



# Does harvest affect genetic diversity in grey wolves?

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## Abstract

Harvest can affect vital rates such as reproduction and survival, but also genetic measures of individual and population health. Grey wolves (*Canis lupus*) live and breed in groups, and effective population size is a small fraction of total abundance. As a result, genetic diversity of wolves may be particularly sensitive to harvest. We evaluated how harvest affected genetic diversity and relatedness in wolves. We hypothesized that harvest would (a) reduce relatedness of individuals within groups in a subpopulation but increase relatedness of individuals between groups due to increased local immigration, (b) increase individual heterozygosity and average allelic richness across groups in subpopulations and (c) add new alleles to a subpopulation and decrease the number of private alleles in subpopulations due to an increase in breeding opportunities for unrelated individuals. We found harvest had no effect on observed heterozygosity of individuals or allelic richness at loci within subpopulations but was associated with a small, biologically insignificant effect on within-group relatedness values in grey wolves. Harvest was, however, positively associated with increased relatedness of individuals between groups and a net gain (+16) of alleles into groups in subpopulations monitored since harvest began, although the number of private alleles in subpopulations overall declined. Harvest likely created opportunities for wolves to immigrate into nearby groups and breed, thereby making groups in subpopulations more related over time. Harvest appears to affect genetic diversity in wolves at the group and population levels, but its effects are less apparent at the individual level given the population sizes we studied.

## KEYWORDS

allelic richness, *Canis lupus*, genetic diversity, grey wolf, harvest, heterozygosity, relatedness

## 1 | INTRODUCTION

Humans have harvested wild animals for millennia. Science and active management play a key role in ensuring such harvest is sustainable in many wildlife populations around the world (Leopold, Kessler, & Cummins, 2018). Much effort has been given to understanding how harvest affects individual vital rates and ultimately population demography (Fryxell, Packer, McCann, Solberg, & Saether, 2010; Jensen, 1996; Mills, 2013; Nichols, Runge,

Johnson, & Williams, 2007). Recently, work has assessed how harvest affects not only vital rates (e.g., survival, reproduction), but also genetic measures of individual and population health (Allendorf, England, Luikart, Ritchie, & Ryman, 2008; Consuegra, DeLeaniz, Serdio, & Verspoor, 2005; Darimont, Fox, Bryan, & Reimchen, 2015; Gaggiotti & Vetter, 1999; Hendry, Gotanda, & Svensson, 2017; Kuparinen & Festa-Bianchet, 2017; Kuparinen, Hutchings, & Waples, 2016; Nabata, Masuda, & Takahashi, 2004; Whitehouse & Harley, 2002).

In some cases, harvest can reduce genetic variation and create spatially based genetic structure in populations (Allendorf et al., 2008; Allendorf, Luikart, & Aitken, 2013). Harvest targeting large individuals can be strongly selective leading to reduced body size and earlier maturation rates in some populations (Jachmann, Berry, & Imae, 1995; Palkovacs, Moritsch, Contolini, & Pelletier, 2018; Swain, Sinclair, & Hanson, 2007; Therkildsen et al., 2019). Small populations can be particularly prone to negative genetic effects associated with harvest due to their small effective population size and inherently reduced genetic diversity overall (Allendorf et al., 2013). Many carnivore populations experience human harvest, yet carnivore populations typically have smaller effective population sizes than species traditionally managed for sustained yield such as ungulates (Frankham, 1995). Thus, carnivore populations may be particularly sensitive to the potentially negative demographic and genetic effects related to harvest (Rick, Moen, Erb, & Starsburg, 2017) including impacts on social structure leading to undesirable hybridization (Bohling & Waits, 2015; Rutledge, White, Row, & Patterson, 2012).

While human harvest is generally found to negatively affect genetic diversity in very small populations of carnivores, it is possible that harvest can increase genetic diversity across multiple scales (Jedrzejewski et al., 2005; Meldrum, 2007). This may be particularly true for carnivores living in groups where breeding opportunities are limited and typically monopolized by a just a few individuals over several breeding seasons. Even low rates of harvest could strongly affect genetic diversity in such populations if breeders are prone to harvest and their death facilitates breeding by unrelated individuals. It is important, however, to consider the scale at which inferences are drawn when studying the effects of harvest on genetic diversity in group-living carnivores. For example, a loss of private alleles within a subpopulation may be concurrent with increases in allelic diversity in the larger meta-population as animals leave subpopulations for breeding opportunities elsewhere (Vonholdt et al., 2010).

