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HARVEST AND PERSISTENCE OF WOLF POPULATIONS:

VARIABLE EFFECTS OF HARVEST ON WOLF PACKS IN THE ROCKY MOUNTAINS

By

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B.S. in Wildlife Biology, The University of Montana, Missoula, Montana 2008

Thesis

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Harvest and persistence of wolf populations: variable effects of harvest on wolf packs in the Rocky Mountains

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Public harvest is a common method used to manage populations of wolves (*Canis lupus*) in North America. Although wolves appear resilient to the effects of harvest management the influences on demography and pack stability are uncertain. Packs generally drive population dynamics for wolves; thus, we were interested in how harvested populations were maintained and how harvest influenced the abundance and distribution of packs. We used noninvasive genetic data collected in Idaho, USA (2008–2014) and Alberta, Canada (2012–2014) to test whether immigration compensated for harvest mortality and helped maintain population densities. We further fit occupancy models to detection data derived from noninvasive genetic samples and hunter surveys from Alberta, Canada (2012–2014) to test the stability of pack abundance and distribution in a harvested population of wolves. We genetically identified 461 unique wolves across our study areas; 762 hunters reported seeing live wolves in southwestern Alberta. We found our hypothesis that immigration did not compensate for harvest mortality was supported. Density of wolves in the U.S. population declined from 15.49 wolves/1000 km^2 (95% credible interval [CRI]: 12.38–18.57) without harvest to 10.20 wolves/1000 km^2 (95% CRI: 7.47–12.90) with harvest, whereas the proportion of long-distance immigrants was low and did not change with harvest (ranged 0.01–0.02, SD = 0.1). Density and proportion of immigrants were similar among study areas where harvest occurred. We also found we could not reject our hypothesis that occurrence of packs was generally stable in a harvested population of wolves. The mean annual probability for wolf pack occupancy ranged 0.72–0.74 and the estimated distribution of wolf packs was consistent over time. Model selection indicated harvest did not have a strong effect on pack occurrence but that the probability of detecting a wolf pack was positively associated with the intensity of harvest for wolves. Although immigration did not appear to compensate for harvest mortality, pack occurrence remained generally stable over time, likely due to movement between packs from within the population. Harvest therefore appears to affect within-pack dynamics, but may not directly affect the number and distribution of packs across a population.

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Thank you.

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Chapter 1

The influence of harvest varies within and across wolf packs in the Rocky Mountains

This research began in 2012 when the Montana Cooperative Wildlife Research Unit (MCWRU) collaborated with Alberta Environment and Parks (AEP) to develop and test a monitoring program for wolves in southwestern Alberta. As we conducted noninvasive genetic surveys and worked with biologists in the region, we grew curious about the persistence of this population. Harvest pressure on wolves appeared high in southwestern Alberta; not all harvest of wolves was reported (Robichaud and Boyce 2010, Webb et al. 2011), AEP did not require hunting licenses or quotas for resident wolf hunters (Webb et al. 2011), and some counties in our study area offered bounties for wolves (Cardston County Council). Despite the high harvest pressure in southwestern Alberta (G. Hale, AEP, personal communication), our field surveys demonstrated wolf packs persisted during our 3-year study. We were therefore interested in how this population was maintained and how strongly harvest influenced the dynamics of the packs we were surveying.

Wolves are generally resilient to harvest (Ballard et al. 1987, Hayes and Harestad 2000, Adams et al. 2008, Webb et al. 2011) and numerous studies hypothesize that harvested populations are maintained by a combination of reproduction and immigration (e.g., Ballard et al. 1987, Hayes & Harestad 2000, etc.). Recent research has demonstrated, however, pup survival and recruitment were low in southwestern Alberta and have declined in other regions of the Rocky Mountains where harvest occurred (Ausband et al. 2015). Thus, changes in reproduction do not appear to compensate for harvest mortality in this region. Although populations of wolves may be able to compensate for harvest if natural mortality declines (Errington 1945, Anderson and Burnham 1976) there is limited empirical evidence that natural mortality decreases in response to low or intermediate levels of harvest mortality (Adams et al. 2008, but see Murray et al. 2010). Reduced emigration may also compensate for harvest (Adams et al. 2008). Given the high harvest pressure in southwestern Alberta however, we hypothesized immigration was most important for maintaining population density and wolf packs in this region (Ballard et al. 1987, Potvin et al. 1992, Jędrzejewska et al. 1996, Larivière et al. 2000, Jędrzejewski et al. 2005).

It is difficult to evaluate compensatory responses to harvest without an experiment or a comparable unharvested population (Sandercock 2011). Wolves in southwestern Alberta have been harvested since the 1980s (Gunson 1992, Robichaud & Boyce 2010), but harvest of wolves in the northern U.S. Rocky Mountains was only recently initiated (U.S. Fish and Wildlife Service [USFWS] 2014). The MCWRU had conducted long-term noninvasive genetic sampling for wolves in central Idaho since 2007. This timeframe corresponded with when wolves were removed from the protection of the Endangered Species Act and public harvest was initiated in Idaho (Montana Fish, Wildlife and Parks [MFWP] 2010, Idaho Department of Fish and Game [IDFG] 2012, Rich et al. 2013, Ausband et al. 2014). We were therefore able to explicitly test whether immigration compensated for harvest mortality in central Idaho. We could also compare the relationship between harvest and immigration in central Idaho to the relationship in southwestern Alberta to evaluate whether this relationship was consistent across harvested populations of wolves.

In Chapter 2, we asked how immigration compensated for harvest mortality in populations of wolves managed with public harvest in the Rocky Mountains. We tested 3 competing hypotheses that 1) immigration compensated, 2) immigration partially compensated, and 3) immigration did not compensate for harvest mortality. We used noninvasive genetic data collected from 10 packs in central Idaho (2007–2014) and 3 packs in southwestern Alberta (2012–2014) to assess the relationship between harvest and immigration. Our hypothesis that immigration did not compensate for harvest mortality was supported. We found population density of wolves in central Idaho declined from 15.49 wolves/1000 km^2 (95% credible interval [CRI]: 12.38–18.57) without harvest to 10.20 wolves/1000 km^2 (95% CRI: 7.47–12.90) with harvest whereas the proportion of long-distance immigrants was low and did not change with harvest (ranged 0.01–0.02, SD = 0.1). The density and proportion of immigrants were similar among study areas where harvest occurred.

In addition to understanding whether compensatory immigration maintained harvested populations of wolves in the Rocky Mountains, we were also interested in the stability of wolf populations managed with public harvest. Packs are the reproductive units of a wolf population and generally drive population dynamics (Peterson et al. 1984, Fuller et al. 2003); thus our research focused on the stability of packs. Frequent loss and reestablishment of packs across space and time (i.e., turnover of packs) may affect demography (Haber 1996, Grewal et al. 2004, Jędrzejewski et al. 2005, Brainerd et al. 2008). Furthermore, frequent changes in the abundance and distribution of packs may affect whether monitoring can provide adequate information necessary for managing populations of wolves. Setting harvest regulations and meeting population objectives for wolves may be more challenging if the abundance and distribution of wolf packs is highly dynamic due to harvest.

In Chapter 3, we evaluated the effect of harvest on occurrence and turnover of packs in a population of wolves managed with heavy harvest in the Canadian Rocky Mountains. We tested two alternative hypotheses that 1) the abundance and distribution of wolf packs was highly dynamic due to harvest or 2) the abundance and distribution of wolf packs was generally stable regardless of harvest. We generated detection data for wolves based on noninvasive genetic samples and observations of live wolves made by hunters. We used occupancy models to estimate the annual abundance and distribution of packs in southwestern Alberta (2012–2014) and then tested the relative influence of harvest and environmental factors on pack occurrence and turnover. We also compared model estimates to wolf genotypes to assess turnover of packs and individuals within packs. We found the mean annual probability for wolf pack occupancy ranged 0.72–0.74 and the estimated distribution of wolf packs was consistent over time. Model selection indicated harvest did not have a strong effect on pack occurrence but that the probability of detecting a wolf pack was positively associated with the intensity of harvest for wolves. Whereas the abundance and distribution of packs appeared stable during our study, we observed frequent turnover of individuals within packs genetically sampled over consecutive years.

This research grew out of curiosity about a harvested population of wolves. Our observations from the field led us to ask questions about how heavily harvested populations were maintained and the stability of packs. Contrary to expectation, immigration does not compensate for harvest mortality in all populations of wolves, yet the abundance and distribution of packs can remain stable despite heavy harvest. Harvest therefore appears to affect within-pack dynamics, but may not directly affect the number and distribution of packs across a population. We hypothesize the level of harvest may affect social stability within packs, thus influencing compensatory immigration and adoption of unrelated adults, which in turn may affect the stability of pack occurrence in harvested populations.

LITERATURE CITED

Adams, L. G., R. O. Stephenson, B. W. Dale, R. T. Ahgook, and D. J. Demma. 2008. Population dynamics and harvest characteristics of wolves in the Central Brooks Range, Alaska.

Anderson, D.R., and Burnham, K.P. 1976. Population ecology of the mallard: VI. the effect of exploitation on survival. U.S. Fish and Wildlife Service Resource Publication No. 128.

Ausband, D. E., L. N. Rich, E. M. Glenn, M. S. Mitchell, P. Zager, D. A. W. Miller, L. P. Waits, B. B. Ackerman, and C. M. Mack. 2014. Monitoring gray wolf populations using multiple survey methods. The Journal of Wildlife Management 78:335–346.

Ausband, D. E., C. R. Stansbury, J. L. Stenglein, J. L. Struthers, and L. P. Waits. 2015. Recruitment in a social carnivore before and after harvest. Animal Conservation 18:415–423.

Ballard, W. B., J. S. Whitman, and C. L. Gardner. 1987. Ecology of an exploited wolf population in South-Central Alaska. Wildlife Monographs 98:1–54.

Brainerd, S. M., H. Andren, E. E. Bangs, E. H. Bradley, J. a Fontaine, W. Hall, Y. Iliopoulos, M. D. Jimenez, E. a Jozwiak, O. Liberg, C. M. Mack, T. J. Meier, C. C. Niemeyer, H. C. Pedersen, H. Sand, R. N. Schultz, D. W. Smith, P. Wabakken, and a P. Wydeven. 2008. The effects of breeder loss on wolves. Journal of Wildlife Management 72:89–98.

Cardston County Council. 2012. Cardston County Council Meeting Minutes. Cardston, Alberta, Canada. < https://cardston.civicweb.net/document/12181>. Accessed 21 April 2017.

Errington, P. L. 1945. Some contributions of a fifteen-year local study of the northern bobwhite to a knowledge of population phenomena. Ecologial Monographs 15:1–34.

Fuller, T. K., L. D. Mech, and J. F. Cochrane. 2003. Wolf population dynamics. Pages 161–191 *in* L. D. Mech and L. Boitani, editors. Wolves: behavior, ecology, and concervation. The University of Chicago Press. Illinois, USA.

Gunson, J. R. 1992. Historical and present management of wolves in Alberta. Wildlife Society

Bulletin 20:330–339.

Haber, G. C. 1996. Biological, conservation, and ethical implications of exploiting and controlling wolves. Conservation Biology 10:1068–1081.

Hayes, R. D., and A. S. Harestad. 2000. Demography of a recovering wolf population in the Yukon. Canadian Journal of Zoology 78:36–48.

Idaho Department of Fish and Game [IDFG] and Nez Perce Tribe. 2012. 2011 Idaho wolf monitoring progress report. Idaho Department of Fish and Game. Boise, Idaho, USA.

Jędrzejewska, B., W. Jędrzejewski, A. N. Bunevich, L. Milkowski, and H. Okarma. 1996. Population dynamics of wolves Canis lupus in Bialowieza primeval forest (Poland and Belarus) in relation to hunting by humans, 1847-1993. Mammal Review 26:103–126.

Jędrzejewski, W., W. Branicki, C. Veit, I. MeĐugorac, M. Pilot, A. N. Bunevich, B. Jędrzejewska, K. Schmidt, J. Theuerkauf, H. Okarma, R. Gula, L. Szymura, and M. Förster. 2005. Genetic diversity and relatedness within packs in an intensely hunted population of wolves Canis lupus. Acta Theriologica 50:3–22.

Larivière, S., H. Jolicoeur, and M. Crete. 2000. Status and conservation of the gray wolf (*Canis lupus*) in wildlife reserves of Quebec. Biological Conservation 94:143–151.

Montana Fish, Wildlife and Parks [MFWP]. 2010. Montana gray wolf conservation and management 2009 annual report. Montana Fish, Wildlife & Parks. Helena, Montana, USA.

Murray, D. L., D. W. Smith, E. E. Bangs, C. Mack, J. K. Oakleaf, J. Fontaine, D. Boyd, M. Jiminez, C. Niemeyer, T. J. Meier, D. Stahler, J. Holyan, and V. J. Asher. 2010. Death from anthropogenic causes is partially compensatory in recovering wolf populations. Biological Conservation 143:2514–2524.

Peterson, R. O., J. D. Woolington, and T. N. Bailey. 1984. Wolves of the Kenai Peninsula, Alaska. Wildlife Monographs 88:1–52.

Potvin, F., H. Jolicoeur, L. Breton, and R. Lemieux. 1992. Evaluation of an experimental wolf reduction and its impact on deer in Papineau-Labelle Reserve, Quebec. Canadian Journal of Zoology 70:1595–1603.

Rich, L. N., R. E. Russell, E. M. Glenn, M. S. Mitchell, J. a Gude, K. M. Podruzny, C. a Sime, K. Laudon, D. E. Ausband, and J. D. Nichols. 2013. Estimating occupancy and predicting numbers of gray wolf packs in Montana using hunter surveys. Journal of Wildlife Management 77:1280–1289.

Robichaud, C. B., and M. S. Boyce. 2010. Spatial and temporal patterns of wolf harvest on registered traplines in Alberta, Canada. Journal of Wildlife Management 74:635–643.

Sandercock, B. K., E. B. Nilsen, H. Brøseth, and H. C. Pedersen. 2011. Is hunting mortality additive or compensatory to natural mortality? Effects of experimental harvest on the survival and cause-specific mortality of willow ptarmigan. Journal of Animal Ecology 80:244–258.

U.S. Fish and Wildlife Service [USFWS], Idaho Department of Fish and Game, Montana Fish, Wildlife & Parks, Wyoming Game and Fish Department, Nez Perce Tribe, National Park Service, Blackfeet Nation, Confederated Salish and Kootenai Tribes, Wind River Tribes, Confederated Colville Tribes, Spokane Tribe of Indians, Washington Department of Fish and Wildlife, Oregon Department of Fish and Wildlife, Utah Department of Natural Resources, and USDA Wildlife Services. 2014. Northern Rocky Mountain wolf recovery program 2013 interagency annual report. M.D. Jimenez and S.A. Becker, eds. USFWS, Ecological Services, 585 Shepard Way, Helena, Montana, USA.

Webb, N. F., J. R. Allen, and E. H. Merrill. 2011. Demography of a harvested population of wolves (*Canis lupus*) in west-central Alberta, Canada. Canadian Journal of Zoology 89:744–752.

Chapter 2

Immigration does not compensate for harvest mortality of wolves in the Rocky Mountains

ABSTRACT

In some harvested populations, demographic processes may change in response to harvest mortality and obscure the effects of harvest on density. Gray wolves (*Canis lupus*) often appear resilient to harvest management, potentially because immigration compensates for harvest mortality and maintains population densities. We used noninvasive genetic samples to estimate the density and proportion of immigrants in a population of wolves before and after harvest was initiated in the northern U.S. Rocky Mountains (2008–2014) and in a population managed with harvest for decades in the Canadian Rocky Mountains (2012–2014). We tested three competing hypotheses that 1) immigration compensated, 2) immigration partially compensated, and 3) immigration did not compensate for harvest mortality. We also hypothesized that any compensatory relationship between harvest and immigration would be similar across populations where harvest occurred. We collected fecal samples from wolves in 13 packs for 3–7 consecutive years, extracted DNA and genotyped 426 unique wolves across 18 microsatellite loci. We classified individuals as residents (n = 370), neighbors (n = 3), short-distance immigrants (n = 16), or long-distance immigrants (n = 23) based on genetic relationships among wolves in our samples. Our hypothesis that immigration did not compensate for harvest mortality was supported. Density of wolves in the U.S. population declined from 15.49 wolves/1000 km^2 (95% credible interval [CRI]: 12.38–18.57) without harvest to 10.20 wolves/1000 km^2 (95% CRI: 7.47–12.90) with harvest, whereas the proportion of long-distance immigrants was low and did not change with harvest (ranged 0.01–0.02, SD = 0.1). Density and proportion of immigrants were similar among study areas where harvest occurred. We hypothesize available breeding opportunities and the social structure of wolf packs may limit the compensatory response of immigration in some populations of wolves managed with low to moderate levels of harvest.

