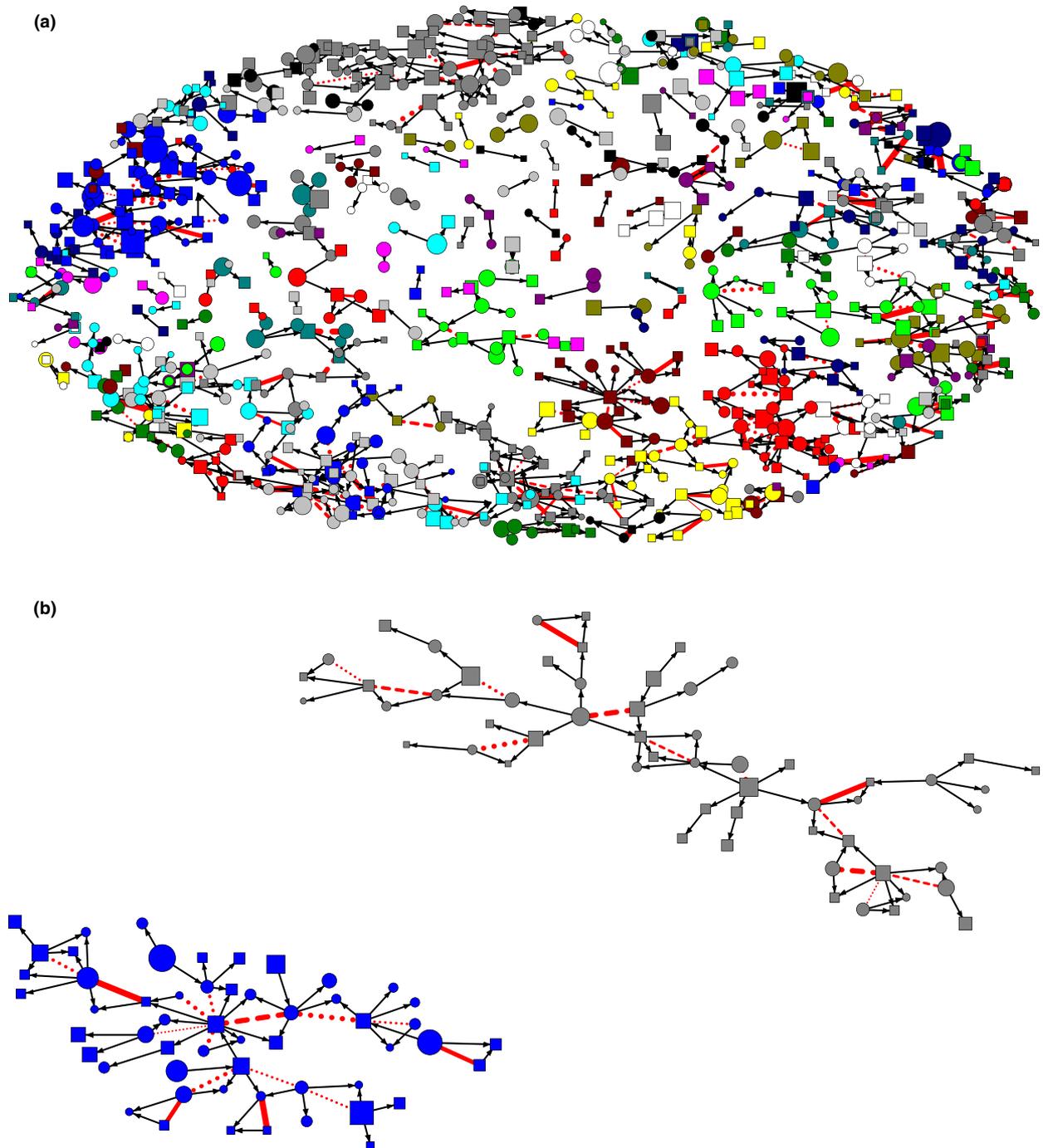


Fig. 2 (a) Social networks of black bears in the Northern Lower Peninsula, Michigan. Nodes are individuals (circles = females, squares = males). The relative size of the symbol indicates the bears' birth year (larger = earlier), and node locations are based on nonmetric multidimensional scaling (not geographic locations of bears). Black lines indicate parent-offspring relationships, and red lines indicate mated pairs. Solid lines are pairs where males were 2 years old or less at the time of mating, dashed are pairs with males 2-5 years old, and dotted are pairs with males 5 years old or older. Colours represent components, whereby all nodes in the component are accessible to one another through a network path. (b) The two largest components in the network, providing an example of the multigenerational nature of our black bear data set.

