



## No inbreeding avoidance in an isolated population of bighorn sheep

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Inbreeding avoidance mechanisms such as mate choice should be selected for when inbreeding produces fitness costs. Several studies, however, suggest that animals tolerate inbreeding despite its costs. We studied inbreeding avoidance in bighorn sheep, *Ovis canadensis*, on Ram Mountain, Alberta, Canada, a population with limited dispersal. We used a randomization procedure to simulate a mean inbreeding coefficient of lambs if mating was random every year, and compared these random mating scenarios with known pairings from 1996 to 2007. We considered three sets of candidate males: all males aged 2 years or more, only males known to reproduce, and all males but accounting for age differences in reproductive success. In all cases, mean cohort inbreeding coefficients did not differ from those expected under random mating. We found no evidence of avoidance of mating between close relatives (half-cousins and higher degrees of relatedness). Mate choice was possibly constrained by the generally high level of relatedness among individuals in the population. Selective pressures for inbreeding avoidance, however, may also be weak for this species because of sex-differential costs of inbreeding, limited opportunities of meeting close relatives and breeding migrations of males. The apparent lack of inbreeding avoidance has important implications for the conservation of small and isolated populations of bighorn sheep, where high levels of inbreeding should be expected.

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Inbreeding occurs when close relatives mate. It can reduce fitness and lead to inbreeding depression, a decline in the value of a trait (Keller & Waller 2002; Snustad & Simmons 2003). When inbreeding depression is substantial, theory predicts the evolution of inbreeding avoidance mechanisms (Pusey & Wolf 1996). Animals may reduce the risk of inbreeding through dispersal, decreasing the chance of meeting relatives where mating occurs (Blouin & Blouin 1988; Pusey & Wolf 1996). Alternatively, philopatric animals may avoid mating with close kin by suppressing offspring reproduction, delaying maturation, or through various kin-recognition mechanisms (Blouin & Blouin 1988). For example, female lions, *Panthera leo*, conceive at an earlier age if their father is evicted from their social group (Hanby & Bygott 1987).

Kin recognition can lead to active mate choice. Although females are generally the choosier sex, there is evidence that males can also be selective (Amundsen & Forsgren 2001; Doutrelant et al. 2008). Many mechanisms of kin recognition have been suggested.

Hansson et al. (2007) proposed that birds avoid mating with conspecifics to which they have been exposed during early development. Mate choice could also be based on smell associated with the major histocompatibility complex (MHC), and therefore, may depend on genotype (Brown & Eklund 1994). This hypothesis has been supported in studies of fish (Landry et al. 2001) and mammals (Piertney & Oliver 2006). Finally, copulations by females with multiple males (Pusey & Wolf 1996) can allow postmating kin recognition, again based on genotype. Chemoreceptors on spermatozoa, eggs, oviduct and ovarian liquid may enable post-copulatory or 'cryptic' choice by females (Eberhard 1996).

Several recent studies failed to detect inbreeding avoidance in natural populations (van Noordwijk et al. 1985; Keller & Arcese 1998; Hansson et al. 2007; Holand et al. 2007; Jamieson et al. 2009; Szulkin et al. 2009). Most of these studies were on birds, except for that of Holand et al. (2007) on reindeer, *Rangifer tarandus*. Inbreeding avoidance, however, has been reported in numerous other studies (reviewed in Pusey & Wolf 1996) on a wide variety of species including ants (Keller & Passera 1993), birds (Blomqvist et al. 2002; but see Griffith & Montgomerie 2003; Eimes et al. 2005) and mammals (Pusey 1990).

Inbreeding avoidance should be selected if its cost is lower than that of inbreeding (Waser et al. 1986). Possible costs of inbreeding avoidance include the loss of breeding opportunities, or higher risk

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of mortality while searching for an unrelated mate (Kokko & Ots 2006). Smith (1979) suggested that inbreeding depression would have to be substantial for inbreeding avoidance to be selected. Recently, Kokko & Ots (2006) tried to estimate inbreeding costs with a model examining changes in the opportunity to select between a related and an unrelated mate, the mate encounter rate and the number of mating opportunities. They estimated that inbreeding avoidance should evolve only if the cost of inbreeding was substantial, and they predicted that inbreeding tolerance should be frequent (Kokko & Ots 2006).

Inbreeding tolerance is expected to be higher in polygynous species than in monogamous species (Waser et al. 1986), based on the argument that mating with kin increases the parent's inclusive fitness (Bengtsson 1978). A female that mates with her brother may help a relative to spread genes that they share, provided that inbreeding has a weak effect or no negative effect on fitness. If a female mates with a close relative without reducing mating opportunities for the male, the female will have a direct benefit from this mating through her  $n$  offspring, and an indirect benefit by increasing the mating success of her male relative ( $m$ ). The female's total inclusive fitness will be  $(1 + r)n$  while it would have been only  $n$  for an unrelated mating (Fisher 1941). In this case there is an advantage for both the female and the male of mating with relatives. In monogamous species, however, mating with relatives does not increase the proportion of genes transmitted to progeny, because the male cannot mate with other females.