KEY WORDS *Canis lupus*, compensatory immigration, gray wolf, harvest, noninvasive genetic sampling, Rocky Mountains

INTRODUCTION

Understanding the relationship between population growth and sustainable harvest is an important aspect of wildlife management. In some populations, growth and total mortality may not change with low levels of harvest due to compensatory changes in natural mortality. As harvest rates increase, however, changes in natural mortality may not be able to compensate for harvest mortality, at which point total mortality will increase and the population will decline (Errington 1945, Anderson and Burnham 1976, Allen et al. 1998). The effects of harvest are often context-dependent and can vary among species or even among populations of a single species (Fuller et al. 2003, Mills 2012, Minnie et al. 2016), creating uncertainty about the extent to which harvest and natural mortality are compensatory across a variety of harvested species (Allen et al. 1998, Pöysä et al. 2004, Sandercock et al. 2011, Wolfe et al. 2015).

Managing carnivores with public harvest can be particularly challenging for this reason (Lieury et al.2015). If compensatory responses to harvest management occur, changes in natural mortality may obscure the effects of harvest on the growth or density of a population and negate management efforts (Ellison 1991, Sandercock et al. 2011, Williams et al. 2002, Wolfe et al. 2015). It may be unclear which, if any, vital rates change in response to harvest or how best to manage harvest to meet population objectives (Herrando-Pérez et al. 2012, Wolfe et al. 2015).

In the Rocky Mountains, wolves (*Canis lupus*) are managed through public harvest to minimize the negative effects of predation on wild ungulates, mitigate conflicts with livestock, and provide opportunities for hunting wolves (Idaho Legislative Wolf Oversight Committee [ILWOC] 2002, Montana Fish, Wildlife & Parks [MFWP] 2002, Bruskotter 2013). This is challenging both sociopolitically (Bruskotter 2013) and biologically, particularly because of the social nature of wolves. Wolves live in groups (i.e., packs) which generally comprise a dominant breeding pair and their offspring of multiple generations (Mech & Boitani 2003); the pack is the reproductive unit in a wolf population and drives population dynamics (Peterson et al. 1984, Fuller et al. 2003). Adult pack members defend a common territory, hunt cooperatively, and assist the breeding pair in raising pups (Packard et al. 2003). The effects of harvest mortality on wolf packs and populations vary depending on the age-class, social-rank, and dispersal-status of the individuals harvested and, thus, can be complex (Fuller et al. 2003, Brainerd et al. 2008, Murray et al. 2010, Sandercock et al. 2011).

Wolf populations appear resilient to the effects of low to intermediate levels of harvest, (i.e., hunting and trapping; Hayes and Harestad 2000, Adams et al. 2008, Webb et al. 2011). Adams et al. (2008) estimated wolf populations can sustain an average harvest rate of ≤ 0.29 and maintain stable densities. Above this rate, several studies found hunting and trapping can regulate wolf densities, leading to population declines (Peterson et al. 1984, Ballard et al. 1987, Person and Russell 2008). These studies suggest harvest mortality in wolf populations is compensatory up to a critical threshold (Anderson and Burnham 1976). Limited evidence exists, however, that natural mortality decreases in response to low or intermediate levels of harvest mortality (Adams et al. 2008, but see Murray et al. 2010), contradicting the compensatory mortality hypothesis.

Some studies posit compensatory changes in reproduction may better explain how populations of wolves sustain harvests with minimal long-term effects to population growth or density (Fuller et al. 2003). Litter size or pup survival within packs may increase to compensate for harvest mortality (Mech 1970, van Ballenberghe et al. 1975), although this hypothesis has limited empirical support (Gasaway et al. 1983, Peterson et al. 1984, Ballard et al. 1987, Potvin et al. 1992). Peterson et al. (1984) hypothesized reproduction could increase because more small packs could reproduce in the same area as fewer large packs where harvest reduced mean size of packs and territories. A proportional increase of pups in a harvested population is more likely related to changes in the composition of a population (e.g., fewer adults and yearlings) however, than a compensatory response in reproduction (Gasaway et al. 1983). Reproductive success is lower in packs when breeder mortality occurs (Brainerd et al. 2008, Borg et al. 2015) which may also limit whether reproduction compensates for harvest. In addition, changes in size and structure of packs can indirectly affect the reproductive success of packs; smaller, less complex packs recruit fewer pups into the adult population, thus reproduction may not offset harvest mortality at all (Ausband et al. 2015).

Fuller et al. (2003) hypothesized compensatory relationships exist between dispersal and harvest, but few studies have evaluated dispersal as a compensatory mechanism for harvest mortality in wolf populations. Dispersal, i.e., the process of leaving a natal pack and joining another or establishing a new pack, is a common life-history trait of wolves and an important process for growth and persistence of wolf populations (Peterson et al. 1984, Fuller et al. 2003, Jimenez et al. 2017). This may be especially true in populations that are harvested (Fuller et al. 2003, Adams et al. 2008). For example, Adams et al. (2008) found emigration can decline in response to harvest, effectively compensating for the effects of harvest mortality on the density of a wolf population.

Increased immigration may also be an important factor compensating for harvest mortality in populations of wolves. Packs may be more receptive to adopting immigrants where harvest rates are high (Grewal et al. 2004, Rutledge et al. 2010). Although targeted removal (Bjorge and Gunson 1985, Fuller et al. 2003, Bradley et al. 2015) and dissolution of packs in response to harvest (Jędrzejewska et al. 1996, Mech and Boitani 2003, Brainerd et al. 2008, Smith et al. 2016) can leave territories unoccupied, numerous studied documented rapid recolonization of vacant territories by local dispersers and immigrants (Ballard et al. 1987, Fuller 1989, Potvin et al. 1992, Hayes & Harestad 2000, Scandura et al. 2011). Immigration may offset harvest mortality by quickly replacing individuals or packs lost to harvest, thus maintaining wolf densities (Ballard et al. 1987, Potvin et al. 1992). This may be particularly true when harvest rates vary across administrative and political boundaries (McCullough 1996); dispersal from lightly-harvested populations may sustain populations of wolves managed under heavier harvest (Forbes and Theberge 1996; Jędrzejewska et al. 1996, Jędrzejewski et al. 2005, Smith et al. 2016). If harvest reduces emigration (Adams et al. 2008) or pup recruitment (Ausband et al. 2015) rates however, fewer wolves may disperse or be available to offset harvest mortality, thus limiting any compensatory response (Small et al. 1991).

Although numerous studies speculated compensatory immigration was important for maintaining harvested populations of wolves (Ballard et al. 1987, Potvin et al. 1992, Jędrzejewska et al. 1996, Jędrzejewski et al. 2005, Larivière et al. 2000), none explicitly tested whether immigration offset harvest mortality. Monitoring dispersal is inherently challenging (Nathan 2001) and evaluating whether a compensatory response to harvest occurs is difficult where wolves are already managed with harvest. Populations of wolves in the Canadian and northern U.S. Rocky Mountains, however, provide a unique opportunity to assess compensatory immigration. Wolves in Idaho, USA were not harvested while listed as endangered under the Endangered Species Act (ESA), but have been harvested since delisting (U.S. Fish and Wildlife Service [USFWS] 2014). In contrast, wolves in Alberta, Canada were managed with harvest for decades (Gunson 1992, Robichaud & Boyce 2010). By comparing a population before and after harvest was initiated, we can explicitly test for a response of immigration to harvest. In addition, comparing immigration among harvested populations will also allow us to assess how general this response is across different harvested populations of wolves.

We evaluated how immigration compensated for harvest mortality in populations of wolves managed with public harvest in the Rocky Mountains. We focused on immigration into packs because packs are the reproductive units within a wolf population (Fuller et al. 2003). We assumed harvest pressure varied spatially because management goals and harvest regulations differed within and across state and provincial boundaries (ILWOC 2002, Idaho Department of Fish and Game [IDFG] 2015*a*, MFWP 2002; 2016), and thus tested three alternative hypotheses. We first hypothesized immigration fully compensated for harvest mortality. If true, we predicted wolf density would remain constant when harvest occurred but that the proportion of new immigrants associated with packs would increase. We next hypothesized immigration only partially compensated for harvest mortality. If true, we expected the density of wolves to decrease but the proportion of new immigrants associated with packs to increase when harvest occurred. We then hypothesized immigration did not compensate for harvest mortality. If true, we predicted the density of wolves to decrease and the proportion of new immigrants associated with packs to decrease or remain constant when harvest occurred. To assess the generality of immigration as a mechanism to offset harvest mortality, we hypothesized the relationship between harvest and compensatory immigration was similar across harvested populations of wolves in the Rocky Mountains. If true, we predicted the patterns between density and immigration would be similar among study areas where harvest occurred.

To test these hypotheses, we used noninvasive genetic data collected in central Idaho prior to and after public harvest of wolves was initiated, and in southwestern Alberta where harvest of wolves occurred throughout our study. We compared the density and proportion of immigrants detected from years when harvest did and did not occur in central Idaho to test for compensatory changes in immigration. We then compared the density and proportion of immigrants detected from only years when harvest occurred in central Idaho and southwestern Alberta to test whether our predictions were generally consistent across study systems.

STUDY AREA

We conducted annual surveys for wolves in 2 study areas in central Idaho and 1 in southwestern Alberta. In Idaho, the east study area was IDFG (Game Management Unit (GMU) 28 (3,388 km^2), and the west study area was GMUs 33, 34, and 35 (3,861 km^2; Fig. 1). The southwestern Alberta study area extended from the Canadian-US border to Trans-Canadian Highway 1, following the British Columbia border but excluded Banff National Park (12,020 km^2; Fig. 1). Both Idaho study areas were dominated by ponderosa pine (*Pinus ponderosa*), lodgepole pine (*P. contorta*), and spruce (*Picea engelmannii*) mixed forests and sagebrush (*Artemisia tridentate*) steppe (IDFG 2015*a*). The western portion of southwestern Alberta study area was mountainous and dominated by Douglas fir (*Pseudotsuga menziesii*), lodgepole pine, and spruce mixed forests, that transitioned through aspen (*Populus tremuloides*) to agricultural land and fescue (*Genus spp.*) dominated grassland in the east (National Regions Committee 2006).

The USFWS reintroduced wolves to central Idaho in 1995 and 1996 as part of the Northern Rocky Mountain (NRM) Wolf Recovery Plan (USFWS 2014). The USFWS removed wolves in the NRM from protection under the ESA twice between 2008 and 2010, during which Idaho initiated a brief public harvest in 2009. The Congress removed wolves in Idaho and Montana from protection under the ESA in 2011 at which time Idaho resumed public harvest (IDFG 2010, USFWS 2011). The annual harvest averaged 23.8% of wolves in central Idaho (SD = 9.2; Ausband et al. 2015). Public harvest of wolves occurred between 30 August and 30 June (IDFG 2015*b*).

The Fish and Wildlife Division of Alberta Environment and Parks (AEP) has managed wolves in southwestern Alberta with public harvest since the 1980s after the population recovered from a rabies eradication program (Gunson 1992, Forbes & Boyd 1996, Robichaud and Boyce 2010). Regional biologists believed harvest pressure on wolves was high, although they did not know the annual harvest rate in our study area (G. Hale, AEP, personal communication); previous research north of our study area reported mean annual harvest rate was 0.34 (Webb et al. 2011). Harvest of wolves on public lands occurred between 1 September and 31 May and year-round on private and leased lands (Gunson 1992, Robichaud & Boyce 2010, Alberta Government 2014*a*, *b*).

METHODS

Field Methods

We collected noninvasive genetic data in central Idaho (2007–2014) in collaboration with IDFG and the Nez Perce Tribe and in southwestern Alberta (2012–2014) in collaboration with AEP. We followed data collection methods described by Ausband et al. (2010) and Stenglein et al. (2011).

We used resource selection function maps for each study area to identify predicted rendezvous sites (i.e., pup-rearing sites; Ausband et al. 2010, Ausband & Mitchell 2011) and surveyed for wolves from mid-June through mid-August of each year. While surveying a site, we recorded the presence of live wolves and wolf sign and collected genetic samples from scat when detected (Ausband et al. 2010). We considered canid scats to be adult wolf if ≥ 2.5 cm in diameter and canid scats at active rendezvous sites to be wolf pup if < 2.5 cm in diameter (Weaver and Fritts 1979). We collected a small sample (pencil eraser sized) of each scat using sterilized forceps and stored it in DMSO/EDTA/Tris/salt solution buffer (Frantzen et al. 1998, Stenglein et al. 2010*a*). We recorded the geographic coordinate location of each scat sampled. In southwestern Alberta we surveyed predicted rendezvous sites in only the southern half of the study area due to budgetary constraints in 2012 (Fig. 2). We surveyed the full southwestern Alberta study area in 2013 and 2014.

Laboratory Methods

We analyzed genetic samples at the Laboratory for Ecological, Evolutionary and Conservation Genetics (LEECG) at the University of Idaho, Moscow, USA to determine the number of unique individuals sampled each year in each study area. We followed DNA extraction and analysis protocols described in detail by Stenglein et al. (2010*b*, 2011) and Stansbury et al. (2014). We screened samples with a mitochondrial DNA species-identification test to remove non-target species and low quality samples (De Barba et al. 2014, Stansbury et al. 2014). We genotyped the remaining samples for individual identification with polymerase chain reaction (PCR) using 9 nuclear DNA microsatellite loci and up to 9 additional microsatellite loci for unique identification and to verify matches or mismatches (Stenglein et al. 2011, Stansbury et al. 2014). We evaluated presence of genotyping errors with Dropout (McKelvey and Schwartz 2005) and Micro-Checker (Van Oosterhout et al. 2004). We identified and sorted matching and unique genotypes with GENALEX (Peakall and Smouse 2006, 2012) and used RELIOTYPE (Miller et al. 2002) to test the accuracy of single capture genotypes. We then analyzed the genotypes using STRUCTURE (Pritchard et al. 2000) to estimate percent coyote, dog and gray wolf ancestry and removed samples with highly probable coyote or dog ancestry (Stansbury et al. 2014). We examined allele frequencies and tested for isolation-by-distance (Mantel test) between study areas and between packs within study areas in GENALEX (Peakall and Smouse 2006, 2012).

Pack Assignment

Following methods described by Stansbury et al. (2016), we used geographic data of sampled scat locations to assign individual wolves to putative packs and to inform genetic analyses. Adult wolves in a pack periodically return to the rendezvous site to guard and provision pups (Packard 2003). Thus, we assigned individuals to a common pack if they were sampled together at ≥ 1 common locations. If an individual did not share a common location with other wolves we considered it a lone wolf.

We used ML-RELATE (Kalinowski et al. 2006) to estimate pairwise relatedness among all individuals and assess relatedness within each pack. We considered an individual genetically related to other wolves in a putative pack if it had pairwise relatedness values at the parent-offspring (PO) or full-sibling (FS) levels ($r = 0.5$) with ≥ 50% of the wolves it was sampled with (Stansbury et al. 2016).

Because wolf packs are typically kin-based units (Mech and Boitani 2003, Rutledge et al. 2010), we assumed wolves shared similar allele frequencies with pack members (Wayne and Vila 2003, Rutledge et al. 2010). We used STRUCTURE to estimate the number of genetic clusters (K), i.e., putative packs, across all study areas and estimated the probability (*q*-value or ancestral value) an individual descended from a given cluster based on similarities in their 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 = 1–28. We used additional study area and year-specific models in STRUCTURE to distinguish whether an individual was assigned to a pack because it was born into the pack or because it was a breeding adult in the pack; we reduced the number of possible clusters to K = 1–15 for these analyses. We then evaluated the most likely number of packs in each study area by comparing STRUCTURE-HARVESTER (Earl and VonHoldt 2011) estimates to the number of packs reported by IDFG, as well as the historic and current packs documented by AEP.

We used GENECLASS2 to probabilistically identify first-generation migrants in each study area (Piry et al. 2004) using the L_home test statistic (Paetkau et al. 2004). For each wolf, we tested the a priori hypothesis that it was sampled with its natal pack and thus shared similar allele frequencies with other wolves it was sampled with. To be consider a first-generation migrant, we required that probability to 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).

Finally, we considered wolves part of the same pack if we identified 2 genetically different groups of individuals, but they were all sampled at the same rendezvous site (Stansbury et al. 2016). This designation helped reduce the likelihood of overestimating pack abundance where breeder replacement or multiple breeders occurred in a single pack (Stansbury et al. 2016).