it is not surprising that bears are more likely to mate with close neighbours (i.e. those whose home ranges overlap their own), as encounter rates with these

bears are likely much higher than with individuals residing further away (Bellemain *et al.* 2006; Costello *et al.* 2009).

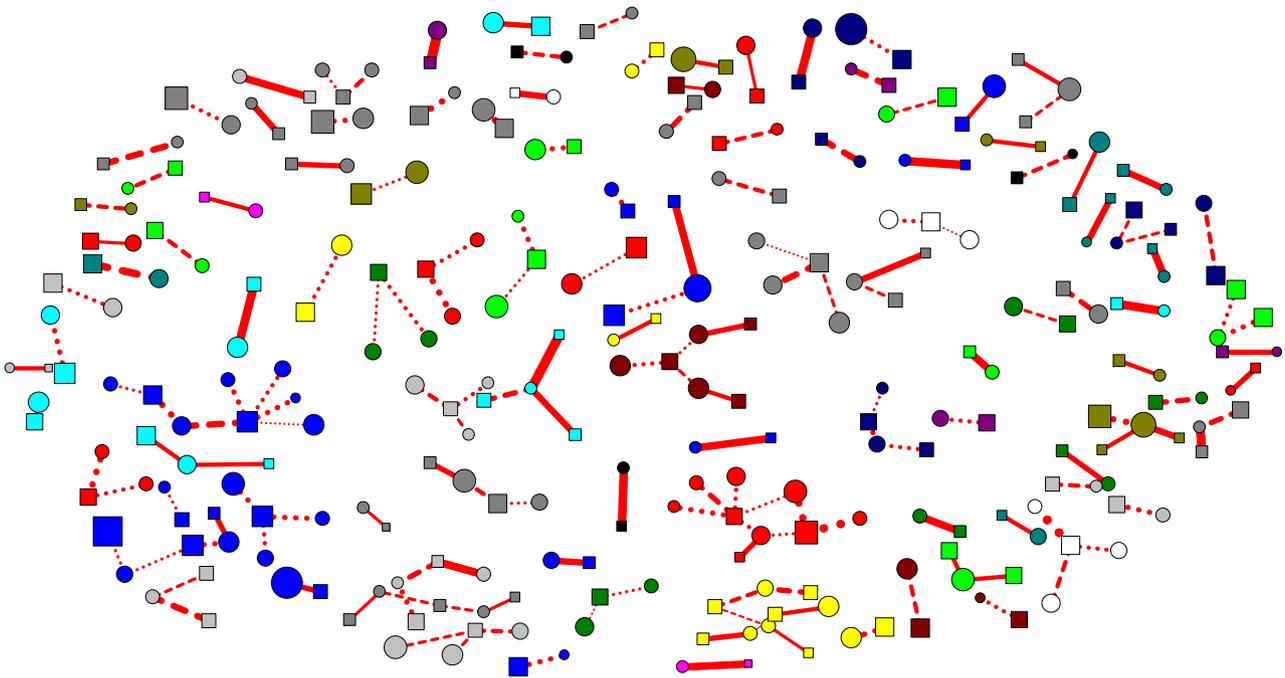


Fig. 3 Network of mated pairs of black bears from the Northern Lower Peninsula, Michigan. Females are represented as circles, males as squares. The relative size of the symbol indicates the bears' birth year (larger = earlier), and locations are based on non-metric multidimensional scaling (not geographic locations of bears). Solid lines are pairs where males were <2 years old, dashed are pairs with males 2–5 years old, and dotted are pairs with males 5 years old or older. Thickness of the line indicates the genetic relatedness of the pair (thicker is more related).