Wolves live and breed in groups where reproduction is typically monopolized by two individuals (Mech & Boitani, 2003), thus effective population size is a small fraction of total population abundance. Wolves are adept dispersers, and dispersing wolves generally comprise 10% of a population (Jimenez et al., 2017). Dispersing wolves typically leave their natal territory at 2–3 years old and travel an average distance of roughly 100 km, although sometimes they travel >300 km (Jimenez et al., 2017). The longevity of wolf breeding pairs can vary widely, and the typical breeding pair lasts just over 2 years (Ausband, 2019). Dispersing wolves can establish a new group once a mate is found, but more commonly in established populations, vacant breeding positions in intact groups are filled by dispersing wolves or by wolves within the group assuming a dominant role and subsequently breeding.

Grey wolves in the Rocky Mountains of Idaho, USA, provide an ideal opportunity for assessing the effects of human harvest on genetic diversity over time. Wolves were reintroduced to central Idaho in 1995–1996 from adjacent extant populations in Alberta and British Columbia, Canada (Bangs & Fritts, 1996). Outside of the reintroduction area in central Idaho, wolf recovery in northern Idaho

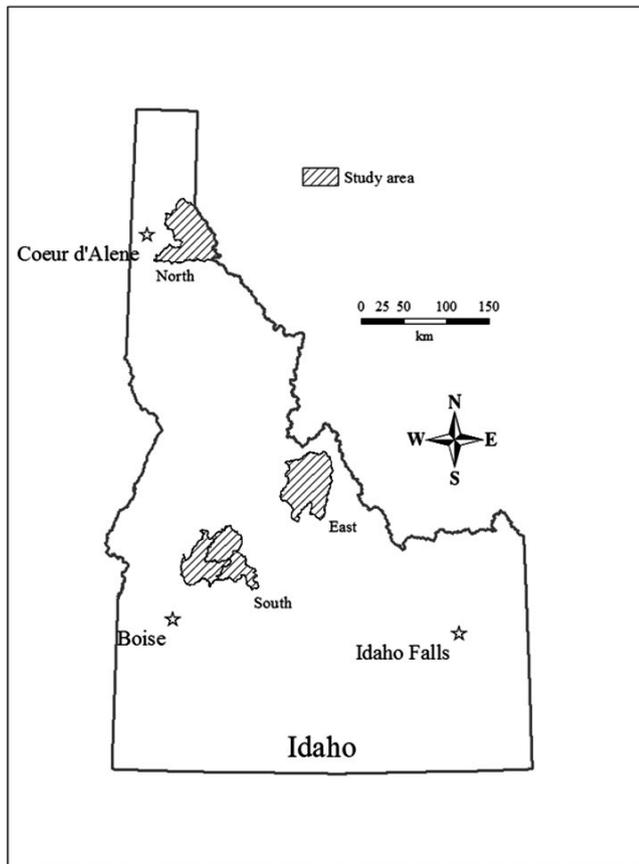
began several years after reintroduction (circa early 2000s) and appears to be largely from natural recolonization by wolves in adjacent British Columbia, Canada populations (Clendenin, Adams, Waits, & Hohenlohe, 2019). Wolves were protected from harvest during the recovery period (1995–2009) yet most wolf mortality was still attributable to humans (e.g., illegal killing, vehicle strikes, harvest in Canada; Murray et al., 2010). Despite sources of anthropogenic mortality, the wolf population throughout Idaho recovered quickly and hunting and trapping began in 2009 (Ausband, 2016). Wolves in several study areas in Idaho have been sampled genetically since before harvest began providing data useful for assessing potential changes in genetic diversity due to changes in population management. Previous assessments of genetic diversity and gene flow in this population of wolves occurred prior to harvest (Vonholdt et al., 2008, 2010) and were strongly influential during litigation about whether to remove Endangered Species Act protections for wolves in the Rocky Mountains (Hebblewhite, Musiani, & Mills, 2010).