Classification of Immigrants

We classified individual wolves as a resident, neighbor, short-distance immigrant, or long-distance immigrant based on results from genetic analyses and location data of where individuals were sampled. We classified an individual as a resident if we could determine it was sampled with its natal pack (Appendix A). Neighboring packs tend to be related (Lehman et al. 1992, Mech and Boitani 2003, Wayne and Vila 2003, VonHoldt et al. 2008, Canigila et al. 2014) because packs often form by splitting, budding, or when wolves disperse to nearby areas (Mech and Boitani 2003, Wayne and Vila 2003, Grewal et al. 2004, Canigila 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 definitively assign it to a natal pack (Appendix A). These individuals were lone wolves located on the periphery of the study area and were 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 pack other than its natal pack in the same study area, i.e., it dispersed within its natal study area (Appendix A). We classified an individual as a long-distance immigrant if it assigned to a study area different from where it was sampled or the individual did not share genetic similarities to wolves from any of the three study areas (Appendix A). We only classified an individual as a short- or long-distance immigrant the first year it was detected with a wolf pack; we reclassified it as a resident in subsequent years. We classified lone wolves detected in the interior of each study area as a short- or long-distance immigrant that was not associated with a pack. We excluded all lone wolves from further analyses because we were interested in compensatory immigration within packs and because changes in sampling after 2009 reduced the likelihood of detecting lone wolves (Table 1). We excluded data collected the first year of sampling in each study area (2007 in central Idaho, 2012 in southwestern Alberta) to avoid misclassifying wolves that may have immigrated prior to that year but were classified as immigrants of that year given it was the first year of sampling. We used these data, however, to help determine whether individuals detected in 2008 (central Idaho) and 2013 (southwestern Alberta) were immigrants of that year.

Minimum Density

Within each study area, we estimated the minimum density of wolves (wolves/1,000 km^2) per year using the number of individuals sampled in each pack and year. If IDFG reported a pack, but we did not sample it that year, we excluded the mean area of a pack's territory (approximately 686 km^2; Ausband et al. 2014) from density estimates. Because sampling varied in southwestern Alberta in 2012 and 2013 we only estimated the minimum density of wolves in southwestern Alberta for 2014.

Effect of Harvest on Density and Immigration

We fit linear models (Table 2) using a Bayesian framework in JAGS (Plummer 2013) and program R 3.2.5 (R Core Team 2016) with the R2jags package (Su and Yajima 2015). We fit general linear mixed models (GLMM) to test for effects of harvest (Y/N) and study area on the minimum density of wolves and included a random effect for year. We used generalized linear models (GLM) to test for effects of harvest, study area, and survey effort (number of predicted sites surveyed per year) on the probability a short- or long-distance immigrant was detected with a pack, respectively (Table 2). We did not include a random effect in models testing for effects on immigration due to small sample sizes; variance on model estimates are therefore biased low. 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.

To test our compensatory immigration hypotheses, we fit a group of models using only data from central Idaho and tested for an effect of harvest on density and immigration before and after harvest was initiated. We then fit a separate group of models that only included data from southwestern Alberta and central Idaho in years when harvest occurred to test whether the relationship between harvest and compensatory immigration was similar across harvested populations of wolves in the Rocky Mountains.

RESULTS

Field Surveys

From 2008–2014, we surveyed 406 and 631 predicted rendezvous sites in the east and west study areas in central Idaho, respectively (Table 1; Ausband et al. 2010). We located 53 active rendezvous sites and collected 7,876 genetic samples. In southwestern Alberta, we surveyed 622 predicted rendezvous sites (2013–2014; Table 1). We located 12 active rendezvous sites and collected 1,270 genetic samples. The majority (85%) of samples were collected in active rendezvous sites across all study areas (Stansbury et al. 2014, Ausband and Bassing 2015).

Classification of Unique Individuals

Success rates for mtDNA species identification tests averaged 93.5% and individual identification success rates ranged 78 – 80% (Stansbury et al. 2016). The probability of identity for siblings ranged 3.54×10^{-4} – 1.18×10^{-3} across study areas (Ausband et al. 2015). Average error rates due to allelic drop-out and false alleles were 4.25% and 0.65%, respectively (Stansbury et al. 2016). The microsatellite analysis yielded 3,247 consensus genotypes between all three study areas. Of those, we identified 149 and 183 unique wolves in the east and west study areas in central Idaho, respectively (Table 1). We genetically recaptured 151 unique wolves ≥ 1 times across years in central Idaho. We identified 94 unique wolves in southwestern Alberta, 19 of which were genetically recaptured ≥ 1 times across years. On average, we detected 44.56 (SD = 14.49) unique individuals per year.

We classified almost all individuals (99.06%) sampled as either a type of resident or immigrant (2008–2014; Appendix A). Of those individuals, we assigned a majority (90.76%) to their natal pack following methods reported by Stansbury et al. (2016). Most wolves (87.68%) were residents and sampled with their natal packs (n = 370). Across all three study areas, we classified few wolves as potential immigrants (n = 39), of which16 were short-distance and 23 long-distance immigrants (Appendix A). Thirteen of the short- distance and 9 of the long-distance immigrants were associated with wolf packs across the three study areas (Fig. 2). We classified 2 wolves as both short-distance and long-distance immigrants in central Idaho. We considered one a lone, long-distance immigrant that eventually dispersed within the study area to fill a breeding vacancy within a pack. A second wolf joined a pack as a long-distance immigrant (non-breeder) and then dispersed locally to become the breeder in a different pack. Of the immigrants that joined a pack in central Idaho, most became a breeder within 1 year of joining (n = 12); in southwestern Alberta most immigrants associated with a pack joined as nonbreeding adults (n = 5). The sex ratio among all immigrants was 7:3 (M:F) and was more male-biased among immigrants that joined packs (18:5). We excluded lone wolves (n = 19) and neighbors (n = 6) from regression analyses.

We found limited evidence of isolation-by-distance among packs within each study area (Mantel r statistic ranged 0.10 – 0.23). The mean minimum density of wolves in central Idaho was 11.80 wolves/1000km^2 (SD = 1.44) in the east study area and 13.12 wolves/1000km^2 (SD = 1.44) in the west study area. Minimum density estimates decreased over time in both central Idaho study areas (Fig. 3). The minimum density of wolves in southwestern Alberta in 2014 was 8.34 wolves/1000km^2 (SD = 2.86).

Effects of Harvest on Density and Immigration

Harvest had a negative effect on the mean minimum density of wolves in central Idaho (Fig. 3; Table 2). The mean minimum density across both central Idaho study areas was 15.49 wolves/1000 km^2 (95% CRI = 12.38–18.57) when harvest did not occur and 10.20 wolves/1000 km^2 (95% CRI = 7.47–12.90) when harvest did occur (Fig. 4). Differences in the east and west study areas did not explain the variation in density of wolves over time (Table 2). Harvest did not affect the proportion of immigrants associated with wolf packs in central Idaho (Table 2). The mean probability that a wolf pack contained a short-distance immigrant was 0.01 (SD = 0.01) when harvest did not occur and 0.02 (SD = 0.01) when harvest did occur. The probability that a wolf pack contained a long-distance immigrant was 0.02 (SD = 0.01) when harvest did not occur and 0.01 (SD = 0.01) when harvest did occur (Fig. 5; Table 2). The proportion of short-distance and long-distance immigrants associated with a wolf pack did not differ by study area in central Idaho. We found no effect of survey effort between the Idaho study areas when we excluded lone wolves and neighbors from regression analyses (Table 2). The minimum density and probability a wolf pack contained an immigrant (short- or long-distance, respectively) when harvest occurred in central Idaho was not different from that in southwestern Alberta (Table 3).

DISCUSSION

In the Rocky Mountains, wildlife managers use public harvest of wolves to manage abundance and to mitigate human-wolf conflicts (ILWOC 2002, Bruskotter 2013). Studies have shown that wolves are resilient to harvest however (Hayes and Harestad 2000, Adams et al. 2008, Webb et al. 2011), and have hypothesized immigration may maintain stable densities within a population despite heavy harvest pressure, negating management efforts (Fuller 1989, Mech 1989, Jędrzejewska et al. 1996, Larivière et al. 2000, Webb 2009). We found little evidence that immigration compensated for harvest mortality of wolves in central Idaho or southwestern Alberta and therefore rejected our hypotheses that immigration fully or partially compensated for harvest mortality in the Rocky Mountains. Whereas previous studies found wolves generally dispersed from populations of higher density and immigrated into populations of lower density (Ballard et al. 1984, Jimenez et al. 2017) we found density and immigration were not directly related. In central Idaho, pack size and number of occupied territories decreased with harvest (IDFG 2014, Ausband et al. *in review*) but the proportion of long-distance immigrants associated with packs did not increase after harvest was initiated. The population of wolves in southwestern Alberta also had a low proportion of long-distance immigrants associated with packs even though it was a low-density population managed with public harvest for several decades (Gunson 1991). We conclude that immigration does not compensate for harvest mortality in all populations of wolves.

Given the harvest rate (23.8%; Ausband et al. 2015) in central Idaho, we found wolf density decreased in response to harvest whereas the proportion of long-distance immigrants associated with packs remained constant regardless of harvest. Similarities between the proportion of long-distance immigrants associated with packs in southwestern Alberta and packs in central Idaho after harvest began suggest this pattern was not specific to just central Idaho. We therefore could not reject our hypothesis that immigration does not compensate for harvest mortality in the Rocky Mountains. Dispersal behavior of wolves may explain why. Dispersing wolves seek breeding opportunities which can be secured by either joining or establishing a pack (Fuller et al. 2003, Mech and Boitani 2003). Attempting to join a pack is risky due to the strong potential for aggression from resident members (i.e., intraspecific strife; Mech 1994), and dispersing wolves may prefer to form new packs (Jimenez et al. 2017). Where populations are expanding or recolonizing, immigrants can successfully establish their own packs and territories

(Mech and Boitani 2003); but in well-established or saturated populations, such as in the Rocky Mountains, an immigrant's only option to find a breeding opportunity may be to join a pack (Mech and Boitani 2003). If breeder mortality from harvest is high in these populations immigration may compensate for harvest mortality primarily through breeder-replacement. In central Idaho, however, Ausband et al. (*in review*) found the frequency of breeder turnover did not increase after harvest was initiated. As a result, there are likely few opportunities for immigrants to compensate for breeder loss in this region, which may explain why the proportion of long-distance immigrants associated with packs did not change after harvest began.

The social structure of packs may further prevent immigrants from replacing nonbreeding pack members lost to harvest. Packs generally accept unrelated adult wolves (i.e., short- or long-distance immigrants) when a breeding position is available or a breeder is overthrown (Packard 2003, Stahler et al. 2002, Jędrzejewski et al. 2005, VonHoldt et al. 2008, Caniglia et al. 2014). Although there are examples of packs adopting unrelated nonbreeding adults (e.g., Rothmen and Mech 1979, Van Ballenberghe 1983, Lehman et al. 1992, Meier et al. 1995, Grewal et al. 2004, Jędrzejewski et al. 2005) we hypothesize it is uncommon when the social structure of a wolf pack is intact (i.e., the breeding pair persists; Mech and Boitani 2003). In our central Idaho study areas, for example, only 2 of the 14 immigrants that joined packs did not assume a breeding position within 1 year of joining (Ausband 2015); one of these immigrants ultimately left to fill a breeding vacancy elsewhere. Despite a 15% decline in mean pack size since harvest was initiated in Idaho (IDFG 2014), we found that immigrants did not frequently replace nonbreeding adults within packs. Thus, packs appear less likely to adopt unrelated adults when the pack social structure is intact (Rutledge et al. 2010) even if additional nonbreeding wolves would help maintain pack size and pup recruitment (Ausband et al. 2015). This may suggest that group augmentation is not the primary evolutionary mechanism driving cooperative breeding in wolves (Clutton-Brock 2002).

Although we rejected our hypotheses that immigration compensates for harvest mortality in the Rocky Mountains, compensatory immigration may explain how populations of wolves persist in regions where harvest mortality is higher. When heavy harvest creates social instability, packs may be more receptive to adopting unrelated nonbreeding adults (Jędrzejewska et al. 1996; Grewal et al. 2004; Jędrzejewski et al. 2005; Brainerd et al. 2008; Webb et al. 2011). In addition, immigrants will establish packs where harvest creates territory vacancies (Bjorge and Gunson 1985, Fuller 1989, Hayes & Harestad 2000, Brainerd et al. 2008, Scandura et al. 2011). In an extreme example of compensatory immigration, Larivière et al. (2000) reported harvest rates ranged from 0 to 193% of the annual wolf populations across 9 wildlife preserves in southern Quebec, Canada, but found that wolf densities were correlated with the previous year's harvest in only 1 preserve. They hypothesized that strong immigration from adjacent areas (McCullough 1996), possibly source-sink dynamics (Delibes et al. 2001), maintained stable populations within preserves. Where harvest rates are high enough to exceed the estimated annual abundance of a population of wolves, immigration appears to be the dominant factor maintaining stable densities (Larivière et al. 2000).

We hypothesize that the relationship between compensatory immigration and harvest exists on a continuum. When harvest mortality is low, the social structure of packs remains relatively intact. Packs are generally composed of closely related individuals (Rutledge et al. 2010) with diverse age structures (Fuller et al. 2003) that maintain long-term territories (Mech and Boitani 2003), all of which likely limit the compensatory response of immigrants to harvest mortality at the pack level. Where harvest mortality is high, however, immigration may not be limited by the social constraints of intact packs and may become an important compensatory mechanism in heavily harvested populations of wolves (Adams et al. 2008). Previous studies that hypothesized compensatory immigration maintained wolf densities reported higher harvest rates than what we observed in central Idaho or likely southwestern Alberta (e.g., Ballard et al. 1987, Potvin et al. 1992, Larivière et al. 2000, Jędrzejewski et al. 2005). These studies would fall toward the higher end of the spectrum we hypothesize for the compensatory relationship between immigration and harvest, which may explain why immigration appears to compensate in these populations but not in the Rocky Mountains. Alternatively, many of these studies focused on subpopulations within much larger wolf populations (e.g., Alaska, USA or northern Canada; Ballard et al. 1987; Hayes and Harestad 2000) whereas our study focused on a peninsular population (central Idaho; USFWS 2016) and one on the eastern-edge of wolf distribution in the Rocky Mountains (southwestern Alberta; Boitani 2003). Differences in human and wolf densities, availability of suitable wolf habitat (Ausband 2016), and whether studies took place in the interior or frontier of wolf distribution (Fuller et al. 2003) may further explain the variable relationship between compensatory immigration and harvest mortality across these populations (Ausband 2016).

The population of wolves in the Rocky Mountains likely falls along the lower end of our hypothesized continuum, although pack structure appeared less stable in southwestern Alberta than in central Idaho. Thus, even across the Rocky Mountains, gradations in the relationship between immigration and harvest may exist. We detected 8 immigrants associated with packs in southwestern Alberta compared to 3 in central Idaho during the last 2 years of our study (2013–2014). In addition, most immigrants (n = 5) joined packs as nonbreeding adults in southwestern Alberta whereas most became breeders in central Idaho; packs in southwestern Alberta appeared more receptive to adopting nonbreeding adults than in central Idaho (Grewal et al. 2004, Jędrzejewski et al. 2005). The majority (75%) of immigrants in southwestern Alberta where not long-distance immigrants however, and dispersed from nearby packs. Short-distance immigrants are already part of the population and their dispersal cannot directly help maintain population densities, but they likely help packs persist as harvest rates increase.

Although we focused on compensatory immigration at the pack level, immigrants unaffiliated with packs may also be important in harvested populations of wolves. Lone wolves are immigrants circulating within a population, seeking opportunities to join or form a pack (Mech and Boitani 2003). Lone wolves typically make up 10–15% of a wolf population (Fuller et al. 2003), thus immigrants unaffiliated with packs may provide a pool of individuals whose loss to harvest would have little consequence for packs or population dynamics (Fuller 1989, Fuller et al. 2003). Due to their naivety in novel environments (Peterson et al. 1984, Smith et al. 2016) and vulnerability to anthropogenic-caused mortality (Person and Russell 2008), harvest may be biased towards lone wolves instead of resident pack members (Peterson et al. 1984, Adams et al. 2008, Webb 2009, Smith et al. 2010); continual replacement of lone wolves by new immigrants may compensate for harvest mortality across a population (Fuller et al. 2003). Most (82%) immigrants we detected in central Idaho 2008–2009 were lone wolves, suggesting a large pool of immigrants unaffiliated with packs may have existed in this region. We could not test whether their abundance represented a compensatory response to harvest however because changes in sampling after 2009 made lone wolves difficult to detect. In addition, unless we genetically recaptured lone wolves over multiple years, we could not differentiate true lone wolves, i.e., floating within the population, from dispersers traveling through the study area.

