

Immigration does not offset harvest mortality in groups of a cooperatively breeding carnivore

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Introduction

Cooperatively breeding species live in social groups in which at least some nonbreeding group members participate in rearing offspring born to the group (Clutton-Brock, 2006). Mortality can affect cooperative breeders in multiple ways, and resulting effects are often more complex than simply subtracting the number of animals that died from total group size. For example, death of a breeder can result in lowered reproductive success of the group and even group dissolution (Brainerd *et al.*, 2008; Loveridge *et al.*, 2010). Harvest by

Abstract

The effects of harvest on cooperatively breeding species are often more complex than simply subtracting the number of animals that died from the group count. Changes in demographic rates, particularly dispersal, could offset some effects of harvest mortality in groups but this is rarely explored with cooperative breeders. We asked whether a cooperatively breeding species known for long-distance dispersal could compensate for the effect of harvest mortality on density by adopting immigrants into the group. We used genetic samples to estimate the minimum density of gray wolves (*Canis lupus*) and proportion of immigrants in groups in the northern US Rocky Mountains after an annual harvest regime was initiated and in the Canadian Rocky Mountains where wolves were managed consistently under an annual harvest regime. We tested whether immigration (1) compensated, (2) partially compensated or (3) did not compensate numerically for harvest mortality in groups and hypothesized immigration would increase with increasing harvest intensity. Density of wolves in groups declined after harvest was initiated whereas immigration into groups was consistently low and did not change with harvest in the US study area. Immigration into groups was similarly low and density even lower in the Canadian study area compared to the US study area. Our results indicate immigration did not compensate for harvest mortality in groups in two separate populations of a cooperatively breeding carnivore. We hypothesize the social structure of wolf groups may limit the potentially compensatory response of immigration in some populations.

humans (i.e. hunting and trapping) can be a particularly disruptive form of mortality in cooperative breeders because it can disproportionately target certain sex and age classes (e.g. breeding adults; Loveridge *et al.*, 2007) or alter reproductive hierarchy (Ausband, Mitchell & Waits, 2017b) in the group. More generally, mortality reduces group size and can lower genetic relatedness resulting in reduced survival and reproduction (Pope, 2000; Courchamp, Rasmussen & Macdonald, 2002). Alternatively, harvest could conceivably increase the reproductive potential of populations. Breeding vacancies can provide opportunities for unrelated individuals to mate,

resulting in multiple breeding individuals and broods within groups (Ausband *et al.*, 2017b, Ausband, 2018). This would lead to long term increases in effective population size of the group and suggests that changes in demographic rates could compensate for harvest mortality at the group-level.

Increased immigration may be a particularly important compensatory mechanism for cooperative breeders that are harvested. The process of dispersal (i.e. leaving one's natal group to join or establish another; Bateman *et al.*, 2013) is a key factor driving the evolution of cooperative breeding (i.e. where groups provide social roles in exchange for access to habitat; Koenig, 2017) and dispersal decisions (e.g. timing, distance) can have marked effects on demography (Bateman *et al.*, 2013). Increased immigration can fully compensate for harvest mortality in some populations of non-cooperatively breeding species (e.g. red fox [*Vulpes vulpes*]; Lieury *et al.*, 2015). Given the social organization of cooperative breeders, immigration could enhance a group's ability to offset harvest mortality by replacing group-members lost to harvest (Larivière, Jolicoeur & Crête, 2000; Grewal *et al.*, 2004). Alternatively, the social structure could preclude dispersers from joining a group, thereby limiting the ability of groups to rebound from the initial population reduction from harvest.

Gray wolves (*Canis lupus*) are a cooperatively breeding carnivore known for long-distance dispersal that also experience sustained harvest throughout most of their current distribution. Adams *et al.* (2008) estimated wolf populations can withstand a mean annual harvest of $\leq 29\%$ and maintain stable densities, suggesting some cooperatively breeding species can compensate for harvest mortality up to a certain threshold; above this annual rate, harvest can lead to population declines in wolves (e.g. Ballard, Whitman & Gardner, 1987; Person & Russell, 2008). There is limited evidence that natural mortality decreases in response to low or intermediate levels of harvest mortality in wolf populations (Adams *et al.*, 2008, but see Murray *et al.*, 2010). Reproductive success is lower in groups when breeder mortality occurs (Brainerd *et al.*, 2008), and groups recruit fewer offspring into the adult population when harvest occurs (Ausband *et al.*, 2015). Thus, changes in natural mortality or reproduction may not be the primary processes compensating for harvest mortality in cooperative breeders like wolves. Conversely, increased immigration into harvested populations of wolves may be an important factor maintaining population density (Ballard *et al.*, 1987; Larivière *et al.*, 2000).

Management of wolves in the Rocky Mountains provided an opportunity to evaluate the relationship between immigration and harvest of a cooperatively breeding species. Wolves in Idaho, USA, were not harvested while listed as endangered under the Endangered Species Act, but have been harvested since delisting in 2009 (U.S. Fish & Wildlife Service, 2014). In contrast, wolves in Alberta, Canada, have been harvested for decades (Robichaud & Boyce, 2010) and at a higher annual rate ($\sim 35\%$ of the population; Webb, Allen & Merrill, 2011) than wolves in Idaho (18% of the population; Idaho Department of Fish & Game [IDFG], unpublished data). Changes in natural mortality and reproduction did not appear to offset harvest mortality in central Idaho (Ausband

et al., 2015; Horne *et al.*, 2019), leaving immigration from adjacent populations as a reasonable explanation for how groups could compensate for harvest mortality in this region. Additionally, immigration is presumably an important process for persistence of heavily harvested populations of wolves, even if natural mortality also declines at higher harvest rates (Adams *et al.*, 2008). Therefore, immigration into groups should be an important compensatory process in south-western Alberta as well.

We tested two sets of hypotheses to evaluate whether immigration into groups offset harvest mortality in populations of cooperatively breeding gray wolves managed with public harvest in the Rocky Mountains. First, we tested alternative hypotheses that immigration would: (1) fully, (2) partially or (3) not compensate numerically for harvest mortality within groups of wolves in central Idaho. We predicted the density of group-dwelling wolves (i.e. wolves associated with packs) would remain constant but the proportion of immigrants in groups would increase if immigration compensated for harvest in groups. If immigration was partially compensatory, we predicted the density of group-dwelling wolves to decrease but the proportion of immigrants in groups to increase. Lastly, if immigration did not compensate for harvest, we predicted the density of group-dwelling wolves to decrease and the proportion of immigrants in groups to decrease or remain constant. Additionally, if compensatory immigration is a common process that offsets harvest mortality in groups, we hypothesized immigration would be higher within groups where the population was harvested at a higher rate. We predicted the proportion of immigrants within groups in south-western Alberta would be greater than those in central Idaho given the differences in rate and history of harvest across these regions of the Rocky Mountains.

To test these hypotheses, we used genetic data collected in central Idaho prior to and after public harvest of wolves were initiated, and in south-western Alberta where long-term harvest occurred. We compared the density of group-dwelling wolves and proportion of immigrants detected in central Idaho before and after harvest began to test our first set of hypotheses. We then compared the density of group-dwelling wolves and proportion of immigrants in central Idaho after harvest was initiated to those in south-western Alberta to test whether immigration was a common compensatory mechanism across multiple harvested populations of wolves.

Materials and methods

Study areas

We conducted annual surveys for wolves in central Idaho, USA and south-western Alberta, Canada. We surveyed Idaho Game Management Unit (GMU) 28 (East study area), and GMUs 33, 34 and 35 (West study area; Fig. 1) from 2007–2016. We surveyed the Alberta study area from 2012 to 2014, which extended from the Canadian-US border to Trans-Canadian Highway 1, following the British Columbia border excluding Banff National Park (Fig. 1).