We assessed how harvest affects genetic diversity and relatedness in a population of grey wolves monitored over a 10-year period. We hypothesized that harvest would (a) reduce relatedness of individuals within groups in a subpopulation, but increase relatedness of individuals between groups in a subpopulation due to increased local immigration, (b) increase individual heterozygosity and average allelic richness across groups in subpopulations and (c) add new alleles to a subpopulation and decrease the number of private alleles in subpopulations due to an increase in breeding opportunities for unrelated individuals.

## 2 | MATERIALS AND METHODS

### 2.1 | Study areas

We sampled wolves in three study areas (north, east and south) that included 5 Game Management Units (GMUs) within Idaho, USA (GMUs 4, 28, 33–35; Figure 1), and considered each study area a subpopulation. All study areas were mountainous regions of primarily United States Forest Service (USFS) lands. Annual temperatures ranged from –13 to 36°C (Western Regional Climate Center, 2016). Annual precipitation ranged from 30 to 130 cm (Western Regional Climate Center, 2016). Elevation ranged from 646 to 3,219 m. The northern study area (GMU 4; 3,189 km<sup>2</sup>) had a maritime climate dominated by Western red cedar (*Thuja plicata*), Douglas fir (*Pseudotsuga menziesii*), Engelmann spruce (*Picea engelmannii*) and lodgepole pine (*Pinus contorta*). The eastern (GMU 28; 3,388 km<sup>2</sup>) and southern (GMUs 33–35; 3,861 km<sup>2</sup>) study areas had a continental climate and were dominated by ponderosa pine (*P. ponderosa*), lodgepole pine, spruce mixed forests and sagebrush (*Artemisia tridentate*) steppe (Mack et al., 2010). Public harvest of wolves began in Idaho in 2009, temporarily ceased in 2010 and began again in 2011. Wolves were harvested using rifles (65.7%) or traps (32.7%) and although the vulnerability of various sex and age classes is currently unknown, breeder turnover did not increase



**FIGURE 1** Study areas (i.e., subpopulations) in Idaho, USA, where wolves were genetically sampled, 2008–2018

after harvest began in two of the study areas examined here (Ausband, 2016; Ausband, Mitchell, & Waits, 2017). Most harvest occurred during September–March with a peak during the big-game rifle hunting season in October–November (Ausband, 2016). The population of wolves in Idaho is robust (approx. 1,000 wolves) and adjacent to large neighbouring populations of wolves in western United States as well as Canada.

## 2.2 | Field methods

From June to August 2008–2018, we collected wolf scats at occupied or recently occupied wolf pup-rearing sites. When available, we used GPS or radio-telemetry locations of wolves to locate pup-rearing sites. In areas with no radio-collared wolves, we surveyed historic pup-rearing sites and sites predicted by a habitat model to have a high probability ( $\geq 70\%$  suitability) of being a pup-rearing site (Ausband et al., 2010). At each predicted site, technicians attempted to find an activity centre (area where pups congregate) through howl surveys (Harrington & Mech, 1982) or by searching the area around wolf GPS clusters and radio-telemetry locations. Once the activity centre was located, 4–8 technicians collected pup and adult scat for 3–5 hr, radiating out from the activity centre up to 500 m to ensure a sufficient sample of adult scats (Ausband

et al., 2010; Stenglein, Waits, Ausband, Zager, & Mack, 2010). Incidental scats found outside of pup-rearing sites were also collected. We collected 125–200 samples per group per year, which generally detected every individual in the group (Stenglein, Waits, Ausband, Zager, & Mack, 2011). We attempted to resample each group every year.