We made several assumptions whose violations could affect our inferences. A misclassification of wolves (resident, neighbor, short-distance, or long-distance immigrant) could have biased the estimated proportion of immigrants in packs and our conclusion about the compensatory response to harvest. We required agreement between 4 metrics to classify wolves based on the genetic relationships among individuals in our samples. Several individuals we classified as immigrants (i.e., short- or long-distance) were also radio-collared and their dispersals were corroborated by IDFG biologists independent of our genetic methods. We excluded known misclassifications (n = 2) from analyses. Because most individuals met our classification requirements we are confident the probability undetected misclassifications occurred was low. Changes in prey density can affect density (Messier 1985, Fuller 1989, Fuller et al. 2003) and likely dispersal (Ballard et al. 1987, Thurber and Peterson 1993, Hayes and Harestad 2000) of wolves; however prey densities remained generally consistent in central Idaho during our study (Ausband et al. 2015). Prey data were not available for southwestern Alberta and we assumed prey density did not influence immigration in this region. Immigration also depends on population densities in other regions (McCullough 1985, Larivière et al. 2000) and immigration during out study could have been affected by changes in densities in source populations. We were unable to measure the density of wolves outside our study areas; however, because we did not observe a change in immigration after harvest was initiated in central Idaho, we do not believe variation in source populations had a strong influence in the relationship we observed between harvest and immigration. Although prey density or the density of wolves in other areas did not appear influential during our study future work should attempt to explicitly incorporate these into analyses.

MANAGEMENT IMPLICATIONS

Immigration is often assumed to be one of the primary mechanisms responsible for maintaining stable densities in harvested populations of wolves. Although this assumption is well-rooted in the literature, compensatory immigration does not necessarily occur in all populations of wolves that are harvested. Therefore, if the goal of management is to allow for population growth of wolves while having a public harvest, managers cannot assume immigration will offset the effects of harvest mortality. If, however, the goal is to reduce the density of wolves with public harvest, managers may not need to be as concerned that immigration will negate management efforts as previous research would suggest. Variation in the relationship between compensatory immigration and harvest mortality likely depends on the annual harvest rate, social behavior of wolves, and connectivity across populations. Understanding this variation will help managers better predict the effects of public harvest on a wolf population of interest and meet management objectives.

Finally, we found harvest had a weak positive effect on short-distance immigrants but a weak negative effect on long-distance immigrants associated with wolf packs after harvest was initiated in central Idaho. The effects of harvest on immigration may have been difficult to detect because our analyses were based on a small sample of immigrants. Continued monitoring of immigrants as harvest management continues would strengthen our ability to determine whether harvest does effect immigration in the Rocky Mountains.

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LITERATURE CITED

Alberta Government. 2014*a*. 2014 Alberta guide to hunting rgulations. <http://albertaregulations .ca/2014-Alberta-Hunting-Regulations.pdf >. Accessed 14 Jan 2015.

Alberta Government. 2014*b*. 2014-2015 Alberta guide to trapping regulations. < http://alberta regulations.ca/Trapping-Regs-2014-15.pdf >. Accessed 14 Jan 2015.

Adams, L. G., R. O. Stephenson, B. W. Dale, R. T. Ahgook, and D. J. Demma. 2008. Population dynamics and harvest characteristics of wolves in the Central Brooks Range, Alaska. Wildlife Monographs 170:1–25.

Allen, M. S., L. E. Miranda, and R. E. Brock. 1998. Implications of compensatory and aditive mortality to the management of selected sprotifish populations. Lake & Reservoirs: Research and Management 3:67–79.

Anderson, D.R., and Burnham, K.P. 1976. Population ecology of the mallard: VI. the effect of exploitation on survival. U.S. Fish and Wildlife Service Resource Publication No. 128.

Ausband, D. E. 2015. Groups and mortality: their effects on cooperative behavior and population growth in a social carnivore. Dissertation, University of Montana, Missoula, USA.

Ausband, D. E. 2016. Gray wolf harvest in Idaho. Wildlife Society Bulletin 40:500–505.

Ausband, D. E., and M. S. Mitchell. 2011. A habitat model for predicting gray wolf rendezvous site locations in southwest Alberta. Missoula, Montana, USA.

Ausband, D., M. Mitchell, K. Doherty, P. Zager, C. Mack, and J. Holyan. 2010. Surveying predicted rendezvous sites to monitor gray wolf populations. Journal of Wildlife Management 74:1043–1049.

Ausband, D. E., M. S. Mitchell, and L. P. Waits. 2017. Effects of breeder turnover and harvest on group composition and recruitment in a social carnivore. *In review*.

Ausband, D. E., C. R. Stansbury, J. L. Stenglein, J. L. Struthers, and L. P. Waits. 2015. Recruitment in a social carnivore before and after harvest. Animal Conservation 18:415–423.

Ballard, W. B., J. S. Whitman, and C. L. Gardner. 1987. Ecology of an exploited wolf population in South-Central Alaska. Wildlife Monographs 98:1–54.

Bjorge, R. R., and J. R. Gunson. 1985. Evaluation of wolf control to reduce cattle predation in Alberta. Journal of Range Management 38:483–487.

Bjorge, R. R., and J. R. Gunson. 1989. Wolf, *Canis lupus*, population characteristics and prey relationships near Simonette River, Alberta. The Canadian Field-Naturalist 103:327–334.

Borg, B. L., S. M. Brainerd, T. J. Meier, and L. R. Prugh. 2015. Impacts of breeder loss on social structure, reproduction and population growth in a social canid. Journal of Animal Ecology 84:177–187.

Boitani, L. 2003. Wolf conservation and recovery. Pages 317 – 340 *in* L. D. Mech and L. Boitani, editors. Wolves: behavior, ecology, and concervation. The University of Chicago Press. Illinois, USA.

Bradley, E. H., H. S. Robinson, E. E. Bangs, K. Kunkel, M. D. Jimenez, J. A. Gude, and T. Grimm. 2015. Effects of wolf removal on livestock depredation recurrence and wolf recovery in Montana, Idaho, and Wyoming. The Journal of Wildlife Management 79:1337–1346.

Brainerd, S. M., H. Andren, E. E. Bangs, E. H. Bradley, J. a Fontaine, W. Hall, Y. Iliopoulos, M. D. Jimenez, E. a Jozwiak, O. Liberg, C. M. Mack, T. J. Meier, C. C. Niemeyer, H. C. Pedersen, H. Sand, R. N. Schultz, D. W. Smith, P. Wabakken, and a P. Wydeven. 2008. The effects of breeder loss on wolves. Journal of Wildlife Management 72:89–98.

Bruskotter, J. T. 2013. The predator pendulum revisited: Social conflict over wolves and their management in the western United States. Wildlife Society Bulletin 37:674–679.

Caniglia, R., E. Fabbri, M. Galaverni, P. Milanesi, and E. Randi. 2014. Noninvasive sampling and genetic variability, pack structure, and dynamics in an expanding wolf population. Journal of Mammalogy 95:41–59.

Clutton-Brock, T. 2002. Breeding together: kin selection and mutualism in cooperative vertebrates. Science 296:69–72.

De Barba, M., J. R. Adams, C. S. Goldberg, C. R. Stansbury, D. Arias, R. Cisneros, and L. P.

Waits. 2014. Molecular species identification for multiple carnivores. Conservation Genetics Resources 6:821–824.

Delibes, M., P. Gaona, and P. Ferreras. 2001. Effects of an attractive sink leading into maladaptive habitat selection. The American Naturalist 158:277–285.

Earl, D. A., and B. M. VonHoldt. 2011. STRUCTURE HARVESTER: a website and program for visualizing STRUCTURE output and implementing the Evanno method. Conservation Genetic Resources 4:359–361.

Ellison, L. N. 1991. Shooting and compenstory mortality in tetraonids. Scandinavian Journal of Onithology 22:229–240.

Errington, P. L. 1945. Some contributions of a fifteen-year local study of the northern bobwhite to a knowledge of population phenomena. Ecologial Monographs 15:1–34.

Forbes, S. H., and D. K. Boyd. 1996. Genetic variation of naturally colonizing wolves in the Central Rocky Mountains. Conservation Biology 10:1082–1090.

Forbes, G. J., and J. B. Theberge. 1996. Cross-boundary management of Algonquin Park wolves. Conservation Biology 10:1091–1097.

Frantzen, M. A., J. B. Silk, J. W. Ferguson, R. K. Wayne, and M. H. Kohn. 1998. Empirical evaluation of preservation methods for faecal DNA. Molecular Ecology 7:1423–1428.

Fuller, T. K. 1989. Population Dynamics of Wolves in North-Central Minnesota. Wildlife Monographs 105:1–41.

Fuller, T. K., L. D. Mech, and J. F. Cochrane. 2003. Wolf population dynamics. Pages 161–191 *in* L. D. Mech and L. Boitani, editors. Wolves: behavior, ecology, and concervation. The University of Chicago Press. Illinois, USA.

Gasaway, W. C., R. O. Stephenson, J. L. Davis, P. E. K. Shepherd, and O. E. Burris. 1983.

Interrelationships of wolves, prey, and man in interior Alaska. Wildlife Monographs 84:1–50.

Grewal, S. K., P. J. Wilson, T. K. Kung, K. Shami, M. T. Theberge, J. B. Theberge, and B. N. White. 2004. A genetic assessment of the eastern wolf (*Canis lycaon*) in Algonquin Provincial Park. Journal of Mammalogy 85:625–632.

Gunson, J. R. 1991. Management plan for wolves in Alberta. Forestry, Lands and Wildlife, Fish and Wildlife Devision. Edmonton, Alberta, Canada.

Gunson, J. R. 1992. Historical and present management of wolves in Alberta. Wildlife Society Bulletin 20:330–339.

Hayes, R. D., and a. S. Harestad. 2000. Demography of a recovering wolf population in the Yukon. Canadian Journal of Zoology 78:36–48.

Herrando-pérez, A. S., S. Delean, B. W. Brook, and J. A. Corey. 2012. Decoupling of component and ensemble density feedbacks in birds and mammals. Ecology 93:1728–1740.

Idaho Department of Fish and Game [IDFG]. 2010. Wolf conservation and management in Idaho, progress report 2009. Idaho Department of Fish and Game, Boise, Idaho, USA.

Idaho Department of Fish and Game [IDFG]. 2014. 2013 Idaho wolf monitoring progress report. Idaho Department of Fish and Game, Boise, Idaho, USA.

Idaho Department of Fish and Game [IDFG]. 2015*a*. 2014 Idaho wolf monitoring progress Report. Idaho Department of Fish and Game, Boise, Idaho, USA.

Idaho Department of Fish and Game [IDFG]. 2015*b*. 2015-2016 & 2016-2017 gray wolf hunting andtrapping seasons and general rules. Idaho Department of Fish and Game, <https://idfg. idaho.gov/sites/default/files/seasons-rules-big-game-wolf_2015-2016.pdf > Accessed 16 Mar 2017.

Idaho Legislative Wolf Oversite Committee [ILWOC]. 2002. Idaho wolf conservation and management plan as amended by the 56th Idaho Legislature, Second Regular Session. <http://fishandgame.idaho.gov/public/docs/ wolves/plan02.pdf>. Accessed 1 Mar 2017.

Jędrzejewska, B., W. Jędrzejewski, A. N. Bunevich, L. Milkowski, and H. Okarma. 1996. Population dynamics of wolves Canis lupus in Bialowieza primeval forest (Poland and Belarus) in relation to hunting by humans, 1847-1993. Mammal Review 26:103–126.

Jędrzejewski, W., W. Branicki, C. Veit, I. MeĐugorac, M. Pilot, A. N. Bunevich, B. Jędrzejewska, K. Schmidt, J. Theuerkauf, H. Okarma, R. Gula, L. Szymura, and M. Förster. 2005. Genetic diversity and relatedness within packs in an intensely hunted population of wolves Canis lupus. Acta Theriologica 50:3–22.

Jimenez, M. D., E. E. Bangs, D. K. Boyd, D. W. Smith, S. A. Becker, D. E. Ausband, S. P. Woodruff, E. H. Bradley, J. Holyan, and K. Laudon. 2017. Wolf dispersal in the rocky mountains, western United States: 1993-2008. The Journal of Wildlife Management DOI: 10.1002/jwmg.21238.

Kalinowski, S. T., A. P. Wagner, and M. L. Taper. 2006. ML-RELATE: A computer program for maximum likelihood estimation of relatedness and relationship. Molecular Ecology Notes 6:576–579.

Larivière, S., H. Jolicoeur, and M. Crete. 2000. Status and conservation of the gray wolf (*Canis lupus*) in wildlife reserves of Quebec. Biological Conservation 94:143–151.

Lehman, N., P. Clarkson, L. D. Mech, T. J. Meier, and R. K. Wayne. 1992. A study of the genetic relationships within and among wolf packs using DNA fingerprinting and mitochondrial DNA. Behavioral Ecology and Sociobiology 30:83–94.

Lieury, N., S. Ruette, S. Devillard, M. Albaret, F. Drouyer, B. Baudoux, and A. Millon. 2015.

Compensatory immigration challenges predator control: An experimental evidence-based approach improves management. The Journal of Wildlife Management 79:425–434.

McCullough, D. R. 1996. Spatially structured populations and harvest theory. The Journal of Wildlife Management 60:1–9.

McKelvey, K. S., and M. K. Schwartz. 2005. DROPOUT: A program to identify problem loci and samples for noninvasive genetic samples in a capture-mark-recapture framework. Molecular Ecology Notes 5:716–718.

Mech, L. D. 1970. The wolf: the ecology and behavior of an endangered species. University of Minnesota Press. Minneapolis, USA.

Mech, L. D. 1989. Wolf population survival in an area of high road density. American Midland Naturalist 121:387–389.

Mech, L. D. 1994. Buffer zones of territories of gray wolves as regions of intraspecific strife. Journal of Mammalogy 75:199–202.

Mech, L. D., and L. Boitani. 2003. Wolf social ecology. Pages 1–34 *in* L. D. Mech and L. Boitani, editors. Wolves: behavior, ecology, and concervation. The University of Chicago Press. Illinois, USA.

Meier, T. J., J. W. Burch, J. D. Mech, and L. G. Adams. 1995. Pack structure and genetic relatedness among wolf packs in a naturally-regulated population. Pages 293–302 *in* L. N. Carbyn, S. H. Fritts, D. R. Seip, editors. Ecology and conservation of wolves in a changing world. Canadian Circumpolar Institude, Edmonton, Canada.

Messier, F. 1985. Solitary living and extraterritorial movements of wolves in relation to social status and prey abundance. Canadian Journal of Zoology 63:239–245.

Miller, C. R., P. Joyce, and L. P. Waits. 2002. Assessing allelic dropout and genotyping reliability using maximum likelihood. Genetics 160 :357–249.

Mills, L. S. 2012. Conservation of wildlife populations: demography, genetics, and management. Second edition. Wiley-Blackwell. West Sussex, UK.

Minnie, L., A. Gaylard, and G. I. H. Kerley. 2016. Compensatory life-history responses of a mesopredator may undermine carnivore management efforts. Journal of Applied Ecology 53:379–387.

Montana Fish, Wildlife and Parks [MFWP]. 2002. Montana wolf conservation and management planning document. Montana Fish, Wildlife and Parks, Helena, Montana, USA.

Montana Fish, Wildlife and Parks [MFWP]. 2016. Montana gray wolf conservation and management 2015 annual report. Montana Fish, Wildlife and Parks, Helena, Montana, USA.

Murray, D. L., D. W. Smith, E. E. Bangs, C. Mack, J. K. Oakleaf, J. Fontaine, D. Boyd, M. Jiminez, C. Niemeyer, T. J. Meier, D. Stahler, J. Holyan, and V. J. Asher. 2010. Death from anthropogenic causes is partially compensatory in recovering wolf populations. Biological Conservation 143:2514–2524.

Nathan, R. 2001. The challenges of studying dispersal. Trends in Ecology and Evolution 16:481–483.

Natural Regions Committee. 2006. Natural regions and subregions of Alberta. Compiled by D.J. Downing and W.W. Pettapiece. Government of Alberta. Pub. No. I/005. Edmonton, Alberta, Canada.

Packard, J. M. 2003. Wolf behavior: reproductive, social, and intelligent. Pages 35–65 *in* L. D. Mech and L. Boitani, editors. Wolves: behavior, ecology, and concervation. The University of Chicago Press. Illinois, USA.

Paetkau D, W. Calvert, I. Stirling, C. Strobeck. 1995. Microsatellite analysis of population structure in Canadian polar bears. Molecular Ecology 4:347–354.

Paetkau, D., R. Slade, M. Burden, and A. Estoup. 2004. Genetic assignment methods for the direct, real-time estimation of migration rate: A simulation-based exploration of accuracy and power. Molecular Ecology 13:55–65.

Peakall, R., and P. E. Smouse, 2006. GENALEX 6: genetic analysis in Excel. Population genetic software for teaching and research. Molecular Ecology 6:288–295.

Peakall, R., and P. E. Smouse. 2012. GenALEx 6.5: Genetic analysis in Excel. Population genetic software for teaching and research-an update. Bioinformatics 28:2537–2539.

Person, D. K., and A. L. Russell. 2008. Correlates of mortality in an exploited wolf population. The Journal of Wildlife Management 72:1540–1549.