Public harvest of wolves in Idaho occurred briefly in 2009 and reoccurred annually starting in 2011 (IDFG and Nez Perce Tribe, 2013). Harvest occurred between 30 August and 30 June (IDFG, 2015). Annual harvest averaged 18.0% of group-dwelling wolves in the Idaho study areas ($SE = 2.9$; IDFG, unpublished data). On average, 14 genetically marked wolves from our sample groups were harvested annually (range = 10–20 wolves). Ungulate densities remained generally consistent in central Idaho during our study (Ausband *et al.*, 2015), and no disease outbreaks were reported (IDFG, unpublished data) that could potentially explain changes in wolf density or immigration.

The Ministry of Alberta Environment and Parks managed wolves in south-western Alberta with public harvest since the 1980s (Robichaud & Boyce, 2010). Harvest pressure was high on regional wolf populations during our study, but precise annual harvest rates were unknown. Previous research adjacent to our study area reported the mean annual harvest rate was 0.34 (Webb *et al.*, 2011); the harvest rate in our study area was likely similar (Alberta Environment and Parks, personal communication). Harvest of wolves on public lands occurred between 1 September and 31 May and year-round on private and leased lands (Alberta Government, 2014*a,b*). Bounties for wolves existed in portions of the study area (Cardston County Council, 2012). At minimum, 71 wolves were reported as harvested in the study area during our study period (Bassing *et al.*, 2019). Prey data were not available, but annual ungulate harvest in our study area was relatively consistent from 2012 to 2014, suggesting no substantial changes in ungulate densities during our study (Alberta Government, 2018).

Field methods

We collected noninvasive genetic data in central Idaho and in south-western Alberta following data collection methods described by Ausband *et al.* (2010) and Stenglein *et al.*

(2010). We used maps of predicted rendezvous sites (i.e. pup-rearing sites; Ausband *et al.*, 2010) to locate sites occupied by groups of wolves and sampled individuals at these sites from mid-June through mid-August (Supporting Information Appendix S1). We recorded the presence and location of live wolves and wolf sign and collected genetic samples from scat when detected (Ausband *et al.*, 2010). To avoid sampling coyote scats which are similar in size to wolf pup scats (Weaver & Fritts, 1979), we only sampled canid scats <2.5 cm in diameter when found within active rendezvous sites where wolves were heard or observed, or abundant (≥ 10) adult wolf scats (≥ 2.5 cm in diameter) were present (Joslin, 1967; Stansbury *et al.*, 2014). In Alberta, we surveyed predicted rendezvous sites in the southern half of the study area in 2012 (Fig. 1) and surveyed the full study area in 2013 and 2014.

Laboratory methods

We analyzed genetic samples at the Laboratory for Ecological, Evolutionary and Conservation Genetics at the University of Idaho, Moscow, USA, following DNA extraction and analysis protocols described by Stenglein *et al.* (2010, 2011) and Stansbury *et al.* (2014). We removed nontarget species and low-quality samples with a mitochondrial DNA species-identification test (De Barba *et al.*, 2014). We genotyped remaining samples for individual identification with PCR using 9–10 nuclear DNA microsatellite loci (Stenglein *et al.*, 2011; Stansbury *et al.*, 2014). We sorted unique and matching genotypes with GENALEX (Peakall & Smouse, 2006, 2012) and used RELIOTYPE (Miller, Joyce & Waits, 2002) to test accuracy of single capture genotypes. We estimated probability of identity (PID) genotypes for siblings and required a minimum of 7–8 loci to confirm a match (Waits, Luikart & Taberlet, 2001; Stansbury *et al.*, 2014). We genotyped samples matching at all but 1–2 loci with up to nine additional microsatellite loci for unique identification and to

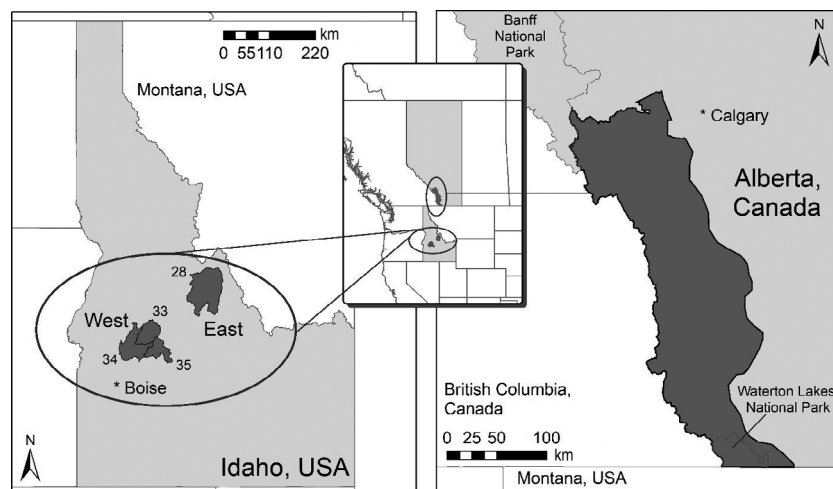


Figure 1 The East (Idaho Game Management Unit 28; 3388 km²) and West (Idaho Game Management Units 33, 34 and 35; 3861 km²) focal study areas in central Idaho, USA, 2007–2016, and the south-western Alberta, Canada study area (12 020 km²), 2012–2014.

verify matches or mismatches (Stenglein *et al.*, 2011; Stansbury *et al.*, 2014). We allowed a 1 locus mismatch when it could be explained by allelic dropout (Adams & Waits, 2007). We evaluated the presence of genotyping errors with Dropout (McKelvey & Schwartz, 2005) and Micro-Checker (van Oosterhout *et al.*, 2004). We analyzed the genotypes using STRUCTURE (Pritchard, Stephens & Donnelly, 2000) and removed samples with highly probable coyote or dog ancestry (Stansbury *et al.*, 2014). We examined allele frequencies and tested for isolation-by-distance (i.e. a positive correlation between geographic and genetic distance; Slatkin, 1993) between study areas and between groups within study areas using 9999 simulated permutations and tested for spatial autocorrelation of pairwise relatedness among individuals in GENALEX.

Group assignment

We used location data of sampled scats to assign individual wolves to putative groups and to inform genetic analyses following methods described by Stansbury *et al.* (2016) and detailed below. Adult wolves in a group periodically return to the rendezvous site to guard and provision pups (Packard, 2003). Thus, we assigned individuals to a common group if they were sampled together at ≥ 1 common location; other wolves we considered lone wolves.

We used ML-RELATE (Kalinowski, Wagner & Taper, 2006) to calculate maximum likelihood estimates of pairwise relatedness among all individuals and assess relatedness within each group. We considered an individual genetically related to other wolves in a putative group if it had pairwise relatedness values at the parent-offspring (PO) or full-sibling (FS) levels ($r = 0.5$) with $\geq 50\%$ of the wolves it was sampled with (Stansbury *et al.*, 2016).

Because wolf groups are typically kin-based units (Mech & Boitani, 2003), we assumed wolves shared similar allele frequencies with group members (Rutledge *et al.*, 2010). We used STRUCTURE to estimate the number of genetic clusters (K), that is, putative groups, across all study areas and estimated the probability (ancestral- or q -value) an individual descended from a given cluster based on similarities in allele frequencies (Pritchard *et al.*, 2000; Stansbury *et al.*, 2016). We used a general admixture model in STRUCTURE assuming correlated allele frequencies within populations but did not provide information about sampling locations; we ran 10 independent model-iterations using 100 000 burn-in and 500 000 MCMC repetitions for $K = 1$ –35. We used additional study area- and year-specific models in STRUCTURE to distinguish whether an individual was born into the group it assigned to or was a breeding adult in the group; we reduced the number of possible clusters to $K = 1$ –15 for these analyses. We then evaluated the most likely number of groups in each study area by comparing STRUCTURE-HARVESTER (Earl & VonHoldt, 2012) estimates to the number of groups reported by agency biologists. Finally, we considered wolves part of the same group if we identified two genetically different groups of individuals, but they were sampled at the same rendezvous site

(Stansbury *et al.*, 2016). This reduced the likelihood of over-estimating group abundance where breeder replacement or multiple breeders occurred in a single group (Stansbury *et al.*, 2016).