## 2.3 | Laboratory methods

DNA analyses were conducted at the University of Idaho's Laboratory for Ecological, Evolutionary and Conservation Genetics. We extracted DNA from scat samples using Qiagen kits (Qiagen) and included a negative control to test for contamination. We first screened all samples in a species-identification test (SpID) using a 3-primer mitochondrial DNA (mtDNA) control region polymerase chain reaction (PCR) to remove nontarget species (e.g., coyote; *Canis latrans*) and low-quality samples. We then attempted to genotype all samples identified during the mtDNA test as wolf or dog (*Canis familiaris*) using 18 nuclear DNA microsatellite loci; FH2001, FH2054, FH2088, FH2137, FH2611, FH2670, FH3725, C09.173, Cxx.119, AHT103, AHT109, AHT121, AHTk200, C05.377, C37.172, Cxx.250, FH2004, FH2010 and FH2145 (Breen et al., 2001; Guyon et al., 2003; Holmes, Strange, Binns, Mellersh, & Sampson, 1994; Ostrander, Sprague, & Rine, 1993). We initially amplified all samples twice for genotyping and required successful amplification of alleles at  $\geq 5$  loci for the sample to continue for an additional 1–3 PCRs, whereas we discarded samples that amplified at  $< 5$  loci. For each locus, we required  $\geq 2$  independent PCR amplifications for consensus of a heterozygote and  $\geq 3$  independent PCR amplifications for consensus of a homozygote. We compared all consensus genotypes and all unique genotypes of previously identified individuals using GENALEX (Peakall & Smouse, 2006) to match samples and distinguish unique genotypes. To avoid overestimation and account for undetected genotyping errors, we grouped samples mismatching by allelic dropout at only 1 locus (e.g., 102, 102 vs. 102, 106) as a single individual (Adams & Waits, 2007). We used Reliotype (Miller, Joyce, & Waits, 2002) to test the accuracy of unique genotypes represented by only 1 noninvasive sample (i.e., single detections) by ensuring the genotype attained a 95% accuracy threshold. Further details regarding laboratory methods can be found in Stenglein, Waits, et al. (2010), Stenglein, De Barba, Ausband, and Waits (2010), Stenglein et al. (2011) and Stansbury et al. (2014).

In 2008 and 2009, we analysed all collected samples. After 2010, we analysed 40 adult and 25 pup samples from each group. If a group had more than two individuals detected only once we analysed additional samples when available to obtain 10 more consensus genotypes. For the three subpopulations combined, we compared genotypes from tissue samples of harvested wolves in fall/winter to genotypes of wolves detected in the previous summer by faecal DNA sampling to estimate a pooled subpopulation harvest rate each year.

## 2.4 | Analyses

Wolf pups do not breed in their first year and are highly related within sibling groups which can bias within-group relatedness high, particularly for small groups. Therefore, we did not include pups in our analyses and used genotypes of wolves  $\geq 1$  year old. We used Program GENALEX 6.503 (Peakall & Smouse, 2006) to calculate observed heterozygosity of individuals, private alleles (i.e., allele observed in a single subpopulation and no others) in subpopulations, and document new alleles in each subpopulation every year. We used Program Coancestry (Wang, 2011) to estimate Trio ML genetic relatedness between all possible pairs of individuals within each subpopulation each year. We calculated average allelic richness at each locus for all groups in each subpopulation in each year using Program FSTAT (Goudet, 2003). Each year, we also estimated allelic richness separately just for groups sampled for the duration of the study to control for new alleles that would have emerged in our data simply due to sampling new groups.

We used Program R (R Core Team, 2013), package "lme4," and generalized linear mixed effects models to predict measures of genetic diversity by subpopulation and as a function of harvest rate during the previous year. We included a random effect for individual identification (heterozygosity models), pairwise comparisons of individuals (e.g., Individual(1)\_Individual(2); relatedness models) and loci (allelic richness models) to account for repeated measures. Specifically, we modelled the following as a function of harvest rate and subpopulation a wolf resided in (a) observed heterozygosity of each individual across 18 loci;

$$H_0 \text{ Individual} = \beta_0 + \beta_1 (\text{previous year's harvest rate}) + \beta_2 (\text{subpopulation}) + \text{RE (individual ID)}$$

(b) pairwise relatedness values between every individual within a group in a subpopulation;

$$r \text{ between individuals within group} = \beta_0 + \beta_1 (\text{previous year's harvest rate}) + \beta_2 (\text{subpopulation}) + \text{RE (pairwise individual ID)}$$

(c) pairwise relatedness values between every individual and others in separate groups within a subpopulation,

$$r \text{ between individuals between groups} = \beta_0 + \beta_1 (\text{previous year's harvest rate}) + \beta_2 (\text{subpopulation}) + \text{RE (pairwise individual ID)}$$

and (d) average allelic richness for each locus in a subpopulation.

$$\text{allelic richness per locus} = \beta_0 + \beta_1 (\text{previous year's harvest rate}) + \beta_2 (\text{subpopulation}) + \text{RE (loci)}$$

$p$ -values for each covariate were estimated using asymptotic Wald tests from package "lme4" in Program R. Lastly, we fit intercept-only null models and compared Akaike's information criterion (AIC; Akaike, 1973) values between our predictive and null models for a coarse assessment of model fit (Appendix S1).