Black bears have a promiscuous mating system that is indicative of strong sexual selection for traits that improve male competitive ability. When male home ranges overlap, dominance hierarchies can form with female access and mating success dominated by large, old males (Barber & Lindzey 1986). Age is typically correlated with body size in bears, and older males can be more adept at locating females in oestrous (Costello *et al.* 2009). In a study of a black bear population in New Mexico, Costello *et al.* (2009) found that intermediate-aged male black bears had the highest reproductive success. These authors presumed that this could result from intermediate-aged male bears showing superior fighting ability due to higher testosterone levels than older males (Garshelis & Hellgren 1994), or that female bears prefer intermediate-aged males because they have demonstrated an ability to survive, yet are not yet suffering from reduced fertility often associated with old age (Brooks & Kemp 2001). Success of intermediate-aged bears could explain the lack of age-assortative mating in NLP black bears.

Our networks (Figs 2 and 3) provided a rare opportunity to characterize multigeneration family groups of black bears in the wild. Due to the long-term nature of our data (spanning 9 years), we were able to identify some larger family groups that contained multiple

generations of parents and offspring and mated individuals (Figs 2b and 3). Many of the large groups contain a few individuals that appear to be largely responsible for genetic cohesion, through ties with multiple different mates and generations of offspring (Fig. 2b). Examination of the family groups also shows that male and female black bears can both have multiple mating partners throughout their lifetimes, but also that the same pair of mates can have multiple offspring together, often produced during different years.

Our finding that mated pairs are more likely to occur at comparatively lower local harvest density was contrary to the expectation that mating would be more likely at higher densities, due to higher mate encounter rates (Zedrosser *et al.* 2007). This finding could be an artefact of the way we generated unmated pairs. More bears occurred in the higher density areas, which meant that more of the unmated pairs were generated from those areas. Therefore, the ratio of mated to unmated pairs may have been much smaller for the high-density areas, which could have influenced the strong negative effect of density we detected. An alternative biological explanation is that reproductive success is more strongly biased towards dominant individuals at high density, and at low density, bears are not reproductively limited by competition, resulting

Table 2 Results of five best-supported social network selection models of black bear mating including AIC values, Δ AIC values and Akaike weights (w_i)

Model parameters*	AIC	Δ AIC	w_i
degree + related + logdistance + density + coexistyears + mestmateage + related*coexistyears + related*mestmateage	1967.6	0.0	0.9355
degree + related + logdistance + density + coexistyears + mestmateage + related*mestmateage	1973.0	5.4	0.0629
degree + related + logdistance + density + coexistyears + mestmateage + related*coexistyears	1980.8	13.2	0.0013
degree + related + logdistance + density + coexistyears + related*coexistyears	1984.9	17.3	0.0002
degree + related + logdistance + density + coexistyears + fage + related*coexistyears	1985.7	18.1	0.0001

See Appendix S2 (Supporting Information) for a full list of candidate model results and parameter estimates.

*related, pairwise maximum-likelihood relatedness; density, harvest location density; logdistance, log of pairwise Euclidean distance; degree, term controlling for effect of multiple mates; coexistyears, number of years a pair coexisted in time; mestmateage, male age at time of mating (or estimated age for unmated pairs; fage, female age at harvest).

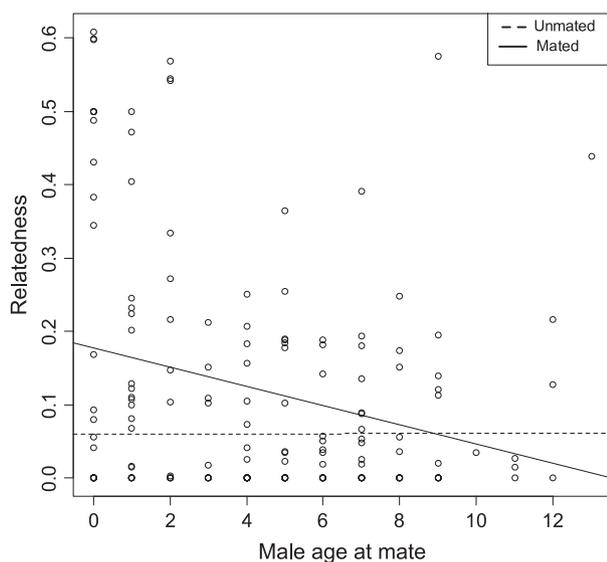


Fig. 4 Relationship between pairwise relatedness and male age at time of mating (for mated pairs, black line, open circles) and average age during coexistence (for unmated pairs, dashed line) of pairs of black bears in the Northern Lower Peninsula, MI, including fitted regression lines.

in a comparatively higher proportion of bears mating at low density vs. high density. Moore *et al.* (2014) found dispersal probability was also negatively related to density of NLP black bears, which could reflect increased competition and suppression of dispersal at higher density (Clobert *et al.* 2009).