Peterson, R. O., J. D. Woolington, and T. N. Bailey. 1984. Wolves of the Kenai Peninsula, Alaska. Wildlife Monographs 88:1–52.

Piry, S., A. Alapetite, J. M. Cornuet, D. Paetkau, L. Baudouin, and A. Estoup. 2004. GENECLASS2: A software for genetic assignment and first-generation migrant detection. Journal of Heredity 95:536–539.

Plummer, M. 2013. JAGS Version 3.4.0 user manual. 1–41.

Potvin, F., H. Jolicoeur, L. Breton, and R. Lemieux. 1992. Evaluation of an experimental wolf reduction and its impact on deer in Papineau-Labelle Reserve, Quebec. Canadian Journal of Zoology 70:1595–1603.

Pöysä, H., J. Elmberg, G. Gunnarsson, P. Nummi, and K. Sjöberg. 2004. Ecological basis of sustainable harvesting: Is the prevailing paradigm of compensatory mortality still valid? Oikos 104:612–615.

Pritchard, J. K., M. Stephens, and P. Donnelly. 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. R Foundation for Statistical Computing, Vienna, Austria.

Robichaud, C. B., and M. S. Boyce. 2010. Spatial and temporal patterns of wolf harvest on registered traplines in Alberta, Canada. Journal of Wildlife Management 74:635–643.

Rutledge, L. Y., B. R. Patterson, K. J. Mills, K. M. Loveless, D. L. Murray, and B. N. White. 2010. Protection from harvesting restores the natural social structure of eastern wolf packs. Biological Conservation 143:332–339.

Sandercock, B. K., E. B. Nilsen, H. Brøseth, and H. C. Pedersen. 2011. Is hunting mortality additive or compensatory to natural mortality? Effects of experimental harvest on the survival and cause-specific mortality of willow ptarmigan. Journal of Animal Ecology 80:244–258.

Scandura, M., L. Iacolina, C. Capitani, A. Gazzola, L. Mattioli, and M. Apollonio. 2011. Fine-scale genetic structure suggests low levels of short-range gene flow in a wolf population of the Italian Apennines. European Journal of Wildlife Research 57:949–958.

Smith, D. W., E. E. Bangs, J. K. Oakleaf, C. Mack, J. Fontaine, D. Boyd, M. Jimenez, D. H. Pletscher, C. C. Niemeyer, T. J. Meier, D. R. Stahler, J. Holyan, V. J. Asher, and D. L. Murray. 2010. Survival of colonizing wolves in the Northern Rocky Mountains of the United States, 1982–2004. Journal of Wildlife Management 74:620–634.

Rothman, R. J., and L. D. Mech. 1979. Scent-marking in lone wolves and newly formed pairs. Animal Behaviour 27:750–760.

Small, R. J., J. C. Holzwart, and D. H. Rusch. 1991. Predation and hunting mortaltiy of ruffed grouse in central Wisconsin. The Journal of Wildlife Management 55:512–520.

Smith, D. W., P. J. White, D. R. Stahler, A. Wydeven, and D. E. Hallac. 2016. Managing wolves in the Yellowstone area: Balancing goals across jurisdictional boundaries. Wildlife Society Bulletin 40:436–445.

Stahler, D. R., D. W. Smith, and R. Landis. 2002. The acceptance of a new breeding male into a wild wolf pack. Canadian Journal of Zoology 80:360-365.

Stansbury, C. R., D. E. Ausband, P. Zager, C. M. Mack, C. R. Miller, M. W. Pennell, and L. P. Waits. 2014. A long-term population monitoring approach for a wide-ranging carnivore: Noninvasive genetic sampling of gray wolf rendezvous sites in Idaho, USA. Journal of Wildlife Management 78:1040–1049.

Stansbury, C. R., D. E. Ausband, P. Zager, C. M. Mack, and L. P. Waits. 2016. Identifying gray wolf packs and dispersers using noninvasive genetic samples. The Journal of Wildlife Management 80:1408–1419.

Stenglein, J. L., M. De Barba, D. E. Ausband, and L. P. Waits. 2010*a*. Impacts of sampling location within a faeces on DNA quality in two carnivore species. Molecular Ecology Resources 10:109–114.

Stenglein, J. L., L. P. Waits, D. E. Ausband, P. Zager, and C. M. Mack. 2010*b*. Efficient, noninvasive genetic sampling for monitoring reintroduced wolves. Journal of Wildlife Management 74:1050–1058.

Stenglein, J. L., L. P. Waits, D. E. Ausband, P. Zager, and C. M. Mack. 2011. Estimating gray wolf pack size and family relationships using noninvasive genetic sampling at rendezvous sites. Journal of Mammalogy 92:784–795.

Su, Y.S. and M. Yajima. 2015. R2jags: A Package for Running JAGS from R. R package version

0.03-06. http://CRAN.R-project.org/package=R2jags.

Thurber, J. M., and R. O. Peterson. 1993. Effects of population density and pack size on the foraging ecology of gray wolves. Journal of Mammology 74:879–889.

U.S. Fish andWildlife Service [USFWS]. 2011. Endangered and threatened wildlife and plants; reissuance of final rule to identify the northern Rocky Mountain population of gray wolf as a distinct population segment and to revise the list of endangered and threatened wildlife. Fed. Regist. 76, USFWS, Denver, Colorado, USA.

U.S. Fish and Wildlife Service [USFWS], Idaho Department of Fish and Game, Montana Fish, Wildlife & Parks, Wyoming Game and Fish Department, Nez Perce Tribe, National Park Service, Blackfeet Nation, Confederated Salish and Kootenai Tribes, Wind River Tribes, Confederated Colville Tribes, Spokane Tribe of Indians, Washington Department of Fish and Wildlife, Oregon Department of Fish and Wildlife, Utah Department of Natural Resources, and USDA Wildlife Services. 2014. Northern Rocky Mountain wolf recovery program 2013 interagency annual report. M.D. Jimenez and S.A. Becker, eds. USFWS, Ecological Services, 585 Shepard Way, Helena, Montana, USA.

U.S. Fish and Wildlife Service [USFWS], Idaho Department of Fish and Game, Montana Fish, Wildlife & Parks, Wyoming Game and Fish Department, Nez Perce Tribe, National Park Service, Blackfeet Nation, Confederated Salish and Kootenai Tribes, Wind River Tribes, Confederated Colville Tribes, Spokane Tribe of Indians, Washington Department of Fish and Wildlife, Oregon Department of Fish and Wildlife, Utah Department of Natural Resources, and USDA Wildlife Services. 2016. Northern Rocky Mountain wolf recovery program 2015 interagency annual report. Northern Rocky Mountain Wolf Recovery Program 2015 Interagency Annual Report. M.D. Jimenez and S.A. Becker, eds. USFWS, Ecological Services, 585 Shepard Way, Helena, Montana, USA.

Van Ballenberghe, V. 1983. Extraterritorial movements and dispersal of wolves in southcentral Alaska. Journal of Mammalogy 64:168–171.

Van Ballenberghe, V., A. W. Erickson, and D. Byman. 1975. Ecology of the timber wolf in northeastern Minnesota. Wildlife Monographs 43:1–43.

Van Oosterhout, C., W. F. Hutchinson, D. P. M. Wills, and P. Shipley. 2004. Micro-Checker: Software for identifying and correcting genotyping errors in microsatellite data. Molecular Ecology Notes 4:535–538.

VonHoldt, B. M., D. R. Stahler, D. W. Smith, D. a Earl, J. P. Pollinger, and R. K. Wayne. 2008. The genealogy and genetic viability of reintroduced Yellowstone grey wolves. Molecular Ecology 17:252–74.

Wayne R.K., and C. Vilà. 2003. Molecular genetic studies of wolves. Pages 218–238 in L. D. Mech and L. Boitani, editors. Wolves: behavior, ecology, and concervation. The University of Chicago Press. Illinois, USA.

Weaver, J. L., and S. H. Fritts. 1979. Comparison of coyote and wolf scat diameters. Journal of Wildlife Management 43:786–788.

Webb, N. F. 2009. Density, demography, and functional responses of a harvested wolf population in west-central Alberta, Canada. Dissertation, University of Alberta, Edmonton, Canada.

Webb, N. F., J. R. Allen, and E. H. Merrill. 2011. Demography of a harvested population of wolves (*Canis lupus*) in west-central Alberta, Canada. Canadian Journal of Zoology 89:744–752.

Williams, B. K., J. D. Nichols, M. J. Conroy. 2002. The use of models in conservation and management. Pages 223 – 242 *in* Analysis and management of animal populations. Academic Press. San Diego, CA, USA.

Wolfe, M. L., D. N. Koons, D. C. Stoner, P. Terletzky, E. M. Gese, D. M. Choate, and L. M. Aubry. 2015. Is anthropogenic cougar mortality compensated by changes in natural mortality in Utah? Insight from long-term studies. Biological Conservation 182:187–196.

Figure 1. A) The east and west focal study areas in central Idaho, USA, 2008–2014, and B) the southwestern Alberta, Canada study area, 2012–2014.

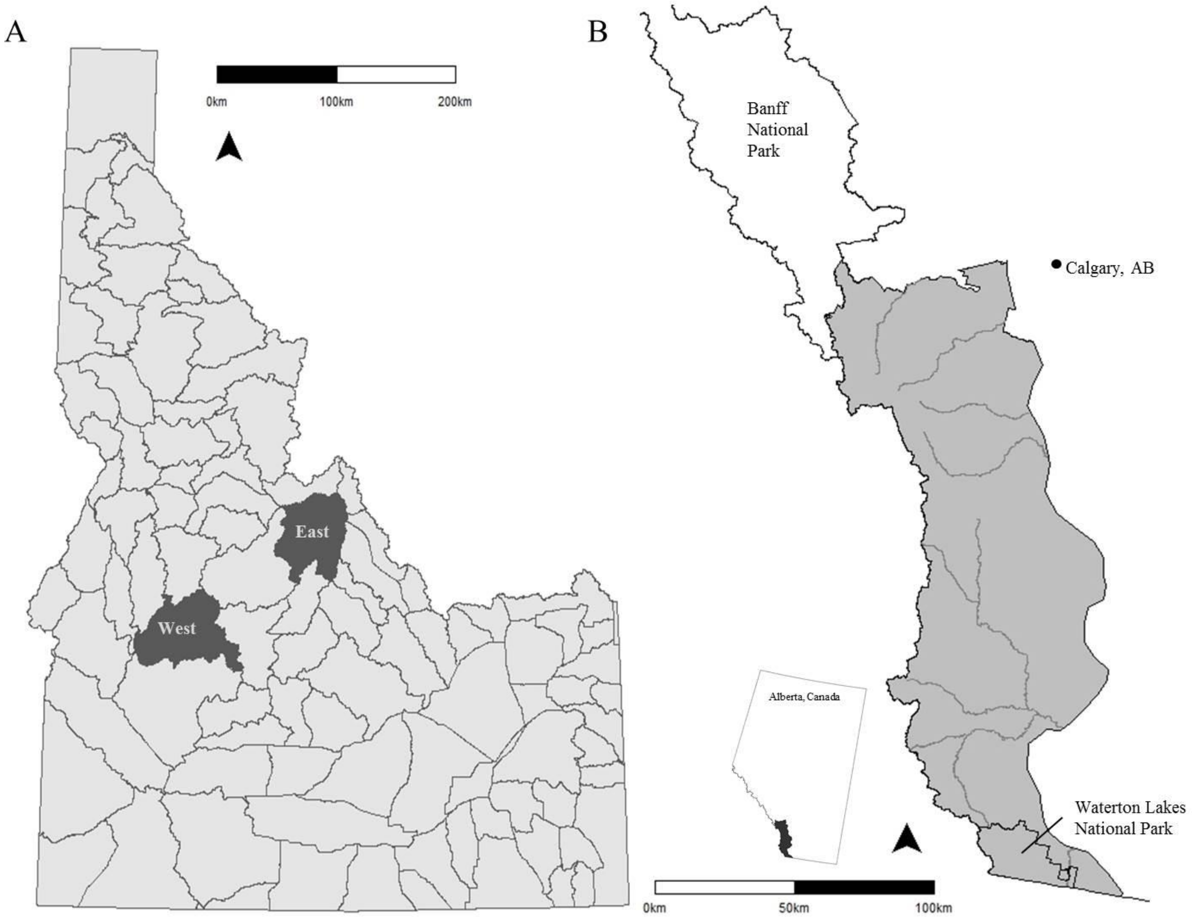

Figure 2. The number of short-distance and long-distance immigrants associated with a wolf pack in central Idaho, 2008–2014. Immigrants not associated with a wolf pack, i.e., lone wolves, were not included.

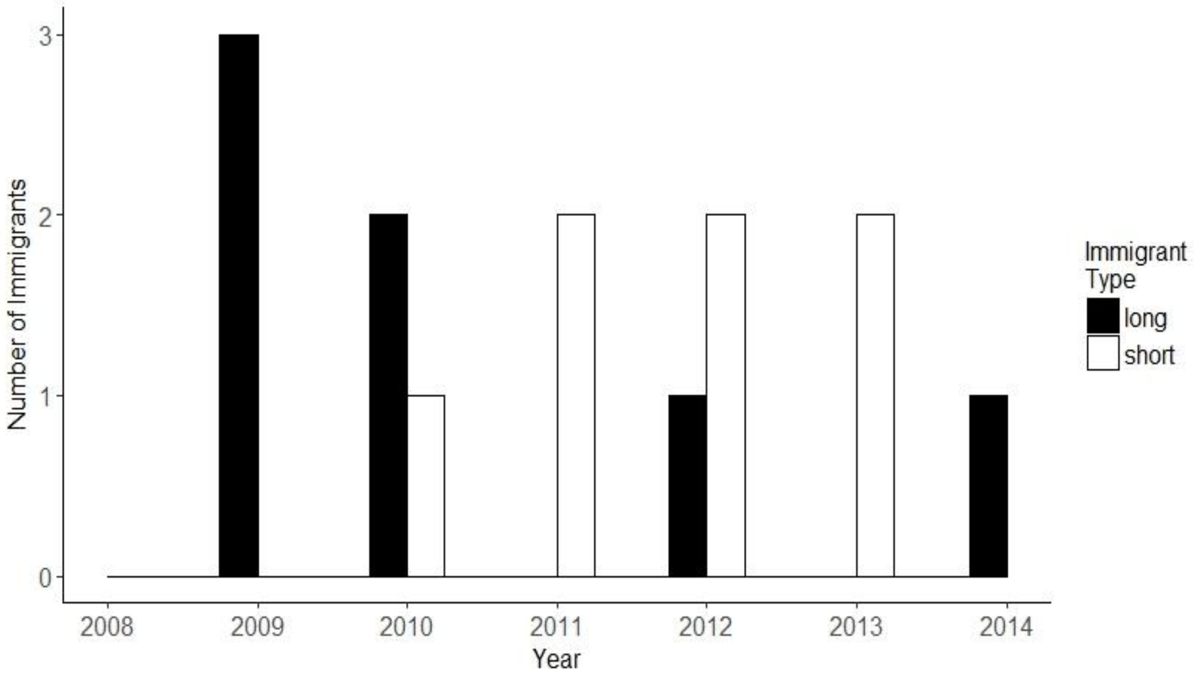

Figure 3. Annual trends in density of wolves for the east and west study areas in central Idaho, 2008–2014. Harvest occurred during autumn-winter of 2009-2010, 2011–2012, 2012–2013, and 2013–2014.