## 3 | RESULTS

We genotyped each adult  $>1$  year old in 5–16 wolf groups from 2008 to 2018 resulting in 629 individual heterozygosity estimates, 2,107 comparisons of relatedness between pairs of individuals within groups in subpopulations, 5,898 comparisons of relatedness between pairs of individuals between groups in subpopulations and 468 measures of average allelic richness at each locus in each subpopulation. Harvest averaged 14.7% annually (range = 0.0–27.6).

Harvest was not associated with a significant increase in observed heterozygosity but was associated with an increase in the relatedness of individuals between groups as well as a significant decrease in relatedness of individuals within groups (Table 1). The association between harvest and the relatedness of individuals between groups was the only biologically meaningful effect size, however (Table 1). Our model predicted a 76% increase in relatedness of individuals between groups as harvest increased to 30%. Annual harvest rate did not have an effect on allelic richness ( $\beta = -.001$ ,  $SE = 0.004$ ). While allelic richness did not differ with harvest, groups sampled for the duration of our study lost 8 alleles and gained 24 previously undetected alleles in each subpopulation since harvest began (Table 2). Alleles lost and gained were both low in frequency (0.03 and 0.02, respectively). Before harvest was initiated in the east and south subpopulations, there were 17 and 14 private alleles, respectively ( $\bar{x}$  frequency = 0.09). Nine years after harvest was initiated, the east and south subpopulations contained fewer private alleles, and they were generally found at low frequencies ( $\bar{x}$  frequency = 0.06; 11 and 11 private alleles, respectively). There were significant differences in

genetic diversity by subpopulation with wolves in north Idaho generally having lower heterozygosity, allelic richness, higher relatedness within and between groups than wolves in the east and south subpopulations, as well as 12 private alleles ( $\bar{x}$  frequency = 0.05; Table 2).

**TABLE 1** Coefficients, statistical significance and relative support for models predicting the effect of harvest rate and subpopulation on genetic diversity metrics in grey wolves (*Canis lupus*), Idaho, USA, 2008–2018

Variable	Coefficient (SE)	t-value (p-value)	n	ΔAIC from null model
Question: Does heterozygosity increase with harvest? Random effect (Individual ID): SD = 0.01				
Harvest rate	0.00005 (0.00)	0.52 (.60)	629	-29.9 <sup>a</sup>
East compared to north subpopulation	0.03 (0.01)	2.38 (.02)		
South compared to north subpopulation	0.03 (0.01)	2.21 (.03)		
Question: Does allelic richness decrease with harvest? Random effect (Loci): SD = 1.35				
Harvest rate	-0.001 (0.004)	-0.29 (.77)	468	13.7
East compared to north subpopulation	0.69 (0.12)	5.48 (<.0001)		
South compared to north subpopulation	0.68 (0.12)	5.52 (<.0001)		
Question: Does relatedness of individuals within groups decrease with harvest? Random effect (Pairwise ID): SD = 0.19				
Harvest rate	-0.0003 (0.0001)	-1.92 (.06)	2,107	6.4
East compared to north subpopulation	-0.066 (0.013)	-4.88 (<.0001)		
South compared to north subpopulation	-0.018 (0.014)	-1.31 (.19)		
Question: Does relatedness of individuals between groups increase with harvest? Random effect (Pairwise ID): SD = 0.06				
Harvest rate	0.003 (0.000)	28.0 (<0.0001)	5,898	38.5
East compared to north subpopulation	-0.08 (0.002)	-33.0 (<0.0001)		
South compared to north subpopulation	-0.09 (0.002)	-29.8 (<0.0001)		

Note: The north subpopulation is the reference category.

<sup>a</sup>Indicates null model had more support than fitted model.

**TABLE 2** Changes in private alleles before and after harvest in three subpopulations<sup>a</sup> of grey wolves (*Canis lupus*), Idaho, USA, 2008–2018

Subpopulation	Private alleles (n) before harvest (2008)	Private alleles (n) after harvest (2018)	Alleles lost (n) since 2008	Alleles gained (n) since 2008
East	17	11	8 (freq. = 0.03)	24 (freq. = 0.02)
North	N/A	12	N/A	N/A
South	14	11	8 (freq. = 0.02)	24 (freq. = 0.03)

<sup>a</sup>North subpopulation not sampled before harvest.