We supplemented Stansbury *et al.* (2016)'s established methods to identify immigrants and used GENECLASS2 (Piry *et al.*, 2004) to probabilistically identify first-generation migrants immigrating into each study area (East, West and Alberta) using the L_{home} test statistic (Paetkau *et al.*, 2004). For each GENECLASS2 model, we considered a population to be the number of wolves sampled in that study area that year ($n = 25$ –74 wolves). To be considered a first-generation migrant, we required the probability an individual wolf was sampled within its natal population be ≤ 0.01 (P -value) based on 100 000 Monte Carlo simulations with the Paetkau *et al.* (2004) resampling algorithm. We used the frequencies-based computation criteria (Paetkau *et al.*, 1995) and assumed a default frequency for missing alleles (0.01).

Classification of individuals

We classified individual wolves as a resident, neighbor, short-distance immigrant or long-distance immigrant based on results from genetic analyses and sampling location data. We required agreement between the 4 metrics above to classify wolves as a type of resident or immigrant (Supporting Information Appendix S2) and excluded individuals we could not classify with confidence ($n = 10$). We classified an individual as a resident if it was sampled with its natal group. Neighboring groups tend to be related because groups often form by splitting (i.e. several wolves split from a group to form a neighboring group), budding (i.e. a single wolf leaves to form a neighboring group with another wolf; Mech & Boitani, 2003) or when wolves disperse to nearby areas (Caniglia *et al.*, 2014). We therefore classified an individual as a neighbor if it was related to wolves within the study area it was sampled in, but we could not assign it to a natal group. These individuals were located on the periphery of the study area and excluded from further analyses. We classified an individual as a short-distance immigrant if it met the genetic criteria for a resident or neighbor but was sampled with a group other than its natal group in the same study area, that is, it dispersed within its natal study area. We classified an individual as a long-distance immigrant if it assigned to a study area different from where it was sampled or did not share genetic similarities to wolves from any of the study areas. We classified an individual as a short- or long-distance immigrant the first year it was detected with a group and reclassified it as a resident in subsequent years. Lone wolves are immigrants circulating within a population, seeking opportunities to join or form a group (Mech & Boitani, 2003). We classified short- or long-distance immigrants as lone wolves if they were detected in the interior of a study area but were not associated with a group. We excluded lone wolves from analyses because we were interested in immigration into groups (but see Supporting Information Appendix S3). We excluded data collected during the first year of sampling in each study area to avoid

misclassifying wolves that may have immigrated prior to that year as new immigrants. We used these data to help determine whether individuals detected in the second year of sampling were immigrants of that year.

Minimum density

We estimated the relative minimum density of group-dwelling wolves (wolves/1000 km²; hereafter, minimum density) per study area per year using the number of individuals sampled in each group and year. We considered these estimates a minimum density because they do not account for imperfect detection of individual wolves within a sampled group, nor do they include lone wolves. If Idaho Department of Fish and Game reported a group, we did not sample that year, we excluded the mean area of a group's territory (686 km²; Ausband *et al.*, 2014) when estimating minimum density to reduce sampling bias in our estimates. We only estimated the minimum density of wolves in south-western Alberta for 2014 because sampling effort varied in prior years.

Effects of harvest on density and immigration

We fit nine generalized linear models (Supporting Information Appendix S6) using a Bayesian statistical approach in JAGS (Plummer, 2003) and program R 3.2.5 (R Core Team, 2016) with the R2jags package (Su & Yajima, 2015). We used the minimum density of group-dwelling wolves and the proportion of immigrants within groups (either short- or long-distance) as three separate response variables, and study area and whether harvest occurred as explanatory variables. All explanatory variables were categorical with two factor levels. To test our first set of hypotheses, we fit two separate linear models to data from only central Idaho to test whether the minimum density of group-dwelling wolves changed when harvest occurred (Yes/No) and if density varied by Idaho study area (East/West) respectively. Using the proportion of short- and long-distance immigrants as two separate response variables, we then fit logistic models with data from only central Idaho to test whether the proportion of wolves that were immigrants within groups changed with harvest and study area respectively. We fit a similar set of linear and logistic models to evaluate whether patterns of immigration were similar across multiple populations of wolves managed with public harvest by combining data collected from central Idaho in years when harvest occurred with data from Alberta. We regressed the effect of study area (Idaho/Alberta) on minimum density of group-dwelling wolves and proportion of short- and long-distance immigrants within groups. All models implicitly included a lag effect for harvest because annual public harvest occurred fall through winter of each year but genetic surveys occurred the following summer.

We ran three independent chains of 30 000 Markov chain Monte Carlo (MCMC) iterations, discarding the first 20 000 iterations and retaining all iterations thereafter for each

model. We used the Gelman–Rubin diagnostic and visually inspected the posterior distribution of each parameter to assess model convergence. We considered a covariate supported if the 95% credible interval (CRI) of the posterior probability distribution of the coefficient did not include zero (Kéry, 2010). We further used a probabilistic approach to interpret the strength of each covariate and calculated the probability that the coefficient was above or below 0 based on the number of iterations where the posterior value of the coefficient was greater than or less than 0 respectively. We considered covariates weakly supported if the 95% CRI overlapped zero but the probability that the effect was above or below 0 was ≥ 0.95 , indicating that the covariate was much more likely to not be 0 than 0. We initially included a random effect for group to account for groups surveyed over multiple years but removed this effect due to convergence issues; variance on coefficient estimates are therefore overly optimistic due to pseudo-replication at the group-level.

Results

Field surveys

We surveyed 1833 predicted rendezvous sites in central Idaho (Supporting Information Appendix S4). We located 70 active rendezvous sites and collected 12 192 genetic samples. In south-western Alberta, we surveyed 622 predicted rendezvous sites (Supporting Information Appendix S4), located 12 active rendezvous sites and collected 1270 genetic samples. The majority (85%) of samples were collected in active rendezvous sites across all study areas.

Classification of individuals

Success rates for mtDNA species identification and individual identification in central Idaho ranged 37–95% and 29–80% respectively (Stansbury *et al.*, 2016, this study); they ranged 71–78% and 41–50% in south-western Alberta. The probability of identity for siblings ranged 3.54×10^{-4} – 1.18×10^{-3} in central Idaho (Ausband *et al.*, 2015) and 7.39×10^{-4} – 1.38×10^{-2} in south-western Alberta. Average error rates per locus due to allelic drop-out and false alleles were 4.25% and 0.65% respectively (Stansbury *et al.*, 2016). The microsatellite analysis yielded 4016 consensus genotypes between all study areas. We identified 210 and 212 unique wolves in the east and west study areas in central Idaho respectively. We recaptured 197 unique wolves ≥ 1 time across years in central Idaho. We identified 91 unique wolves in south-western Alberta, 19 of which were recaptured ≥ 1 time across years. On average, we detected 101.78 (SD = 21.08) unique individuals annually.