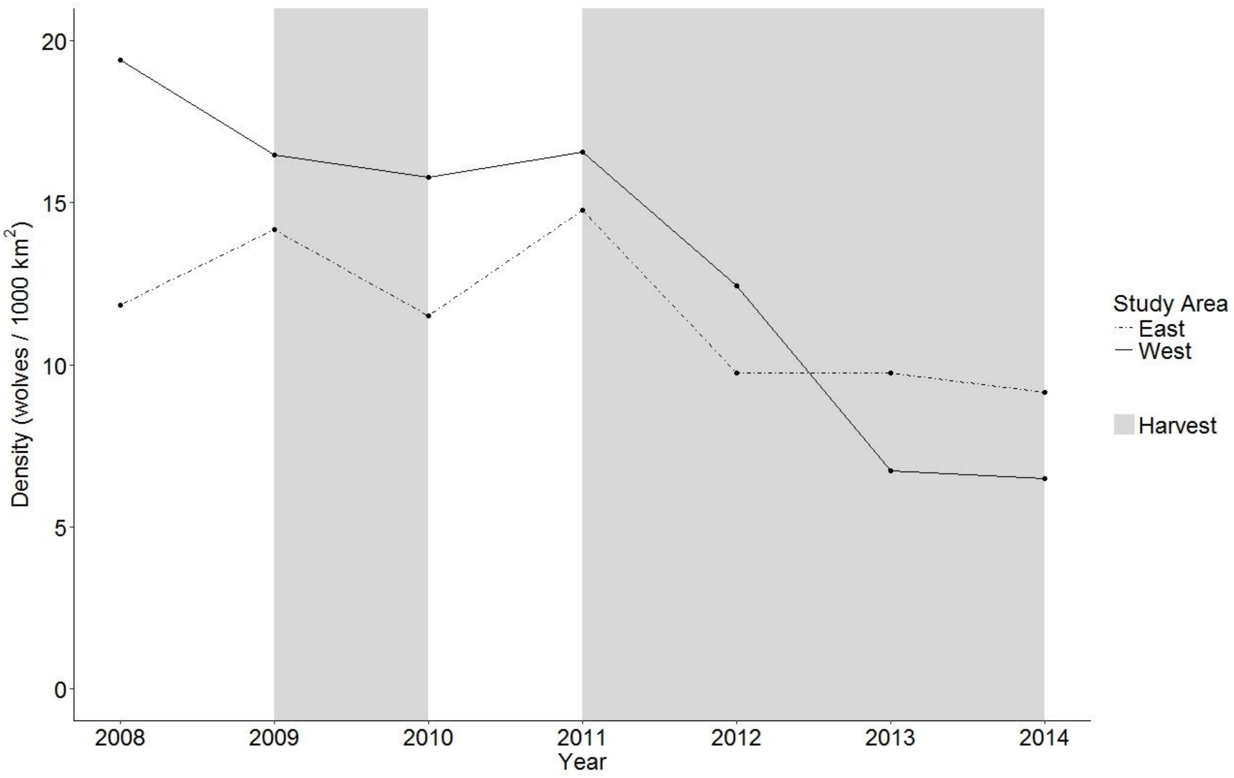

Figure 4. Effect of harvest on mean density of wolves across both study areas in central Idaho, comparing the density of wolves in years when harvest did not occur (2008, 2010) to the density of wolves in years when harvest did occur (2009, 2011–2014).

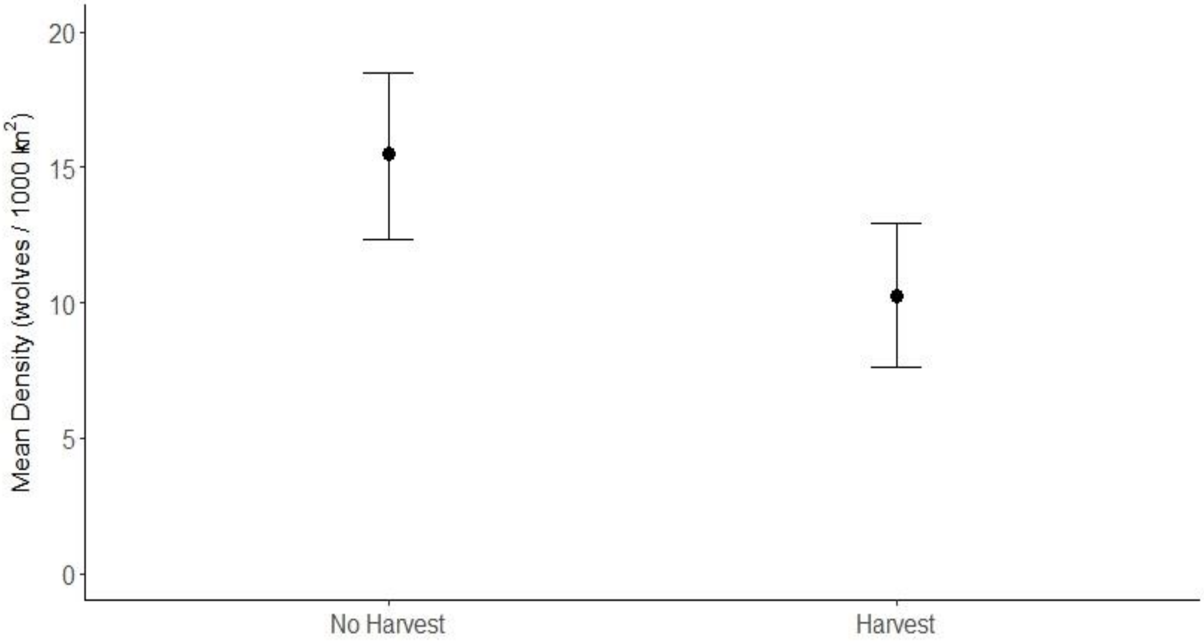

Figure 5. Effect of harvest on the probability a short- or long-distance immigrant is associated with a wolf pack in central Idaho, 2008–2014, respectively.

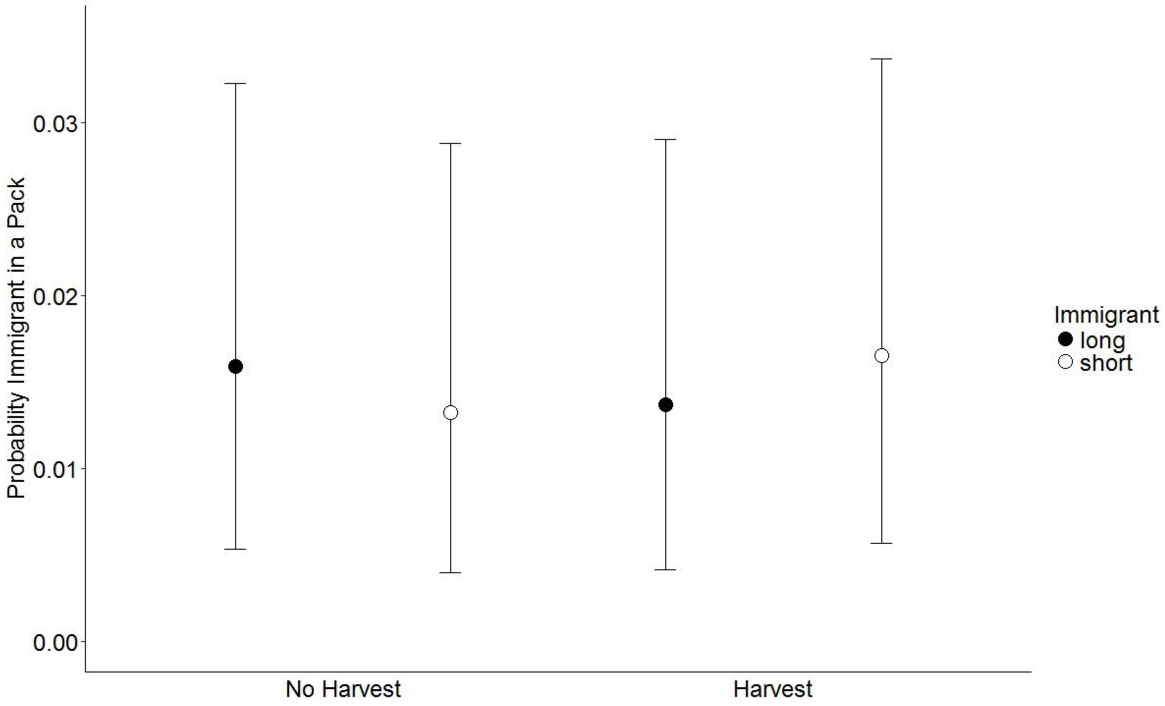

Table 1. Summary of sampling and classification results of gray wolves in central Idaho, USA and southwestern Alberta, Canada, 2008–2014. For each year in each central Idaho (East and West) and southwestern Alberta (Alberta) study areas we report the number of predicted sites surveyed, number of rendezvous sites detected (Rend.), number of consensus genotypes (*n*), and the number of individuals classified as either a short-distance (SDI) or long-distance immigrant (LDI) associated with packs (in packs) and the total number detected (i.e., including lone wolves; All).

Year	Study area	Sites surveyed	Rend. sites detected	Consensus genotypes (*n*)	SDI in packs	All SDI	LDI in packs	All LDI
2008	East	148	3	36	0	0	0	2
2008	West	173	5	46	0	1	0	3
2009	East	149	4	54	0	0	2	7
2009	West	166	6	50	0	0	1	4
2010	East	3	3	39	0	0	2	2
2010	West	41	5	63	1	2	0	1
2011	East	4	3	50	1	1	0	0
2011	West	25	5	64	1	1	0	0
2012	East	20	3	34	0	1	0	0
2012	West	47	6	48	2	2	1	1
2013	East	47	2	33	1	1	0	0
2013	West	78	3	26	1	1	0	0
2013	Alberta	301	2	37	3	4	0	0

2014	East	35	3	31	0	0	0	0
2014	West	101	2	26	0	1	1	1
2014	Alberta	321	10	76	3	3	2	2

Table 2. Model structure and results from 3 separate regression analyses testing for effects of harvest (Y/N), study area (East and West), and survey effort (number of predicted sites surveyed per year) on the density of wolves (number of wolves/1000 km^2), the probability a wolf pack contained a long-distance immigrant (LDI), and the probability a wolf pack contained a short-distance immigrant (SDI) in central Idaho, 2008–2014. Model deviance and standard error (SD), Deviance Information Criterion (DIC), fixed effect parameters, coefficient estimates and standard deviation (SD), and the lower and upper limits of the 95% credible interval (95% CRI) for each parameter are reported.

Model	Response[a]	Deviance (SD)	DIC[b]	Parameter[c]	Estimate (SD)	Lower 95% CRI	Upper 95% CRI
Harvest[d]	Density	31.75 (3.28)	37.1				
				Intercept	15.49 (1.57)	12.34	18.57
				Harvest	-5.29 (2.08)	-9.39	-1.14
Area[d]	Density	79.05 (2.89)	83.2				
				Intercept	11.55 (1.62)	8.31	14.77
				Area	1.86 (2.28)	-2.70	6.36
Harvest	LDI	45.14 (2.01)	47.2				
				Intercept	-4.22 (0.46)	-5.20	-3.40
				Harvest	-0.17 (0.65)	-1.50	1.10

Area	LDI	44.75 (1.87)	46.5				
				Intercept	-4.01 (0.43)	-4.91	-3.24
				Area	-0.69 (0.68)	-2.08	0.61
Effort	LDI	45.11 (2.39)	47.90				
				Intercept	-4.30 (0.52)	-5.41	-3.37
				Effort	-7.98 (0.01)	-0.01	0.01
Harvest	SDI	47.52 (2.23)	50.0				
				Intercept	-4.43 (0.50)	-5.49	-3.53
				Harvest	0.25 (0.65)	-1.00	1.51
Area	SDI	47.69 (2.15)	50.0				
				Intercept	-4.41 (0.51)	-5.52	-3.52
				Area	0.20 (0.66)	-1.08	1.54
Effort	SDI	46.71 (2.32)	49.40				
				Intercept	-3.50 (0.47)	-4.47	-2.63
				Effort	-0.02 (0.01)	-0.04	0.00

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[a] Model type depended on response variable where general linear mixed models were used if density (wolves/1000 km^2) was the response variable and logistic regression models were used when the response variable was whether a wolf pack contained a long-distance immigrant (LDI) or a short-distance immigrant (SDI), respectively.

[b] DIC values are only comparable among models with the same response variable.

[c] No harvest = indicator variable for harvest covariate; East study area = indicator variable for study area covariate.

[d] Models included a random effect for year.

Table 3. Model results from 3 separate regression analyses testing for differences in mean minimum density of wolves (number of wolves/1000 km^2), the probability a wolf pack contained a long-distance immigrant (LDI), and probability a wolf pack contained a short-distance immigrant (SDI) across three study areas (East and West in central Idaho and southwestern Alberta) for only years when harvest occurred, 2009 and 2011–2014. Model deviance and standard error (SD), Deviance Information Criterion (DIC), fixed effect parameters, coefficient estimates and standard deviation (SD), and the lower and upper limits of the 95% credible interval (95% CRI) for each parameter are reported.

Response[a]	Deviance (SD)	DIC[b]	Parameter[c]	Estimate (SD)	Lower 95% CRI	Upper 95% CRI
Density[d]	48.52 (3.63)	55.2				
			Intercept	9.97 (1.97)	5.96	13.84
			West	0.37 (2.79)	-5.22	5.21
			Alberta	-3.61 (4.39)	-12.32	5.90
LDI	37.84 (2.19)	40.20				
			Intercept	-3.90 (0.54)	-4.98	-2.98
			West	-0.57 (0.80)	-2.23	0.92
			Alberta	-0.28 (0.81)	-1.98	1.24
SDI	58.63 (2.36)	61.40				
			Intercept	-3.99 (0.52)	-5.08	-3.04
			West	0.19 (0.70)	-1.20	1.55
			Alberta	0.97 (0.65)	-0.25	2.27

[a] Model type depended on response variable where general linear mixed models were used if density (number of wolves/1000 km^2) was the response variable and logistic regression models were used when the response variable was whether a wolf pack contained a long-distance immigrant (LDI) or a short-distance immigrant (SDI), respectively.

[b] DIC values are only comparable among models with the same response variable.

[c] No harvest = indicator variable for harvest covariate; East = indicator variable for study area covariate.

[d] Density model included a random effect for year.

Chapter 3

Stable abundance and distribution of packs in a harvested population of wolves

ABSTRACT

Harvest can influence the demography of wild populations in a variety of ways. For gray wolves (*Canis lupus*), harvest should affect the abundance and distribution of packs, but the frequency of change in pack occurrence (i.e., turnover) and relative effect of harvest compared to environmental factors is unclear. We used noninvasive genetic sampling, hunter surveys, and occupancy models to evaluate the effect of harvest on occurrence and turnover of packs in a population of wolves managed with heavy harvest in the Canadian Rocky Mountains, 2012–2014. We tested two alternative hypotheses that 1) the abundance and distribution of wolf packs was highly dynamic due to harvest or 2) the abundance and distribution of wolf packs was generally stable regardless of harvest. We found the mean annual probability for wolf pack occupancy ranged 0.72–0.74 and the estimated distribution of wolf packs was consistent over time, 2012–2014. Our top model indicated wolf pack occupancy was positively associated with forest cover and the probability of detecting a wolf pack was positively associated with the intensity of harvest for wolves in that area. We observed frequent turnover of individuals within packs genetically sampled consecutive years but not of entire packs. Because turnover of packs occurred infrequently during our study, we could not reject our hypothesis that occurrence of packs was generally stable in a harvested population of wolves. Packs in southwestern Alberta were connected to the larger Canadian Rocky Mountain wolf population and we hypothesize short-distance dispersal from nearby packs outside our study area helped promote pack stability. Our results suggest that heavy harvest is unlikely to have strong effects on the abundance and

distribution of wolf packs when populations are well-connected, but that harvest appears to strongly influence turnover of individuals within packs.

KEY WORDS *Canis lupus*, distribution, gray wolves, harvest, noninvasive genetic surveys, occupancy model, wolf pack

INTRODUCTION

Public harvest is commonly used to manage wildlife populations and mitigate human-wildlife conflicts. Harvest can affect the demography of wild populations in numerous ways, such as alter the age and sex structures (Ginsberg & Milner-Gulland 1994, Milner et al. 2007), reproductive rate (Knowlton 1972, Ausband et al. 2015), and ultimately growth (Pauli and Buskirk 2007) of a population. Understanding how populations respond to harvest can help wildlife managers evaluate the efficacy of management and inform future decisions (Williams et al. 2002, Mills 2012).

Populations of gray wolves (*Canis lupus*) are managed with harvest across most of their range in North America (Boitani 2003). Because of the social behavior of wolves, the response of wolf populations to harvest may be more complex than for other exploited species (Rutledge et al. 2010). Wolf packs are the reproductive units in a wolf population and drive population dynamics (Fuller et al. 2003); the effects of harvest at the pack-level will affect individual pack members (Brainerd et al. 2008) and potentially the larger population (Haber 1996).

Harvest should affect the abundance and distribution of wolf packs in a population (Jędrzejewska et al. 1996, Fuller et al. 2003) but the demographic consequences of this relationship are poorly understood. Loss of wolves in a pack can create social instability, leading to pack dissolution and territory abandonment (Meier et al. 1995, Jędrzejewska et al. 1996, Brainerd et al. 2008, Smith et al. 2016), and entire packs may be removed through lethal control actions to reduce predation on livestock (Bradley et al. 2015). Frequent loss of packs to harvest can lead to decreased population growth, reproductive success, or relatedness within and among packs (Grewal et al. 2004, Jędrzejewski et al. 2005, Brainerd et al. 2008), which may have long-term effects for populations managed with heavy harvest (Haber 1996, Brainerd et al. 2008). Alternatively, packs that persist provide a source of dispersing wolves to recolonize vacant territories (Bjorge and Gunson 1985, Ballard et al. 1987, Hayes and Harestad 2000, Mech and Boitani 2003, Brainerd et al. 2008); thus, the loss and reestablishment of packs across space and time (i.e., turnover of packs) may have little effect on demography if dispersers can quickly recolonize unoccupied territories (Larivière et al. 2000, Fuller et al. 2003).