One of the strongest predictors of mating in our study system was relatedness. On average, mated pairs were more closely related than unmated pairs. We also found an interaction between relatedness and male age, such that mated pairs containing young males were more likely to be closely related to one another than unmated pairs. This result is contrary to our expectations, particularly because NLP black bears exhibit the

typical mammalian pattern of female philopatry and male-biased dispersal (Moore *et al.* 2014) that usually reduces the risk of inbreeding. However, male dispersal is not absolute in the NLP black bears, with approximately 30% of male bears remaining in or near their natal home ranges (Moore *et al.* 2014). Furthermore, the probability of dispersal increases with age, so younger males are more likely to be closer to their natal ranges (Moore *et al.* 2014). The higher level of inbreeding we documented between females and young males is likely attributable to the above factors, which may also be driven to some extent by the high harvest experienced by this population. In spite of the high harvest, the population has remained at a relatively stable population size (averaging ~1600 bears over the last 10 years), which is indicative of a high growth rate due to overall high resource availability (D. Etter, unpublished, MDNR).

Approximately 13–29% of NLP black bears are harvested annually, and harvest is only restricted for sows with cubs, and cubs themselves. Traits associated with male reproductive and competitive success are also desirable to hunters (Coltman *et al.* 2003; Allendorf *et al.* 2008). As such, larger, older males may be selectively exploited, which can cause a reduction in the average age of individuals, a skewed sex ratio, lower density of large old males and lower age at first reproduction (Czetwertynski *et al.* 2007; Milner *et al.* 2007). High turnover of dominant males may increase reproductive success and decrease dispersal probability for young subordinate males via reduced male–male competition and increased female encounter rates (Zedrosser *et al.* 2007). Previous studies have shown that young males are more reproductively successful at lower density, as they are better able to locate unattended females (Costello *et al.* 2009). In the NLP, the median age of all bears harvested over the last 12 years is two ($N = 1538$ females, 1979 males) (D. Etter, unpublished, MDNR). Female bears with cubs may experience less harvest

pressure than males, and may have a higher probability of living to older age, thus putting males at risk of inbreeding if they do not disperse from their natal home ranges. In the absence of direct kin recognition mechanisms, which black bears are not known to possess (Costello *et al.* 2008), spatial distribution of individuals and social interactions between males and females are important determinants of mating patterns and subsequent levels of inbreeding. Alteration of these social and spatial patterns, by exploitation, can therefore have profound and undesirable effects on natural mating patterns.

In conclusion, we have shown that in the absence of behavioural observations, genetic parentage analysis provides a means to identify relationships and that quantitative social network analysis is a powerful way of characterizing the factors that affect mating patterns in animals (Pinter-Wollman *et al.* 2013). Mating in American black bears is primarily driven by male age and spatial proximity. Our finding that young male bears are more related to their mates than expected warrants further attention, particularly if this result is linked to a disruption of the spatial and social structure due to harvest.

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Data accessibility

Data used in this study, including bear microsatellite genotypes, sexes, estimated ages and harvest locations, are available for download on Dryad (doi:10.5061/dryad.c61q0).

Supporting information

Additional supporting information may be found in the online version of this article.

Appendix S1 Details of parentage simulation.

Appendix S2 Generalized logistic regression models of black bear mated (1) and unmated (0) pairs, including AIC values, change in AIC, relative.

Appendix S3 Results of model reanalysis using varying distance thresholds for generation of unmated pairs of black bears. Distribution of distances.

Appendix S4 Cross nested random effects (p2) model.

Table S1 Parameter estimates for main model terms using cross-nested random effects (p2) model.