## 4 | DISCUSSION

The impact of harvest on genetic diversity and structure is receiving increasing focus in the conservation biology and management literature (Allendorf et al., 2008; Coltman et al., 2003; Hendry et al., 2017; Jedrzejewski et al., 2005; Kuparinen et al., 2016; Kuparinen & Festa-Bianchet, 2017; Pigeon, Festa-Bianchet, Coltman, & Pelletier, 2016; Uusi-Heikkilä et al., 2015). Harvest can affect genetic diversity in complex ways, particularly in populations with limited breeding opportunities and small effective population sizes such as cooperatively

breeding carnivores. Harvest can potentially create breeding vacancies in such populations and thus strongly affect genetic diversity if new migrants join groups. We found harvest had no effect on observed heterozygosity of individuals and was associated with a small, biologically insignificant effect ( $\beta = -.0003$ ) on within-group relatedness values in grey wolves. Harvest was, however, positively associated with increased relatedness of individuals between groups and a net gain (+16) of alleles into groups in subpopulations monitored since harvest began, although the number of private alleles in subpopulations declined.

Assessing the effects of harvest on genetic diversity can be difficult in part because there are multiple measures of diversity (e.g., allelic richness, heterozygosity,  $N_B$ ; Clendenin et al., 2020) that can be affected by the scale at which inferences are drawn. Each measure of diversity can be lost at different rates and have different ecological and evolutionary consequences in a population (Allendorf et al., 2013). For example, a harvested population of an abundant species can show healthy estimates of heterozygosity over time yet still lose rare (and perhaps important) alleles depending on the phenotypic traits targeted through harvest (e.g., black coat colour, large body size). If the loss of rare alleles exceeds the underlying mutation rate, the evolutionary potential of a population can be compromised (Kuparinen & Festa-Bianchet, 2017). It is worthwhile to assess results that seemingly contrast because population structure can influence measures of genetic diversity at different spatial and temporal scales. For example, we found that observed individual heterozygosity was unaffected by harvest. The number of private alleles in subpopulations, however, declined, and relatedness between groups in subpopulations increased. This suggests harvest can affect genetic diversity at the group and population levels while its effects remain less apparent at the individual level given the population sizes we studied. Overall, we estimated multiple measures of genetic diversity in wolves and found our study populations to have relatively high values across a range of genetic metrics. While harvest does appear to increase relatedness between groups, heterozygosity remains high and new alleles continue to arise in our study populations.

In addition to disentangling multiple measures of genetic diversity, inferences about the effect of harvest on diversity are also contingent on population size and the potential for immigration. The population of wolves in Idaho is robust and adjacent to large neighbouring populations of wolves in western United States as well as Canada. Based on increases, albeit very small, in individual heterozygosity and new alleles it appeared breeding vacancies were filled by unrelated wolves. We documented several instances of immigration and subsequent gene flow during our study (Ausband, Mitchell, Stansbury, Stenglein, & Waits, 2017; Stansbury, Ausband, Zager, Mack, & Waits, 2016) and recent work assessing genetic structure also found evidence for gene flow among our subpopulations (Clendenin et al., 2019). Rutledge et al. (2010) found similar results in Algonquin Park; during harvest, groups were more likely to contain unrelated individuals than when harvest was absent. Our results suggest harvest created opportunities for unrelated wolves to enter groups and breed even though previous work in two of our study areas (east and south) through 2015 did not find an increase in breeder turnover after harvest. We note, however, that we included individuals from a third population here (north) as well as several more years of data from all study areas. Additionally, we assessed metrics of genetic diversity, and although previous work (Ausband, 2016) measured breeder replacement, it did not assess the resulting genetic consequences of such turnover.