We classified almost all individuals (98.07%) sampled as either a type of resident or immigrant. We assigned a majority (91.29%) to their natal group; most wolves (89.16%) were residents and sampled with their natal groups ($n = 428$). Across all three study areas, we classified few wolves as potential immigrants ($n = 51$), of which 29 were short-distance and 23 long-distance immigrants (Supporting

Information Appendix S4). We counted 1 wolf as both a short- and long-distance immigrant in central Idaho because it joined a group as a long-distance immigrant and then dispersed locally to a different group. Twenty-two of the short- and 12 of the long-distance immigrants were sampled with other wolves and considered to have successfully joined a group. Of those in central Idaho, most became a breeder within 1 year of joining ($n = 18$); in south-western Alberta most immigrants associated with a group joined as nonbreeding adults ($n = 8$). We excluded lone wolves ($n = 18$) and neighbors ($n = 4$) from further analyses (but see Supporting Information Appendix S3). Several individuals that we classified as immigrants were also radio-collared ($n = 7$; 29% of immigrants) and their dispersals were corroborated by agency biologists independent of our genetic methods.

We found no evidence of isolation-by-distance among groups within each study area (p -value = 0.215) and modest evidence of isolation-by-distance across study areas (p -value = 0.06; Supporting Information Appendix S5). Relatedness among wolves was spatially autocorrelated up to 20 km (Supporting Information Appendix S5).

Effects of harvest on density and immigration

The mean minimum density of group-dwelling wolves in central Idaho was 11.78 wolves/1000 km² (95% CRI = 9.28–14.29) in the east study area and 12.19 wolves/1000 km² (95% CRI = 9.74–14.65) in the west study area, 2008–2016. Estimates of minimum density declined in the years following sustained harvest in both central Idaho study areas, although the change was most pronounced in the west study area (Fig. 2). The mean minimum density of wolves in south-western Alberta in 2014 was 6.17 wolves/1000 km² (95% CRI = 1.71–10.74).

The mean minimum density of group-dwelling wolves in central Idaho was negatively associated with harvest when harvest occurred (Table 1). Study area did not explain the variation in density of group-dwelling wolves as well as the effect of harvest in central Idaho (Table 1). The mean minimum density across both central Idaho study areas declined from 15.19 wolves/1000 km² (95% CRI = 13.12–17.23) when harvest did not occur to 10.40 wolves/1000 km² (95% CRI = 8.96–11.89) when harvest did occur.

We found no association between harvest and the probability that a group included long-distance immigrants in central Idaho but detected a weak difference between central Idaho study areas (Fig. 3; Table 2). The proportion of wolves in a group that were long-distance immigrants was 0.02 (95% CRI = 0.01–0.03) in central Idaho regardless of whether harvest occurred. There was a high probability (0.95, based on 30 000 MCMC iterations) that the effect of study area on the proportion of a group comprising long-distance immigrants was <0 , indicating a weak difference between central Idaho study areas where the proportion was smaller in the west study area compared to the east (Table 2). We found no difference in the proportion of

short-distance immigrants before and after harvest or between study areas in central Idaho (Table 2).

We found weak differences in the minimum density and probability that a group comprised short-distance immigrants when comparing south-western Alberta to central Idaho in years with harvest. The minimum density of wolves was lower in south-western Alberta (6.17 wolves/1000 km² [95% CRI = 1.71–10.74] in 2014) compared to central Idaho (10.39 wolves/1000 km² [95% CRI = 8.57–12.19]), whereas groups in south-western Alberta comprised a larger proportion of short-distance immigrants (0.07 [95% CRI = 0.03–0.13]) than in central Idaho (0.03 [95% CRI = 0.02–0.05]; Table 3). The proportion of long-distance immigrants in a group did not differ between south-western Alberta and central Idaho in years with harvest (0.02 [95% CRI = 0.00–0.05]; Table 3).

Discussion

We found little evidence to support our hypotheses that immigration compensated for harvest mortality within groups of wolves in the Rocky Mountains. The proportion of long-distance immigrants within groups did not change in response to harvest in central Idaho, despite a negative correlation between harvest and the minimum density of group-dwelling wolves, indicating that immigration did not compensate for harvest mortality at the group-level in this population. Group size, recruitment of offspring and the number of occupied territories of wolves also declined in central Idaho after harvest was initiated (IDFG and Nez Perce Tribe, 2014; IDFG and Nez Perce Tribe, 2015; Ausband *et al.*, 2017a), further supporting our findings that immigration did not buffer groups from the effects of harvest. We also found that the proportion of long-distance immigrants within groups were similarly low in south-western Alberta and central Idaho. This suggests that differences in density, harvest rate and history of harvest management between these regions did not influence immigration into groups. Although it does not support our hypothesis that immigration would be higher where harvest was higher, it does suggest that compensatory immigration within groups is not as common as assumed and that the observed lack of response of immigration within groups in central Idaho may be similar in other populations of wolves managed under different harvest regimes.

Although compensatory immigration can offset the numeric consequences of harvest in some solitary species (e.g. Lieury *et al.*, 2015), we hypothesize that the social behavior of cooperative breeders complicates this relationship. Dispersal is driven by group- and population-level influences in cooperative breeders (Solomon & French, 1997; Koenig, Dickinson & Emlen, 2016). Dispersing individuals seek breeding opportunities by joining or establishing a group (Solomon & French, 1997; Fuller, Mech & Cochrane, 2003). Attempting to join a group is risky due to potential aggression from resident members (Schaffner & French, 1997; Cassidy *et al.*, 2015). Where populations are expanding or recolonizing, immigrants can successfully

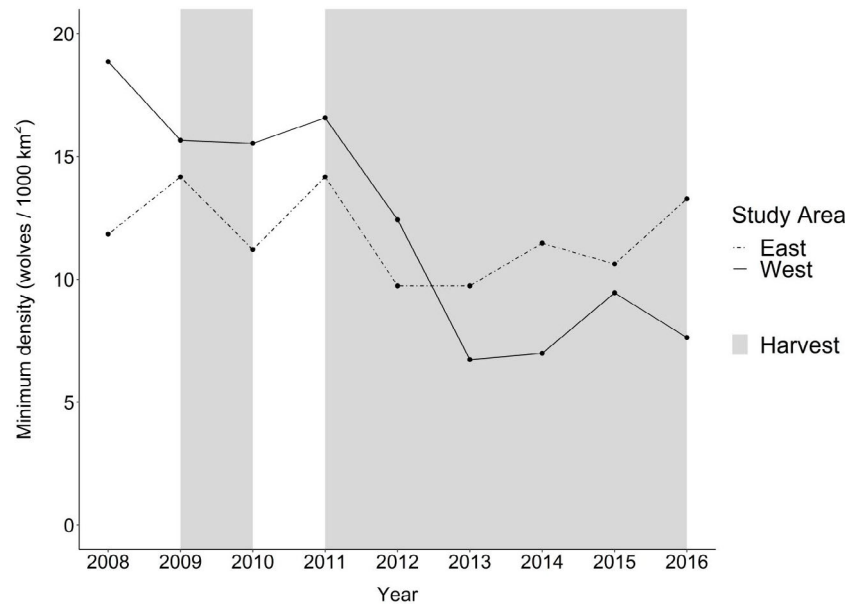


Figure 2 Annual trends in the relative minimum density of group-dwelling wolves for the east and west study areas in central Idaho, 2008–2016. Harvest occurred during autumn–winter of 2009–2010, 2011–2012, 2012–2013, 2013–2014, 2014–2015 and 2015–2016.

Table 1 Models testing for effects of harvest (Yes/No) and study area (East/West) on relative minimum density of wolves (number of wolves/1000 km²) in central Idaho, 2008–2016

Response	Predictor ^a	Estimate (SD)	Lower 95% CRI	Upper 95% CRI	Probability above/below 0 ^b
Density	Intercept	11.78 (1.25)	9.29	14.29	
	Study area	0.41 (1.75)	−3.10	3.88	0.60
Density	Intercept	15.19 (1.03)	13.12	17.23	
	Harvest	−4.79 (1.27)	−7.28	−2.25	0.99

Coefficient estimates and standard deviation (SD), lower and upper limits of the 95% Bayesian credible interval (CRI) and probability that the coefficient estimate was above or below 0 are reported for each predictor variable.