We took advantage of a detailed pedigree to investigate inbreeding avoidance in an isolated population of bighorn sheep, *Ovis canadensis*. Previous research on this population revealed a substantial negative effect of inbreeding on the survival of female lambs, suggesting a selective pressure for inbreeding avoidance. Inbred female lambs ( $f > 0$ ) had to weigh about 60% more than non-inbred ones ( $f = 0$ ) to have a similar probability of overwinter survival (Rioux-Paquette 2010). No inbreeding depression for overwinter survival was detected for male lambs, whose survival was much lower than that of female lambs.

The study population experiences almost no immigration and most breeders are philopatric. However, because bighorn sheep are highly polygynous (Coltman et al. 2002), they could be tolerant to inbreeding. We used a randomization method to compare yearly mean inbreeding coefficients with those expected from random matings. We used three sets of candidate males to represent different mating scenarios: all males that were present during the rut, only males that reproduced each year, and all males present during the rut but accounting for age differences in reproductive success. We also examined whether individuals avoided mating with close relatives.

## METHODS

### Study Area

We studied bighorn sheep on Ram Mountain, Alberta, a mountainous complex (elevation 1080–2170 m) 30 km east of the Canadian Rockies (52°N, 115°W) with 38 km<sup>2</sup> of alpine and subalpine habitat. The population is isolated and philopatric. Since 1988, only three immigrant males have been known to contribute to reproduction. Bighorn sheep on Ram Mountain have been monitored from late May to late September since 1972. Sheep are captured several times each summer in a corral trap baited with salt. Males are marked with ear tags and females with collars. All research protocols were approved by the Université de Sherbrooke Animal Care Committee, affiliated with the Canadian Council for Animal Care (Certificate MFB2008-3). During 40 years of research and about 10 400 captures of over 1000 individuals, capture

operation led to only three sheep deaths and two broken bones. Since 1975, over 98% of sheep 1 year of age and older have been marked. We know precisely which individuals were present each year as the resighting rate is over 99% for females and 96% for males (Jorgenson et al. 1997). Between 1975 and 1981, the population was maintained at approximately 30 adult females by yearly removal of females (Jorgenson et al. 1997). When removals stopped, the population increased, peaking at 103 adult females in 1992. The population then declined to a minimum of 15 resident adult females in 2007 primarily because of density-dependent recruitment (Festa-Bianchet et al. 1995; Portier et al. 1998) and subsequent high cougar, *Puma concolor*, predation in 1998–2002 (Festa-Bianchet et al. 2006). Despite the cessation of high cougar predation, the population included only 21 locally born adult females in 2009. Introductions of sheep from another population in 2004 and in 2007 have so far had a minor impact on the population genetic structure.

Bighorn sheep have a polygynous mating system (Hogg 1987) with older, heavy males with large horns obtaining most paternities (Coltman et al. 2002). Age and body size are also positively correlated with male dominance status (Pelletier & Festa-Bianchet 2006). Yet, subordinate males sire up to 40% of lambs through alternative mating strategies (Hogg & Forbes 1997). So far, no variable associated with mating success of subordinate males has been identified.

### Pedigree Building and Candidate Males

Maternal links were established by field observations of associations between marked females and lambs. Paternal links were based on genetic data from microsatellites. Sampling for DNA analyses began in 1988. Until 1993, blood samples were taken from all captured individuals. Tissue collection resumed in 1997 when hairs were collected from captured sheep. Since 1998, a small piece of ear tissue has been collected from each sheep using a biopsy punch. Polymerase chain reaction (PCR) amplification was executed at 32 ungulate-derived loci that showed no evidence of linkage disequilibrium (Coltman et al. 2005). Paternities were assigned using CER-VUS version 3.0 (Kalinowski et al. 2007) with a 95% confidence interval. We used COLONY version 2.0 (Wang 2004) to identify paternal half-siblings among unassigned offspring. A provisional dummy identity was given to the shared, unsampled father. Paternity was assigned to 350 of 524 lambs born since 1988. The pedigree included 1017 individuals and extended up to seven generations for some lambs born in 2007 and 2008. We calculated the inbreeding coefficient  $f$ , which gives the probability that two alleles at a given locus are identical by descent (Crow & Kimura 1970), using Pedigree Viewer version 5.5 (<http://www-personal.une.edu.au/~bkinghor/pedigree.htm>). We did not calculate relatedness between mating partners as it is equivalent to twice the inbreeding coefficient. We assumed that parents were related when their offspring's inbreeding coefficient  $f$  was different from 0. To assess the expected yearly level of inbreeding in the population if sheep mated at random, we used the pedigree to estimate the inbreeding coefficient value for dummy offspring that would have resulted from potential matings between each male and each female. We analysed these new pedigrees with Pedigree Viewer and calculated the inbreeding coefficient for each of these matings. This manipulation generated an estimated inbreeding coefficient for each possible male–female combination each year in the study population.

A major obstacle to an assessment of inbreeding avoidance in nature is identifying which males are possible mates. The study population is highly isolated, so we are confident that males alive in late September were present during the rut 2 months later. However, we do not know whether some males from the nearby

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