Efforts were made to capture and release wolves into central Idaho (our east and south subpopulations) that were genetically diverse (Bangs & Fritts, 1996), and central Idaho wolves do indeed

have relatively high estimates of individual heterozygosity (0.76,  $SD = 0.10$ ) 25 years after reintroduction. Wolves naturally recolonizing north Idaho show lower heterozygosity than those in central Idaho, but it is still quite high (0.71,  $SD = 0.09$ ). It is possible that the effects of harvest can increase genetic diversity at a local scale while simultaneously decreasing it at a broad scale if subpopulations become more similar over time due to increased immigration and breeding opportunities. Harvest, at the rates we observed, did not appreciably affect observed heterozygosity or allelic richness of wolves in three subpopulations across a broad area, however. Indeed, the heterozygosity we observed during our study (0.76) is higher than that of the founding wolves originally reintroduced to central Idaho, albeit from different loci (0.70; Vonholdt et al., 2010). Very high harvest rates or harvest that disproportionately targets breeders may affect heterozygosity quite strongly (Allendorf et al., 2013; Larson, Jameson, Etnier, Fleming, & Bentzen, 2002; Whitehouse & Harley, 2002), but we did not observe this during our study.

Although harvest was not associated with a biologically significant reduction in relatedness of individuals within groups as found by others (Rutledge et al., 2010), harvest was associated with a positive increase in relatedness of individuals between groups in subpopulations and a decline in the number of private alleles in subpopulations. These findings suggest that harvest may have created opportunities for wolves to immigrate into nearby groups and breed, thereby making groups in an area more related over time. Although alleles may have been lost simply due to genetic drift, our assertion that harvest played a role in patterns of allelic diversity is supported by our finding of 24 previously undetected alleles now present (albeit at a low frequency) in wolf groups monitored since harvest began. Naturally occurring mutation in microsatellites can create new alleles even in the absence of animals moving between groups, but the mutation rate ( $1.1 \times 10^{-2}$  to  $3.9 \times 10^{-3}$ ; Francisco, Langston, Mellersh, Neal, & Ostrander, 1996; Irion et al., 2003; Lingaas et al., 1997) is likely to be relatively low compared to the rate of influx of new alleles from immigration. Harvest may be selective for certain phenotypic traits, as has been documented in many harvested species (Haldane, 1942; Hengeveld & Festa-Bianchet, 2011; Jachmann et al., 1995), but it has also been suggested that harvest of large mammals is not always a force of strong directional selection (Mysterud, 2011). We currently do not know if harvest is selective for certain phenotypic traits in wolves. We measured allelic richness at neutral loci (i.e., those not under selection), however, thus any potential effect of harvest on alleles that manifest in desirable phenotypes (e.g., large body size, black coat colour) would have gone undetected.

Wolves that recolonized north Idaho largely through natural dispersal from neighbouring British Columbia populations had lower individual heterozygosity, allelic richness, and were more highly related to one another both within and between groups than wolves in the reintroduced populations of central Idaho. We suspect this is because natural recolonization in north Idaho occurred over the last 15 years and was likely initiated by a small number of founding individuals, whereas wolves reintroduced to central Idaho 25 years ago comprised 35 individuals from several different wolf

groups originating in Alberta and British Columbia, Canada (Bangs & Fritts, 1996). We posit that wolves in north Idaho will exhibit similar genetic diversity measures to those in central Idaho within several more generations as wolves disperse into the area from nearby recovered populations in Montana and British Columbia.

We used a natural experiment (before and after harvest) and a 10-year study to add a valuable empirical assessment of the genetic effects of harvest on a social carnivore. Harvest can affect mating system dynamics and thus gene flow, relatedness and diversity in wolves. The harvest rates we observed led to a small increase in diversity yet also increased the relatedness of individuals between groups in subpopulations. Increased genetic diversity is commonly associated with increased fitness, and one could argue that some level of harvest may increase effective population size and individual fitness relative to unharvested populations of similar total abundance and low propensity for interspecific hybridization. Our inferences highlight the importance of evaluating the effects of harvest in a variety of species and study systems and are most applicable to robust populations ( $\geq 1,000$  individuals) of social carnivores with long-distance dispersal capabilities and few landscape barriers to dispersal.

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#### AUTHOR CONTRIBUTIONS

D.E.A. conducted fieldwork, performed analyses and wrote manuscript. L.A. supervised genetic laboratory work and wrote manuscript.

#### DATA AVAILABILITY STATEMENT

Genetic metrics (i.e., heterozygosity, relatedness) for individuals used in this study data can be downloaded at <https://doi.org/10.13140/RG.2.2.33041.66409> (Ausband and Waits, 2020).

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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