^aNo harvest: indicator variable for harvest covariate; East: indicator variable for study area covariate.

^bThe computed probability that a negative coefficient estimate was <0 and a positive coefficient estimate was >0 respectively.

establish their own groups in unoccupied habitat (Mech & Boitani, 2003); but in established populations where competition is high, for example, the Rocky Mountains, an immigrant's only option to find a breeding opportunity may be to join a group (Mech & Boitani, 2003; VonHoldt *et al.*, 2008). If breeder mortality from harvest were high in these populations, immigration could presumably compensate through breeder replacement. In central Idaho however, Ausband *et al.* (2017b) found the frequency of breeder turnover did not increase after harvest was initiated. Similarly, most breeding pairs appeared to be left intact in a harvested population adjacent to our south-western Alberta study area

(Webb *et al.*, 2011). As a result, there were likely few opportunities for immigrants to compensate for breeder loss in the regions we studied and this may explain why the proportion of long-distance immigrants associated with groups did not change with harvest.

The social structure of cooperatively breeding groups may further prevent immigrants from replacing nonbreeding group members lost to harvest. Groups typically only accept unrelated adults to fill a breeding position (Baker & Dietz, 1996, Caniglia *et al.*, 2014, but see Lehman *et al.*, 1992). We hypothesize groups may be less likely to adopt unrelated adults when the group social structure is intact, that is, when the breeding pair persists (Rutledge *et al.*, 2010; Wiley & Ridley, 2018). In Idaho, only 6 of the 24 immigrants that joined groups did not become breeders within 1 year of joining (Ausband, 2015); one of these immigrants ultimately left to fill a breeding vacancy elsewhere. Despite a 20% decline in mean group size since harvest was initiated in Idaho (IDFG and Nez Perce Tribe, 2014, 2015), immigrants did not frequently replace nonbreeding adults within groups even if additional nonbreeding members would help maintain group size and offspring recruitment (Ausband *et al.*, 2015).

Extrinsic factors (e.g. harvest) can force groups to be flexible in their social organization, leading to variation in social structure between populations (Schradin, 2013). Given we found no evidence that immigration changed in response to harvest in our study areas, yet numerous studies posit immigration compensates for harvest mortality in other populations (e.g. Ballard *et al.*, 1987; Larivière *et al.*, 2000), we speculate that the relationship between immigration and harvest is non-linear. When harvest mortality in groups is low and generally nonselective of breeding status, the social structure of groups remains relatively intact (Wallach *et al.*, 2009; Rutledge *et al.*,

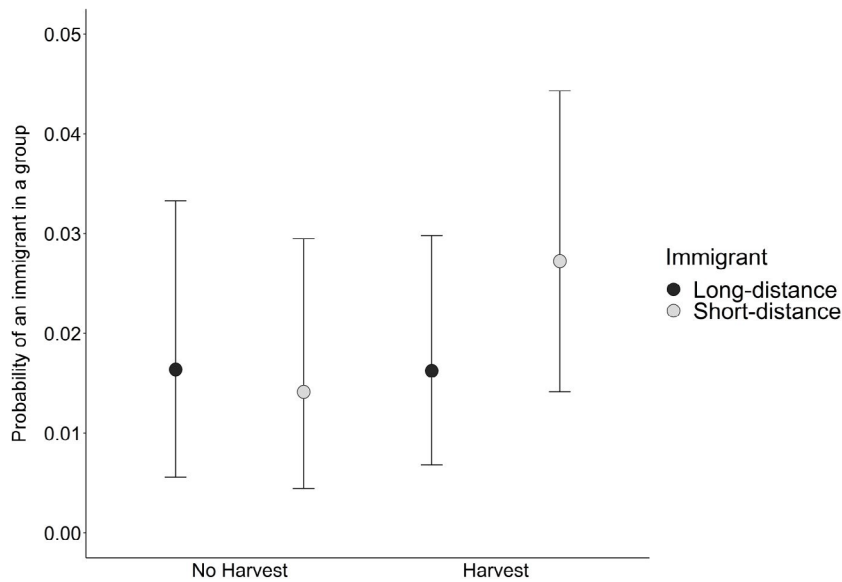


Figure 3 Effect of harvest on the probability a short- or long-distance immigrant was associated with a wolf group in central Idaho, 2008–2016 respectively. Error bars represent 95% Bayesian credible intervals.

Table 2 Models testing for effects of harvest (Yes/No) and study area (East/West) on the proportion of wolves in a group that were long-distance immigrants (LDI) and short-distance immigrants (SDI) in central Idaho, 2008–2016

Response	Predictor ^a	Estimate (SD)	Lower 95% CRI	Upper 95% CRI	Probability above/below 0 ^b
LDI	Intercept	-3.80 (0.32)	-4.55	-3.17	
	Study area	-1.00 (0.63)	-2.30	0.18	0.95
LDI	Intercept	-4.19 (0.46)	-5.18	-3.37	
	Harvest	0.02 (0.58)	-1.10	1.20	0.51
SDI	Intercept	-3.88 (0.37)	-4.65	-3.21	
	Study area	0.04 (0.51)	-0.96	1.05	0.53
SDI	Intercept	-4.35 (0.49)	-5.41	-3.49	
	Harvest	0.74 (0.56)	-0.31	1.90	0.91

Coefficient estimates and standard deviation (SD), the lower and upper limits of the 95% Bayesian credible interval (CRI) and probability that the coefficient estimate was above or below 0 are reported for each predictor variable.

^aNo harvest: indicator variable for harvest covariate; East study area: indicator variable for study area covariate.

^bThe computed probability that a negative coefficient estimate was <0 and a positive coefficient estimate was >0 respectively.

2010). Many group-living carnivores comprise closely related individuals (Clutton-Brock, 2002) that maintain long-term territories and pair bonds (Mech & Boitani, 2003; Ausband, 2019), all of which may limit immigration from offsetting harvest mortality at the group level. Studies hypothesizing compensatory immigration maintained wolf densities reported higher harvest rates than what we observed in our study (e.g.

Table 3 Models testing for differences in mean minimum density of wolves (number of wolves/1000 km²), and the probability a wolf group contained either a long-distance immigrant (LDI) or short-distance immigrant (SDI) between Alberta and central Idaho when harvest occurred, 2010 and 2012–2016

Response ^a	Predictor ^b	Estimate (SD)	Lower 95% CRI	Upper 95% CRI	Probability above/below 0 ^c
Density	Idaho	10.39 (0.92)	8.57	12.19	
	Alberta	-4.22 (2.44)	-9.04	0.67	0.96
LDI	Idaho	-3.98 (0.34)	-4.70	-3.35	
	Alberta	-0.14 (0.75)	-1.72	1.22	0.55
SDI	Idaho	-3.46 (0.27)	-4.03	-2.96	
	Alberta	0.88 (0.46)	-0.04	1.75	0.97

Coefficient estimates and standard deviation (SD), the lower and upper limits of the 95% Bayesian credible interval (CRI) and probability that the coefficient estimate was above or below 0 are reported for each predictor variable.

^aLinear regression was used when density was the response variable; resulting coefficient estimates are unscaled. Logistic regression was used when LDI and SDI were the response variables; resulting coefficient estimates are on the logit scale.

^bThe central Idaho study area was the indicator variable (i.e. intercept).

^cThe computed probability that a negative coefficient estimate was < 0 and a positive coefficient estimate was > 0 respectively.