Frequent changes in abundance and distribution of packs may complicate management of harvested populations of wolves even if there are few demographic consequences. Social instability and turnover of packs can change boundaries (Jędrzejewska et al. 1996, Haber 1996, Mech and Boitani 2003), size (Peterson et al. 1984), or use (Haber et al. 1996) of territories. Such changes may affect the quality or quantity of data collected because tracking frequent changes in pack occurrence can be challenging; this may ultimately affect a manager’s ability to assess the status of a population, set harvest limits and seasons, or achieve population objectives for wolves. Frequent turnover of packs may also alter the rate of wolf-livestock conflicts. Hayes et al. (1991) found predation rates on wild prey increased for colonizing pairs and packs severely reduced after lethal removal; this behavior could extend to predation on livestock as well. If non-depredating packs dissolve in response to harvest, surviving or colonizing wolves may begin to prey on livestock (Bjorge and Gunson 1985, Harper et al. 2008). In addition, studies found lethal removal, particularly of entire packs, reduced the likelihood of future depredations locally (Bjorge and Gunson 1985, Bradley et al. 2015) but did not reduce them population-wide (Harper et al. 2008). Frequent turnover of packs may therefore affect conflicts with livestock depending on the frequency of pack replacement (Bradley et al. 2015) and individual traits of wolves recolonizing vacant territories (Bjorge and Gunson 1985). Understanding the frequency of turnover of packs and associated factors will help monitoring efforts provide accurate and sufficient information to managers, and help managers mitigate conflicts and meet population objectives for wolves.

Studies in Idaho and Montana showed the abundance and distribution of wolf packs was primarily associated with habitat features and prey densities (Rich et al. 2013, Ausband et al. 2014). These studies were largely conducted in the absence of harvest however, prior to removal of wolves from protection under the Endangered Species Act (Montana Fish, Wildlife and Parks [MFWP] 2010, Idaho Department of Fish and Game [IDFG] 2012, Rich et al. 2013, Ausband et al. 2014). Public harvest has since became increasingly liberalized in Idaho and Montana (MFWP 2015*b*, Ausband 2016) but the relative influence of harvest on the occurrence and turnover of wolf packs in the Rocky Mountains is unclear.

Unlike in Idaho and Montana where harvest management was only recently implemented (U.S. Fish and Wildlife Service [USFWS] 2009), wolves in the Canadian Rockies have been managed with public harvest for decades (Boitani 2003). In southwestern Alberta for example, harvest mortality was consistently high for wolves, although the exact harvest rate was unknown because not all public harvest was reported (Robichaud and Boyce 2010, Webb et al. 2011, G. Hale, Alberta Environment and Parks [AEP], personal communication). Because wolves in southwestern Alberta have been managed with public harvest since the 1980s (Gunson 1992) the likelihood of detecting any potential relationship between harvest and occurrence of wolf packs is higher than in Idaho and Montana, where public harvest only recently began. Evaluating the effect of long-term heavy harvest on pack turnover in this region can therefore help inform management of harvested populations of wolves throughout the Rocky Mountains.

We tested two hypotheses to evaluate the effect of harvest on occurrence and turnover of packs in a population of wolves managed with heavy harvest in the Canadian Rocky Mountains. We hypothesized that the abundance and distribution of wolf packs was highly dynamic due to harvest and predicted that pack occupancy changed frequently in association with harvest of wolves in southwestern Alberta. Alternatively, we hypothesized that the abundance and distribution of wolf packs was generally stable regardless of harvest and predicted infrequent changes in occupancy associated with harvest of wolves in southwestern Alberta. We then evaluated the relative importance of harvest compared to environmental factors that have already been shown to explain pack occupancy in the Rocky Mountains to determine the dominant factors driving pack abundance and distribution in a harvested population of wolves.

We used occupancy models to estimate the abundance and distribution of wolf packs in southwestern Alberta and evaluate the frequency with which pack occurrence changed. Occupancy models use detection/non-detection data to estimate the probability landscape patches (i.e., sample units) are occupied by a species of interest given imperfect detection of that species (i.e., occupancy; MacKenzie et al. 2002). Previous occupancy-based studies found close agreement between independent model and radiotelemetry-based estimates of occupancy, abundance, and distribution of wolves, demonstrating the ability of occupancy modelling frameworks to monitor wolves across broad-spatial scales (Rich et al. 2013, Ausband et al. 2014). As a result, wildlife management agencies in Idaho and Montana currently use occupancy models to monitor wolves (Rich et al. 2013, Ausband et al. 2014, IDFG 2015, MFWP 2015*a*); it would be beneficial, however, to evaluate whether occupancy-based monitoring can provide information to managers about pack dynamics (e.g., turnover) in a harvested population of wolves. Accordingly, we generated occupancy models using detection data collected from noninvasive genetic surveys and observations of wolves made by hunters and then tested for changes in occupancy across space and time. We then estimated and compared the effects of harvest and environmental factors on the probability of occupancy to evaluate the relative influence of harvest on abundance and distribution of packs. Finally, as an independent test of whether occupancy models could measure the frequency of turnover of packs, we compared site-specific estimates of occupancy to individual wolf genotypes derived from the genetic data. This allowed us to compare predicted changes in occupancy to the dynamics of genetically marked wolf packs and evaluate the efficacy of using occupancy models to monitor the frequency of turnover of packs in a harvested population of wolves.

METHODS

Study Area

Southwestern Alberta was the southeastern extent of gray wolf distribution in the Canadian Rocky Mountains (Gunson 1991, Boitani 2003). Our study area encompassed 30,000 km^2, extending from the Canadian-United States border north to the Brazeau River but excluded Banff and Jasper National Parks (Fig. 1). Our study area was mountainous in the west along the British Columbia border, dominated by Douglas fir (*Pseudotsuga menziesii*), lodgepole pine (*Pinus contorta*), and spruce (*Picea engelmannii*) mixed forests, that abruptly transition through aspen (*Populus tremuloides*) stands to fescue (*Festuca* spp.) dominated grassland and agricultural land in the east (National Regions Committee 2006, Desserud et al. 2010). Our study area was predominantly public Crown land under the jurisdiction of the Alberta provincial government but included Waterton Lakes National Park. Oil and gas extraction, timber harvest, outdoor recreation, and livestock and crop production occurred throughout the study area, except for within Waterton Lakes National Park (National Regions Committee 2006).

Rendezvous Site Surveys and Genetic Analyses

We surveyed for wolves in southwestern Alberta for 3 years (2012 – 2014). We collected DNA from wolves in collaboration with AEP, following methods described by Ausband et al. (2010) and Stenglein et al. (2011). We used a predictive habitat model to identify potential wolf rendezvous sites (i.e., pup-rearing sites used in summer; Ausband et al. 2010, Ausband and Mitchell 2011) and conducted noninvasive genetic surveys between mid-June and late-August of each year (Ausband et al. 2010, Ausband and Bassing 2015). We recorded the presence and geographic location of wolf sign and collected a genetic sample from scat when detected (Ausband et al. 2010, Stenglein et al. 2010*b*; 2011). We classified canid scats as adult wolf if ≥ 2.5 cm in diameter and canid scats in active rendezvous sites as wolf pup if < 2.5 cm in diameter (Weaver and Fritts 1979). We collected a small sample (pencil eraser sized) from the side of each scat using sterilized forceps and stored it in DMSO/EDTA/Tris/salt solution buffer (Frantzen et al. 1998; Stenglein et al. 2010*a*). Due to budgetary constraints, we surveyed for wolves across the southern third of our study area in 2012 and the southern half of our study area in 2013 and 2014 (Ausband and Bassing 2015).

We analyzed fecal samples at the Laboratory for Ecological, Evolutionary and Conservation Genetics (LEECG) at the University of Idaho, Moscow, USA to identify individuals sampled each year. We followed DNA extraction and analysis protocols described by Stenglein et al. (2010*b*, 2011) and Stansbury et al. (2014). We used a mitochondrial DNA species-identification test to screen and remove non-target species and low quality samples (De Barba et al. 2014, Stansbury et al. 2014). We genotyped the remaining samples with PCR using 9 nuclear DNA microsatellite loci and up to 9 additional microsatellite loci to identify individuals and verify matches or mismatches (Stenglein et al. 2011, Stansbury et al. 2014). We used GENALEX (Peakall and Smouse 2006, 2012) to identify and sort matching and unique genotypes and RELIOTYPE (Miller et al. 2002) to test the accuracy of single capture genotypes. We used STRUCTURE (Pritchard et al. 2000) to estimate percent coyote, dog and gray wolf ancestry of each genotype and removed samples with highly probable coyote or dog ancestry (Stansbury et al. 2014).

Hunter Surveys

We surveyed registered ungulate hunters for observations of live wolves made during the hunting season through an online hunter reporting form used by AEP at the end of each hunting season (Rich et al. 2013, Ausband et al. 2014, Ausband and Bassing 2015). Ungulate hunting seasons occurred from 1 September – 20 January of the next year (Alberta Government 2014) and hunters reported observations made within each week of the hunting season (Ausband and Bassing 2015). We surveyed hunters who hunted in the southern half of our study area after the 2012 season and the entire study area after the 2013 and 2014 seasons.

We excluded hunter observations when only single wolves were reported, only wolf sign (i.e., tracks or howling) was reported, inadequate location data were reported, or an observation was made outside the hunting season (Rich et al. 2013, Ausband et al. 2014). We truncated hunter survey data to include only observations of wolves made September – December to avoid violating the assumption of population closure (MacKenzie et al. 2002). We then estimated point locations for hunter observations of wolves based on the centroid of the Section, Township, Range, and Meridian reported for each sighting using program R 3.2.5 (R Core Team 2016).

Detection Histories and Covariates

We used observation data from both survey methods to generate detection histories of wolf packs in southwestern Alberta following methods described by Rich et al. (2013) and Ausband et al. (2014). We arbitrarily superimposed a grid of 1,000 km^2 cells across the study area; each cell represented a sample unit. The size of cells was based on the estimated average territory size of wolf packs (Rich et al. 2013, Ausband et al. 2014) in southwestern Alberta based on limited GPS collar location data (A. Morehouse, University of Alberta, unpublished data) and published estimates from wolf packs within the southwest and west central regions of Alberta (Webb 2009, Hebblewhite 2006, N. Webb, [AEP], personal communication). We plotted observations from both survey methods across the gridded study area in program R 3.2.5 (R Core Team 2016) to generate detection histories for each year (i.e., 3 primary sampling periods, 1 Jun – 31 Dec). Each annual detection history consisted of 9 sampling occasions; 1 based on the unique genotypes observed through rendezvous site surveys (Ausband et al. 2014), and 8 from hunter surveys where we consolidated weekly observations of wolves into 2-week sampling periods. To account for potential false-positive detections in our data (Royle and Link 2006, Miller et al. 2011), we allowed for multiple detection states (i.e., uncertain and certain) in the hunter survey data (Miller et al. 2011, Miller et al. 2013, Ausband et al. 2014). We then relaxed this requirement because analyses indicated little evidence of false-positive detections in our dataset. For both survey methods, we assumed detecting a pack in one sample unit was independent of detections in other sample units, the probability of detecting wolves was not correlated between survey methods, and the population was closed to changes in pack occupancy during each primary sampling period (i.e., no colonization or local extinction of packs from Jun – Dec each year; MacKenzie et al. 2002, 2003, 2006).

We assessed the relationship of 6 environmental and management covariates and 2 survey effort covariates on wolf pack occupancy and detection (Table 1). We estimated and categorized harvest intensity of wolves (i.e., low, medium, or high) based on the area-weighted reported number of wolves trapped in Registered Fur Management Areas (RFMA) and shot in Wildlife Management Units (WMU) each year (wolves harvested/km^2; 2011–2014). We tested for immediate and one-year lag effects (Robichaud and Boyce 2010) of harvest intensity on occupancy and detection probabilities of wolves. We estimated and categorized area-weighted density of reported cattle (i.e., low, medium, or high density/km^2) using a combination of reported stocking rates for non-overlapping grazing allotments and leases on public (AEP) and private lands (Agriculture and Agri-Food Canada). We calculated percent forest cover from the ABMI Wall-to-wall Land Cover Map (2010) based on 30 m^2 spatial-resolution Landsat satellite imagery (Alberta Biodiversity Monitoring Institute 2012) in each sample unit. We derived mean ruggedness (TRI; terrain ruggedness index) for each sample unit from 25 m^2 resolution digital elevation models (DEM; AEP). We also tested whether the proportion of a sample unit in the study area predicted occupancy of wolf packs in southwestern Alberta (Rich et al. 2013). We evaluated the relationship between survey effort and detection probability by calculating the number of predicted rendezvous sites surveyed and estimating the area-weighted number of hunter days in each WMU (hunter days/km^2) per year for each sample unit as measures of rendezvous site survey and hunter effort, respectively (Rich et al. 2013, Ausband et al. 2014). We centered and scaled all covariates based on their individual means and standard deviations per year. Finally, we tested for collinearity among the covariates and excluded highly correlated covariates ($r \geq |0.6|$; Zuur et al. 2010).

Occupancy Models

We fit dynamic (multi-season) and single season occupancy models (Table 2) using a Bayesian framework (Royle and Kéry 2007, Kéry and Schaub 2012) in JAGS (Plummer 2013) and program R 3.2.5 (R Core Team 2016) with the R2jags package (Su and Yajima 2015) to test for changes in occupancy of wolf packs in southwestern Alberta. We allowed both parameterizations of the model to account for false-positive detections in the data (Miller et al. 2011); based on initial model results, we refit the models assuming no false-positive detections in the data (Table 2). We then tested the effects of environmental, management, and detection effort on abundance and distribution of packs using the best performing parameterization of the model (Table 2, 3). We tested covariates on detection probability, allowing detection probability to vary by survey method, and then used the best supported model for detection probability to test hypothesized effects of covariates on occupancy. We retained only models that successfully converged to compute the Watanabe-Akaike information criteria (or Widely Applicable Information Criteria; WAIC) for model comparison and selection (Watanabe 2010; Gelman et al. 2014; Hooten and Hobbs 2015) using the loo package (Vehtari et al. 2016). We considered models within 10 ΔWAIC and considered covariates in each model supported if the 95% credible interval (CRI) posterior distributions did not include 0 (Kéry 2010). We ran 3 independent chains of 300,000 Markov chain Monte Carlo iterations, discarding the first 150,000 iterations, with a thinning rate of 4 for all models.

Estimating Mean Pack Size and Turnover of Packs

We estimated number of packs and abundance of wolves for each year based on area occupied and the mean territory and pack size in southwestern Alberta (MFWP 2014). We assumed mean territory size was 1,000 km^2, minimal overlap between territories, and territory and pack size did not change per year (Rich et al. 2013, Ausband et al. 2014). We use the lme4 package (Bates et al. 2015) in Program R (R Core Team 2016) to estimate mean pack size based on the number of unique individuals genetically assigned to packs in southwestern Alberta each year. Following methods described by Stansbury et al. (2016), we assigned an individual to a putative pack if it was sampled at ≥ 1 common locations with other wolves and STRUCTURE (Pritchard et al. 2000) analyses estimated it shared common ancestry ($q \geq 0.7$) with wolves it was sampled with, or ML-RELATE (Kalinowski et al. 2006) analyses estimated it was related to ≥ 50% of the wolves it was sampled with at the parent-offspring or full-sibling ($r \geq 0.5$) level. If an individual did not meet the genetic requirements but was sampled at ≥ 1 common locations with other wolves it was also assigned to the pack. We compared putative pack assignments to pack pedigree analyses (Ausband 2015) to evaluate pack membership for each pack in each year and determined if whole pack turnover occurred (i.e., entirely new individuals assigning to a pack each year). We only considered packs in years when the active rendezvous site was detected (i.e., did not include partially sampled packs).

RESULTS

Rendezvous Site and Hunter Surveys

We surveyed 1,042 predicted rendezvous sites in southwestern Alberta from 2012–2014 (mean = 347, SD = 64). We located 15 active rendezvous sites and collected 1,709 genetic samples (Table 4). The majority (85%) of the genetic samples were collected in active rendezvous sites. We identified 129 unique genotypes, 20 of which we genetically recaptured ≥ 2 times across years. On average we identified 53 (SD = 21) unique wolves per year (Table 4).

We received 8,327 responses to our hunter surveys, 2012–2014 (mean = 2776 hunters/year, SD = 518; Table 4). Of those responses, 762 hunters reported seeing ≥ 2 live wolves during the ungulate hunting season, 2012–2014 (mean = 254 hunters/year, SD = 97).

Forty-nine hunter observations of ≥ 2 live wolves did not provide adequate data for analyses and were excluded. Between 10 and 15% of the reported observations of wolves were made on private land, 2012–2014.