>40% reported by Ballard *et al.*, 1987, 74% reported by Larièvre *et al.*, 2000). Where harvest mortality is high, immigration may no longer be limited by the social constraints of intact groups and could become an important process maintaining heavily harvested populations of wolves and other cooperatively breeding species (Courchamp, Grenfell & Clutton-Brock, 1999; Adams *et al.*, 2008).

We hypothesize that social structure, density and harvest intensity interact to determine the extent to which immigration compensates for harvest mortality within groups of cooperatively breeding species. Kin-selection predicts group structure is primarily based on relatedness where individuals gain 'indirect' fitness benefits from assisting relatives (Hamilton, 1964a, 1964b; Clutton-Brock, 2002). When harvest is relatively low or a new source of mortality, kin-selection might be most influential in determining group size and whether groups are receptive to immigrants. Conversely, group augmentation theory predicts that individuals have greater survival or reproduction in larger groups and will therefore benefit from accepting new group members even if they are unrelated (Kokko, Johnstone, Clutton-Brock, 2001). If density is low and harvest mortality high, groups may therefore augment with unrelated individuals to maintain group size. Temporal stochasticity in the environment (e.g. annual variation in harvest mortality) might further influence group structure, leading to groups being more receptive of unrelated adoptees during years of higher mortality (Schradin, 2013; Shen *et al.*, 2017).

Although the effect was weak, we found the proportion of a group comprising short-distance immigrants was greater in south-western Alberta than central Idaho. The proportion of short-distance immigrants may respond positively to intermediate levels of harvest because local dispersers may already have knowledge of surrounding territories (via extraterritorial forays; Mech & Boitani, 2003) and can respond quickly to opportunities created by harvest to join nearby groups (Rothman & Mech, 1979; Messier, 1985). Although the dispersal of short-distance immigrants cannot directly maintain population densities (i.e. they are already part of the population), we speculate they might increase the likelihood of group-persistence as harvest rates increase by augmenting group size (Wayne, 1996; Caniglia *et al.*, 2014).

Immigrants unaffiliated with groups (i.e. lone wolves) may also be important in harvested populations of cooperative breeders. Due to their naiveté in novel environments (Peterson, Woolington, Bailey, 1984) and vulnerability to anthropogenic mortality (Person & Russell, 2008), harvest may be biased towards lone individuals instead of resident group members (Adams *et al.*, 2008); continual replacement of lone wolves by new immigrants may compensate for harvest mortality across a population (Fuller *et al.*, 2003). Any response of immigration to harvest may be more apparent at the population-level than the group-level (e.g. Supporting Information Appendix S3).

Our study underscores the complexity of managing cooperatively breeding species with harvest. Recognizing that immigration into groups does not always offset harvest mortality, and that this may vary with harvest rate, population density and social structure of groups, can help managers better predict the effects of public harvest on cooperative breeders. In particular, it is important to consider that immigration may not maintain density within groups and population growth at the group-level may slow with even moderate levels of harvest. If the goal of harvest is to reduce density within groups, this means immigration may not negate management efforts.

Finally, immigration depends on surrounding population densities and harvest rates (McCullough, 1996; Larivière *et al.*, 2000). We assumed areas with lower or no harvest (e.g. parks and wilderness areas, neighboring states) provided dispersers to our study areas; a greater understanding of how neighboring populations are connected under varying harvest regimes could also inform harvest management of cooperatively breeding carnivores.

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References

- Adams, J.R. & Waits, L.P. (2007). An efficient method for screening faecal DNA genotypes and detecting new individuals and hybrids in the red wolf (*Canis rufus*) experimental population area. *Conserv. Genet.* **8**, 123–131.
- Adams, L.G., Stephenson, R.O., Dale, B.W., Ahgook, R.T. & Demma, D.J. (2008). Population dynamics and harvest characteristics of wolves in the Central Brooks Range, Alaska. *Wildlife Monographs* **170**, 1–25.
- Alberta Government (2014a). 2014–2015 Alberta guide to trapping regulations. <https://open.alberta.ca/dataset/8ccfe254-37d4-42fd-a8ec-fc08fa2fe687/resource/55310a0a-eedb-47ce-8361-f48a01623302/download/2085585-2014-2015-alberta-guide-trapping-regulations.pdf>.
- Alberta Government (2014b). 2014 Alberta guide to hunting regulations. <https://open.alberta.ca/dataset/995b1ca1-0e65-4204-b432-98e4d6ccbf46/resource/900b95bc-7163-4896->

- a77b-ccb932a3b4d0/download/2092895-2014-alberta-guide-hunting-regulations.pdf
- Alberta Government (2018). *Hunter harvest*. <https://mywildalberta.ca/hunting/hunters-harvest.aspx>.
- Ausband, D.E. (2015). *Groups and mortality: their effects on cooperative behavior and population growth in a social carnivore*. Dissertation. University of Montana, Missoula, MT.
- Ausband, D.E. (2018). Multiple breeding individuals within groups in a social carnivore. *J. Mammal.* **99**, 836–844.
- Ausband, D.E. (2019). Pair bonds, reproductive success, and rise of alternate mating strategies in a social carnivore. *Behav. Ecol.* **30**, 1618–1623.
- Ausband, D.E., Mitchell, M.S., Doherty, K., Zager, P., Mack, C.M. & Holyan, J. (2010). Surveying predicted rendezvous sites to monitor gray wolf populations. *J. Wildl. Manage.* **74**, 1043–1049.
- Ausband, D.E., Rich, L.N., Glenn, E.M., Mitchell, M.S., Zager, P., Miller, D.A.W., Waits, L.P., Ackerman, B.B. & Mack, C.M. (2014). Monitoring gray wolf populations using multiple survey methods. *J. Wildl. Manage.* **78**, 335–346.
- Ausband, D.E., Stansbury, C.R., Stenglein, J.L., Struthers, J.L. & Waits, L.P. (2015). Recruitment in a social carnivore before and after harvest. *Anim. Conserv.* **18**, 415–423.
- Ausband, D.E., Mitchell, M.S., Stansbury, C.R., Stenglein, J.L. & Waits, L.P. (2017a). Harvest and group effects on pup survival in a cooperative breeder. *Proc. Roy. Soc. B: Biol. Sci.* **284**, 1–8.
- Ausband, D.E., Mitchell, M.S. & Waits, L.P. (2017b). Effects of breeder turnover and harvest on group composition and recruitment in a social carnivore. *J. Anim. Ecol.* **86**, 1094–1101.
- Baker, A.J. & Dietz, J.M. (1996). Immigration in wild groups of golden lion tamarins (*Leontopithecus rosalia*). *Am. J. Primatol.* **38**, 47–56.
- Ballard, W.B., Whitman, J.S. & Gardner, C.L. (1987). Ecology of an exploited wolf population in south-central Alaska. *Wildl. Monogr.* **98**, 1–54.
- Bassing, S.B., Ausband, D.E., Mitchell, M.S., Lukacs, P., Keever, A., Hale, G. & Waits, L. (2019). Stable pack abundance and distribution in a harvested wolf population. *J. Wildl. Manage.* **83**, 577–590.
- Bateman, A.W., Ozgul, A., Nielsen, J.F., Coulson, T. & Clutton-Brock, T.H. (2013). Social structure mediates environmental effects on group size in an obligate cooperative breeder, *Suricata suricatta*. *Ecology* **94**, 587–597.
- Brainerd, S.M., Andr n, H., Bangs, E.E., Bradley, E.H., Fontaine, J.A., Hall, W., Iliopoulos, Y., Jimenez, M.D., Jozwiak, E.A., Liberg, O., Mack, C.M., Meier, T.J., Niemeyer, C.C., Pedersen, H.C., Sand, H., Schultz, R.N., Smith, D.W., Wabakken, P. & Wydeven, A.P. (2008). The effects of breeder loss on wolves. *J. Wildl. Manage.* **72**, 89–98.
- Caniglia, R., Fabbri, E., Galaverni, M., Milanese, P. & Randi, E. (2014). Noninvasive sampling and genetic variability, pack structure, and dynamics in an expanding wolf population. *J. Mammal.* **95**, 41–59.
- Cardston County Council. (2012). *Cardston County council meeting minutes*. Cardston, Alberta, Canada. <http://cardston.civicweb.net/document/12181>
- Cassidy, K.A., MacNulty, D.R., Stahler, D.R., Smith, D.W. & Mech, L.D. (2015). Group composition effects on aggressive interpack interactions of gray wolves in Yellowstone National Park. *Behav. Ecol.* **26**, 1352–1360.
- Clutton-Brock, T. (2002). Breeding together: kin selection and mutualism in cooperative vertebrates. *Science* **296**, 69–72.
- Clutton-Brock, T.H. (2006). Cooperative breeding in mammals. In *Cooperation in primates and humans: mechanisms and evolution*: 173–190. Kappeler, P.M. & van Schaik, C.P. (Eds). Berlin, Germany: Springer.
- Courchamp, F., Grenfell, B. & Clutton-Brock, T. (1999). Population dynamics of obligate cooperators. *Proc. R. Soc. B: Biol. Sci.* **266**, 557–563.
- Courchamp, F., Rasmussen, G.S.A. & Macdonald, D.W. (2002). Small pack size imposes a trade-off between hunting and pup-guarding in the painted hunting dog *Lycaon pictus*. *Behav. Ecol.* **13**, 20–27.
- De Barba, M., Adams, J.R., Goldberg, C.S., Stansbury, C.R., Arias, D., Cisneros, R. & Waits, L.P. (2014). Molecular species identification for multiple carnivores. *Conserv. Genet. Resour.* **6**, 821–824.
- Earl, D. & VonHoldt, B. (2012). STRUCTURE HARVESTER: a website and program for visualizing STRUCTURE output and implementing the Evanno method. *Conserv. Genet. Resour.* **4**, 359–361.
- Fuller, T.K., Mech, L.D. & Cochrane, J.F. (2003). Wolf population dynamics. In *Wolves: behavior, ecology, and conservation*: 161–191. Mech, L.D. & Boitani, L. (Eds). Illinois: The University of Chicago Press.
- Grewal, S.K., Wilson, P.J., Kung, T.K., Shami, K., Theberge, M.T., Theberge, J.B. & White, B.N. (2004). A genetic assessment of the eastern wolf (*Canis lycaon*) in Algonquin Provincial Park. *J. Mammal.* **85**, 625–632.
- Hamilton, W.D. (1964a). The genetical evolution of social behavior. I. *J. Theor. Biol.* **7**, 17–52.
- Hamilton, W.D. (1964b). The genetical evolution of social behavior II. *J. Theor. Biol.* **7**, 17–52.
- Horne, J.S., Ausband, D.E., Hurley, M.A., Struthers, J., Berg, J.E. & Groth, K. (2019). Integrated population model to improve knowledge and management of Idaho wolves. *J. Wildl. Manage.* **83**, 32–42.
- Idaho Department of Fish and Game [IDFG] and Nez Perce Tribe. (2013). *2012 Idaho wolf monitoring progress report*. <https://idfg.idaho.gov/old-web/docs/wolves/reportAnnual12.pdf>
- Idaho Department of Fish and Game [IDFG] and Nez Perce Tribe. (2014). *2013 Idaho wolf monitoring progress report*.

- <https://idfg.idaho.gov/old-web/docs/wolves/reportAnnual13.pdf>
- Idaho Department of Fish and Game [IDFG] and Nez Perce Tribe. (2015). *2014 Idaho wolf monitoring progress report*. Boise, Idaho. <https://idfg.idaho.gov/old-web/docs/wolves/reportAnnual14.pdf>.
- Idaho Department of Fish and Game [IDFG]. (2015). *2015–2016 & 2016–2017 gray wolf hunting and trapping seasons and general rules*. https://idfg.idaho.gov/sites/default/files/seasons-rules-big-game_2015-2016.pdf
- Joslin, P.W.B. (1967). Movements and home sites of timber wolves in Algonquin Park. *Am. Zool.* **7**, 279–288.
- Kalinowski, S.T., Wagner, A.P. & Taper, M.L. (2006). ML-RELATE: a computer program for maximum likelihood estimation of relatedness and relationship. *Mol. Ecol. Notes* **6**, 576–579.
- Kéry, M. (2010). *Introduction to WinBUGS for ecologists: Bayesian approach to regression, ANOVA, mixed models and related analyses*. Burlington: Academic Press.
- Koenig, W.D. (2017). What drives cooperative breeding? *PLoS Biol.* **15**, e2002965.
- Koenig, W.D., Dickinson, J.L. & Emlen, S.T. (2016). Synthesis: cooperative breeding in the twenty-first century. In *Cooperative breeding in vertebrates: studies of ecology, evolution, and behaviour*: 353–374. Koenig, W.D. & Dickinson, J.L. (Eds). Cambridge, United Kingdom: Cambridge University Press.
- Kokko, H., Johnstone, R.A. & Clutton-Brock, T.H. (2001). The evolution of cooperative breeding through group augmentation. *Proc. R. Soc. B: Biol. Sci.* **268**, 187–196.
- Larivière, S., Jolicoeur, H. & Crête, M. (2000). Status and conservation of the gray wolf (*Canis lupus*) in wildlife reserves of Quebec. *Biol. Cons.* **94**, 143–151.
- Lehman, N., Clarkson, P., Mech, L.D., Meier, T.J. & Wayne, R.K. (1992). A study of the genetic relationships within and among wolf packs using DNA fingerprinting and mitochondrial DNA. *Behav. Ecol. Sociobiol.* **30**, 83–94.
- Lieury, N., Ruelle, S., Devillard, S., Albaret, M., Drouyer, F., Baudoux, B. & Millon, A. (2015). Compensatory immigration challenges predator control: An experimental evidence-based approach improves management. *J. Wildl. Manage.* **79**, 425–434.
- Loveridge, A.J., Searle, A.W., Murindagomo, F. & Macdonald, D.W. (2007). The impact of sport-hunting on the population dynamics of an African lion population in a protected area. *Biol. Cons.* **134**, 548–558.
- Loveridge, A.J., Hemson, G., Davidson, Z. & Macdonald, D.W. (2010). African lions on the edge: Reserve boundaries as ‘attractive sinks’. In *Biology and conservation of wild felids*: 284–304. Macdonald, D. W. & Loveridge, A.J. (Eds). New York, NY: Oxford University Press.
- McCullough, D.R. (1996). Spatially structured populations and harvest theory. *J. Wildl. Manage.* **60**, 1–9.
- McKelvey, K.S. & Schwartz, M.K. (2005). DROPOUT: a program to identify problem loci and samples for noninvasive genetic samples in a capture-mark-recapture framework. *Mol. Ecol. Notes* **5**, 716–718.
- Mech, L.D. & Boitani, L. (2003). Wolf social ecology. In *Wolves: behavior, ecology, and conservation*: 1–34. Mech, L.D. & Boitani, L. (Eds). Illinois: The University of Chicago Press.
- Messier, F. (1985). Solitary living and extraterritorial movements of wolves in relation to social status and prey abundance. *Can. J. Zool.* **63**, 239–245.
- Miller, C.R., Joyce, P. & Waits, L.P. (2002). Assessing allelic dropout and genotype reliability using maximum likelihood. *Genetics* **160**, 357–366.
- Murray, D.L., Smith, D.W., Bangs, E.E., Mack, C., Oakleaf, J.K., Fontaine, J., Boyd, D., Jiminez, M., Niemyer, C., Meier, T.J., Stahler, D., Holyan, J. & Asher, V.J. (2010). Death from anthropogenic causes is partially compensatory in recovering wolf populations. *Biol. Cons.* **143**, 2514–2524.
- Packard, J.M. (2003). Wolf behavior: reproductive, social, and intelligent. In *Wolves: behavior, ecology, and conservation*: 35–65. Mech, L.D. & Boitani, L. (Eds). Illinois: The University of Chicago Press.
- Paetkau, D., Calvert, W., Stirling, I. & Strobeck, C. (1995). Microsatellite analysis of population structure in Canadian polar bears. *Mol. Ecol.* **4**, 347–354.
- Paetkau, D., Slade, R., Burden, M. & Estoup, A. (2004). Genetic assignment methods for the direct, real-time estimation of migration rate: a simulation-based exploration of accuracy and power. *Mol. Ecol.* **13**, 55–65.
- Peakall, R. & Smouse, P.E. (2006). GENALEX 6: genetic analysis in Excel. Population genetic software for teaching and research. *Mol. Ecol. Notes* **6**, 288–295.
- Peakall, R. & Smouse, P.E. (2012). GenALEX 6.5: Genetic analysis in Excel. Population genetic software for teaching and research—an update. *Bioinformatics* **28**, 2537–2539.
- Person, D.K. & Russell, A.L. (2008). Correlates of mortality in an exploited wolf population. *J. Wildl. Manage.* **72**, 1540–1549.
- Peterson, R.O., Woolington, J.D. & Bailey, T.N. (1984). Wolves of the Kenai Peninsula, Alaska. *Wildl. Monogr.* **88**, 1–52.
- Piry, S., Alapetite, A., Cornuet, J.M., Paetkau, D., Baudouin, L. & Estoup, A. (2004). GENECLASS2: a software for genetic assignment and first-generation migrant detection. *J. Hered.* **95**, 536–539.
- Plummer, M. (2003). JAGS: a program for analysis of Bayesian graphical models using Gibbs sampling. In *Proceedings of the 3rd International Workshop on Distributed Statistical Computing*: **124**, 1–10. Vienna, Austria.
- Pope, T.R. (2000). Reproductive success increases with degree of kinship in cooperative coalitions of female red howler monkeys (*Alouatta seniculus*). *Behav. Ecol. Sociobiol.* **48**, 253–267.
- Pritchard, J.K., Stephens, M. & Donnelly, P. (2000). Inference of population structure using multilocus genotype data. *Genetics* **155**, 945–959.

- R Core Team. (2016). *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. <https://www.r-project.org/>.
- Robichaud, C.B. & Boyce, M.S. (2010). Spatial and temporal patterns of wolf harvest on registered traplines in Alberta, Canada. *J. Wildl. Manage.* **74**, 635–643.
- Rothman, R.J. & Mech, L.D. (1979). Scent-marking in lone wolves and newly formed pairs. *Anim. Behav.* **27**, 750–760.
- Rutledge, L.Y., Patterson, B.R., Mills, K.J., Loveless, K.M., Murray, D.L. & White, B.N. (2010). Protection from harvesting restores the natural social structure of eastern wolf packs. *Biol. Cons.* **143**, 332–339.
- Schaffner, C.M. & French, J.A. (1997). Group size and aggression: 'recruitment incentives' in a cooperatively breeding primate. *Anim. Behav.* **54**, 171–180.
- Schradin, C. (2013). Intraspecific variation in social organization by genetic variation, developmental plasticity, social flexibility or entirely extrinsic factors. *Philos. Trans. R. Soc. B: Biol. Sci.* **368**, 20120346.
- Shen, S.-F., Emlen, S.T., Koenig, W.D. & Rubenstein, D.R. (2017). The ecology of cooperative breeding behaviour. *Ecol. Lett.* **20**, 708–720.
- Slatkin, M. (1993). Isolation by distance in equilibrium and non-equilibrium populations. *Evolution* **47**, 264–279.
- Solomon, N.G. & French, J.A. (1997). *Cooperative breeding in mammals*. New York, NY: Cambridge University Press.
- Stansbury, C.R., Ausband, D.E., Zager, P., Mack, C.M., Miller, C.R., Pennell, M.W. & Waits, L.P. (2014). A long-term population monitoring approach for a wide-ranging carnivore: noninvasive genetic sampling of gray wolf rendezvous sites in Idaho, USA. *J. Wildl. Manage.* **78**, 1040–1049.
- Stansbury, C.R., Ausband, D.E., Zager, P., Mack, C.M. & Waits, L.P. (2016). Identifying gray wolf packs and dispersers using noninvasive genetic samples. *J. Wildl. Manage.* **80**, 1408–1419.
- Stenglein, J.L., Waits, L.P., Ausband, D.E., Zager, P. & Mack, C.M. (2010). Efficient, noninvasive genetic sampling for monitoring reintroduced wolves. *J. Wildl. Manage.* **74**, 1050–1058.
- Stenglein, J.L., Waits, L.P., Ausband, D.E., Zager, P. & Mack, C.M. (2011). Estimating gray wolf pack size and family relationships using noninvasive genetic sampling at rendezvous sites. *J. Mammal.* **92**, 784–795.
- Su, Y.-S. & Yajima, M. (2015). *R2jags: a package for running JAGS from R*.
- U.S. Fish and Wildlife Service. (2014). *Northern Rocky Mountain wolf recovery program 2013 interagency annual report*. Helena, Montana.
- Van Oosterhout, C., Hutchinson, W.F., Wills, D.P.M. & Shipley, P. (2004). Micro-Checker: software for identifying and correcting genotyping errors in microsatellite data. *Mol. Ecol. Notes* **4**, 535–538.
- VonHoldt, B.M., Stahler, D.R., Smith, D.W., Earl, D.A., Pollinger, J.P. & Wayne, R.K. (2008). The genealogy and genetic viability of reintroduced Yellowstone grey wolves. *Mol. Ecol.* **17**, 252–274.
- Waits, L.P., Luikart, G. & Taberlet, P. (2001). Estimating the probability of identity among genotypes in natural populations: cautions and guidelines. *Mol. Ecol.* **10**, 249–256.
- Wallach, A.D., Ritchie, E.G., Read, J. & O'Neill, A.J. (2009). More than mere numbers: the impact of lethal control on the social stability of a top-order predator. *PLoS ONE* **4**, e6861.
- Wayne, R.K. (1996). Conservation genetics in the Canidae. In *Conservation genetics: case histories from nature: 75–118*. Avise, J.C. & Hamrick, J.L. (Eds). New York, NY: Chapman & Hall.
- Weaver, J.L. & Fritts, S.H. (1979). Comparison of coyote and wolf scat diameters. *J. Wildl. Manage.* **43**, 786–788.
- Webb, N.F., Allen, J.R. & Merrill, E.H. (2011). Demography of a harvested population of wolves (*Canis lupus*) in west-central Alberta, Canada. *Can. J. Zool.* **89**, 744–752.
- Wiley, E.M. & Ridley, A.R. (2018). The benefits of pair bond tenure in the cooperatively breeding pied babbler (*Turdoides bicolor*). *Ecol. Evol.* **8**, 7178–7185.

Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1. Predicting wolf rendezvous site habitat.

Appendix S2. Genetic criteria to classify wolves.

Appendix S3. Lone wolves and harvest.

Appendix S4. Sampling and classification results.

Appendix S5. Tests for genetic distance and spatial autocorrelation.

Appendix S6. Data and code for statistical analyses.