Occupancy Models

Precision of model estimates and convergence success indicated the single season parameterization of models best described occupancy of wolf packs in southwestern Alberta (Table 2). The dynamic parameterization of the model did not fit our data as well as the single-season parametrizations. Model estimates were more variable than single-season estimates and precision of transition probabilities (e.g., colonization) were highly variable. Dynamic models indicated the mean probability an unoccupied sample unit would become occupied (i.e., colonization) was low whereas the mean probability an occupied sample unit remained occupied the next year (i.e., patch survival) was high (Table 2).

The probability of detecting a wolf pack was generally consistent across years and increased with harvest intensity (Table 5, 6). We were more likely to detect a wolf pack through rendezvous site surveys than hunter surveys (Table 5). The mean probability of falsely detecting a wolf pack in an unoccupied sample unit was 0.00 (annual 95% CRIs ranged 0.00–0.03) when false-positives detections were accounted for in the single season occupancy model (Table 2). The mean probability of falsely detecting a wolf pack in an unoccupied sample unit ranged 0.00–0.02 over the 3-year study period when false-positives detections were accounted for in the dynamic model (Table 2).

The mean annual probability a sample unit was occupied by a wolf pack (i.e., occupancy) ranged 0.72–0.74 over the 3-year study period (Table 5). Probabilities of occupancy were generally highest in the north and through the center of the study area where the Rocky

Mountains transition into foothills (Fig. 2). The estimated distribution of wolf packs was consistent over time, with little variation in the probability of occupancy for individual sample units, 2012–2014 (Fig. 2; Table 5, 6). On average, we estimated 23.41 (95% CRI: 20.32–26.34) wolf packs occupied approximately 23,406 km^2 (95% CRI: 20,322–26,338 km^2) each year in southwestern Alberta. Pack size averaged 6.76 (95% Confidence Interval [CI]: 5.53–9.45) wolves across years. Based on the estimated number of packs and mean pack size, we estimated 160 (95% CRI: 123–186), 156 (95% CRI: 126–183), and 160 (95% CRI: 129–187) wolves occupied southwestern Alberta in 2012, 2013, and 2014, respectively. The top model indicated the probability a sample unit was occupied by a wolf pack was positively related to forest cover and the probability of detecting a wolf pack with either survey method was positively related to harvest intensity (Table 6).

We detected few instances of whole-pack turnover but frequent turnover of individuals within 3 different packs sampled consecutive years, based on genetic analyses. We detected turnover in 1 pack when a group of wolves (n = 12) were genetically sampled in 2012 but not detected genetically again while an entirely new group of wolves (n = 9) were detected in the same area the next year. We detected turnover of breeders in 6 pack-years; dispersers from other packs replaced 4 breeders, a subordinate pack member replaced 1 breeder, and 1 breeder's replacement was unknown but the pack successfully reproduced that year.

DISCUSSION

Harvest of wolves has been a common management practice in the Canadian Rocky Mountains (Gunson 1991, Boitani 2003, Robichaud and Boyce 2010, Webb et al. 2011), but the relationship between harvest and dynamics of pack occurrence was unclear. Harvest may lead to frequent changes in abundance and distribution of packs which may affect demography (Jędrzejewska et al. 1996, Haber 1996) or the ability of managers to monitor packs, meet population objectives for wolves, set harvest regulations, and reduce conflicts with livestock. Understanding the frequency of turnover and the relative effect of harvest on pack occurrence will therefore allow managers to evaluate the efficacy of harvest and inform decisions for wolf management.

We found little evidence occupancy of wolf packs changed frequently in southwestern Alberta, thus we rejected our hypothesis that the abundance and distribution of packs was highly dynamic in a heavily harvested population of wolves. Despite intensive harvest occurring during our study (mean = 114.75 harvested wolves reported per year, SD = 56.94) we found there was a low probability the occupancy state of an individual sample unit changed over time. In addition, most packs genetically sampled during consecutive years persisted even when some individuals were likely lost to harvest. Because turnover of packs occurred infrequently during our study, we could not reject our hypothesis that abundance and distribution of packs would remain generally stable in a harvested population of wolves.

Contrary to expectations, our best supported models did not include harvest on occupancy. Models that did include harvest suggested a weak negative relationship between harvest intensity and occupancy of wolf packs but this relationship was uncertain (95% CRIs contained 0 and models converged poorly). This suggests that public harvest had little influence on the abundance or distribution of wolf packs in southwestern Alberta. Human density and anthropogenic disturbances (e.g., road or building density) have been negatively associated with habitat selection and use by wolves at fine spatiotemporal scales (i.e., within kilometers or hours; Whittington et al. 2005, Hebblewhite and Merrill 2008, Llaneza et al. 2012) but our results suggest human activity, specifically public harvest, may not be strong enough to influence occurrence of wolf packs in southwestern Alberta over several years. In addition, most packs likely experienced some harvest mortality each year (Webb et al. 2011); if harvest was not heavy enough to frequently remove or dissolve packs, packs likely persisted because surviving members could maintain their territories. Alternatively, if harvest generally targeted dispersing wolves over residents (Peterson et al. 1984, Person and Russell 2008) harvest of wolves may have had relatively little effect on established packs.

Even under heavy harvest management, environmental factors had a stronger influence than harvest on the distribution and abundance of wolf packs in southwestern Alberta. Similar to Rich et al. (2013), we found forest cover was positively associated with the probability of occupancy. High forest cover may provide security habitat for wolves inhabiting human-dominated landscapes (Llaneza et al. 2012) and may be associated with the distribution of wild prey (Llaneza et al. 2012, Kittle et al. 2015) in southwestern Alberta. Prey availability generally determines wolf distribution and densities (Fuller 1989, Boitani 2003, Fuller et al. 2003) and was strongly predictive of wolf occupancy in Idaho and Montana (Rich et al. 2013, Ausband et al. 2014). We were unable to estimate prey density or distribution in southwestern Alberta but research in the U.S. Rocky Mountains found elk (*Cervus elaphus*) selected for forests and shrublands over grasslands as snowpack decreased (Proffitt et al. 2011); wild ungulates may prefer forested habitats to grasslands and agricultural lands during summer and fall in southwestern Alberta. In addition, previous research documented wild prey densities were highest at lower elevations in the foothills of west central Alberta (Webb 2009) which corresponded with the highest probabilities of occupancy in our study.

Once harvest reaches a certain intensity however, logically it should have a strong negative effect on the occurrence of wolf packs (Ballard et al. 1987). Thus, at some point the relative effect of harvest should become more important for determining the abundance and distribution of packs than our results suggest. This may be particularly true for colonizing populations and ones on the edge of their range that are at low densities or poorly connected to other populations (Fuller et al. 2003, Brainerd et al. 2008). Comparing packs in southwestern Alberta to ones in Idaho and Montana may illustrate this relationship between harvest and connectivity. Wolves in southwestern Alberta exist on the eastern edge of wolf distribution in the Canadian Rocky Mountains (Gunson 1991, Boitani 2003) but were genetically connected to wolves in British Columbia (Cullingham et al. 2016) and likely northern Alberta (Gunson 1991). Although we found little evidence of long-distance immigration into this region (Chapter 1), short-distance dispersal from nearby packs outside our study area likely occurred, thus promoting pack persistence in southwestern Alberta. Conversely, wolves in Idaho and Montana are part of a relatively isolated, peninsular population (USFWS 2016). Anecdotal evidence suggests numerous packs in central Idaho, for example, have dissolved since harvest was initiated but some territories were not recolonized and remain unoccupied (IDFG 2012, 2016). Because this population is not as well connected to others, metapopulation theory suggests harvest may have a stronger negative effect on the abundance and distribution of packs in Idaho and Montana than what we observed in southwestern Alberta (Levins 1969, Hanski 1991).

Harvest appeared to have a stronger effect on turnover of individuals within packs (Webb et al. 2011) compared to turnover of entire packs. We genetically identified 129 unique wolves in the southern half of our study area but recaptured only 20 in more than 1 year and only 4 in all 3 years; hunters and trappers reported harvesting 71 wolves in the same area during our study. We observed frequent turnover of breeders in packs genetically sampled consecutive years and packs appeared more receptive to adopting nonbreeding adults than in other portions of the Rocky Mountains (Chapter 1). Although frequent breeder loss may lead to pack dissolution (Brainerd et al. 2008) we found little evidence of this in southwestern Alberta, and we hypothesize rapid replacement of breeding adults may explain how packs appeared to persist despite frequent turnover of individuals. Most breeding adults were replaced by local dispersers or by an individual within the pack. In addition, most harvest coincided with the breeding season and the pulse in dispersal typical for wolves in the Rocky Mountains (i.e., late winter – early spring; Mech and Boitani 2003, Webb et al. 2011, Jimenez et al. 2017). Replacement of breeding adults can occur rapidly under these conditions (Rothman and Mech 1979, Fritts and Mech 1981, Stahler et al. 2002, Mech and Boitani 2003), thus breeder turnover may have occurred quickly, preventing the destabilizing effects of breeder loss on the pack (Ballard et al. 1987). This also demonstrates pack stability and occupancy were generally maintained from within the population, contrary to the hypothesis that harvested populations of wolves are often sustained by immigrants dispersing into the population (Ballard et al. 1987, Haight et al. 1998, Hayes and Harestad 2000, Fuller et al. 2003).

Interestingly, we found detection probability was positively associated with harvest of wolves. Contrary to concerns that harvest may reduce density (Gasaway et al. 1983, Fuller 1989) or influence behaviors (Gunson 1992, Webb et al. 2009) of wolves to the point that detecting wolf packs was more difficult than in unharvested populations, we found detection probability was highest in areas where heavy harvest occurred. We hypothesize that this is because harvest intensity may be positively associated with density of wolves. Because abundance can strongly affect detection probability (Royle and Nichols 2003, MacKenzie et al. 2006), surveys may be more likely to detect wolf packs in sample units where wolf densities, and associated harvest intensity, are highest. Alternatively, we hypothesize harvest intensity may reflect areas of higher quality habitat that attract wolves regardless of mortality risk (i.e., attractive sinks; Delibes et al.

2001, Novaro et al. 2005). Even if harvest removes a high proportion of wolves in these areas, dispersers may quickly backfill and maintain local wolf densities enough that the probability surveys will detect wolves is still high.

Occupancy models have been shown to be suitable for monitoring the abundance and distribution of wolves (Ausband et al. 2014), even in harvested populations. We found harvest did not affect our ability to detect wolf packs and survey methods yielded sufficient detection data to estimate the annual abundance and distribution of wolf packs in southwestern Alberta.

We made several assumptions in our study that, if violated, could have affected our ability to detect turnover or evaluate the influence of harvest on the occurrence of packs. We assumed we would be able to detect turnover of packs using occupancy models. If a wolf pack recolonized a vacant territory faster than the rate at which sampling occurred (i.e., rescue effect; Brown and Kodrick-Brown 1977), sample units would appear continuously occupied over time and we would have failed to detect turnover of packs. We detected one instance of whole-pack turnover with genetic analyses that was not detected by the occupancy models; the time within or between primary periods may be biologically irrelevant in a heavily harvested population of wolves and unsuitable for testing our hypotheses about turnover of packs. Genetic analyses and occupancy model estimates were generally consistent, however; thus, the data suggest occupancy was generally stable during our study. We also assumed the number of wolves reported harvested by hunters and trappers accurately reflected harvest in southwestern Alberta. Because not all public harvest of wolves was reported (Gunson 1992, Robichaud and Boyce 2010, Webb et al. 2011) and was reported by WMU (not precise harvest locations; AEP), our estimated intensity of wolf harvest may have biased the estimated relationships between harvest, occupancy, and detection of wolves. Previous research and documentation of wolf distribution and harvest in this region (Robichaud and Boyce 2010, Webb et al. 2011), however, suggest the estimated relationships are reasonable.

MANAGEMENT IMPLICATIONS

Understanding whether harvest affects pack occupancy and turnover can help managers evaluate whether monitoring is accurately tracking population trends, thus providing reliable information necessary for meeting population objective, managing depredations, and setting harvest regulations. Our results suggest that heavy harvest is unlikely to have strong effects on the abundance and distribution of wolf packs when populations are well-connected, but might in peninsular populations. Harvest does appear to strongly influence turnover of individuals within packs but local dispersal may stabilize pack dynamics and occupancy. Annual monitoring using occupancy models is reliable for estimating the number and distribution of wolf packs at broad spatial scales, even in harvested populations of wolves, but may not be reliable for estimating the frequency of turnover of packs if changes in occupancy occur faster than an annual time-step. If managers are interested in monitoring turnover of packs in heavily harvested populations of wolves we recommend reducing the duration of time between primary sampling periods to increase the likelihood of observing changes in occupancy probabilities, if they occur.

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LITERATURE CITED

Agriculture and Agri-Food Canada. 2011. Interpolated census of agriculture to soil landscapes of Canada v3.0 and water survey of Canada sub-sub drainage areas v5.0. National Land and Water Information Service. Ontario, Canada.

Alberta Government. 2014. 2014 Alberta guide to hunting rgulations. <http://albertaregulations.ca/2014-Alberta-Hunting-Regulations.pdf >. Accessed 14 Jan 2015.

Ausband, D. E. 2015. Groups and mortality: their effects on cooperative behavior and population growth in a social carnivore. Dissertation, University of Montana, Missoula, USA.

Ausband, D. E. 2016. Gray wolf harvest in Idaho. Wildlife Society Bulletin 40:500–505.

Ausband, D. E., and S. B. Bassing. 2015. Final Report for testing monitoring techniques for wolves in southwest Alberta. Montana Cooperative Wildlife Research Unit, Missoula, Montana, USA.

Ausband, D. E., and M. S. Mitchell. 2011. A habitat model for predicting gray wolf rendezvous site locations in southwest Alberta. Montana Cooperative Wildlife Research Unit, Missoula, Montana, USA.

Ausband, D., M. Mitchell, K. Doherty, P. Zager, C. Mack, and J. Holyan. 2010. Surveying Predicted Rendezvous Sites to Monitor Gray Wolf Populations. Journal of Wildlife

Management 74:1043–1049.

Ausband, D. E., L. N. Rich, E. M. Glenn, M. S. Mitchell, P. Zager, D. A. W. Miller, L. P. Waits, B. B. Ackerman, and C. M. Mack. 2014. Monitoring Gray Wolf Populations Using Multiple Survey Methods. The Journal of Wildlife Management 78:335–346.

Ausband, D. E., C. R. Stansbury, J. L. Stenglein, J. L. Struthers, and L. P. Waits. 2015. Recruitment in a social carnivore before and after harvest. Animal Conservation 18:415–423.

Bates D., M. Maechler, B. Bolker, and S. Walker. 2015. Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67:1–48.

Ballard, W. B., J. S. Whitman, and C. L. Gardner. 1987. Ecology of an exploited wolf population in South-Central Alaska. Wildlife Monographs 1–54.

Boitani, L. 2003. Wolf conservation and recovery. Pages 317 – 340 *in* L. D. Mech and L. Boitani, editors. Wolves: behavior, ecology, and concervation. The University of Chicago Press. Illinois, USA.

Bjorge, R. R., and J. R. Gunson. 1985. Evaluation of wolf control to reduce cattle predation in Alberta. Journal of Range Management 38:483–487.

Bradley, E. H., H. S. Robinson, E. E. Bangs, K. Kunkel, M. D. Jimenez, J. A. Gude, and T. Grimm. 2015. Effects of wolf removal on livestock depredation recurrence and wolf recovery in Montana, Idaho, and Wyoming. The Journal of Wildlife Management 79:1337–1346.

Brainerd, S. M., H. Andren, E. E. Bangs, E. H. Bradley, J. A. Fontaine, W. Hall, Y. Iliopoulos, M. D. Jimenez, E. a Jozwiak, O. Liberg, C. M. Mack, T. J. Meier, C. C. Niemeyer, H. C. Pedersen, H. Sand, R. N. Schultz, D. W. Smith, P. Wabakken, and A. P. Wydeven. 2008.

The effects of breeder loss on wolves. Journal of Wildlife Management 72:89–98.

Brown, J. H. J. H., and A. Kodric-Brown. 1977. Turnover rates in insular biogeography: effect of immigration on extinction. Ecology 58:445–449.

Cullingham, C. I., C. D. Thiessen, A. E. Derocher, P. C. Paquet, J. M. Miller, J. A. Hamilton, and D. W. Coltman. 2016. Population structure and dispersal of wolves (*Canis lupus*) in the Canadian Rocky Mountains. Journal of Mammalogy 97:839–851.

De Barba, M., J. R. Adams, C. S. Goldberg, C. R. Stansbury, D. Arias, R. Cisneros, and L. P. Waits. 2014. Molecular species identification for multiple carnivores. Conservation Genetics Resources 6:821–824.

Delibes, M., P. Gaona, and P. Ferreras. 2001. Effects of an Attractive Sink Leading into Maladaptive Habitat Selection. The American Naturalist 158:277–285.

Desserud, P., C. C. Gates, B. Adams, and R. D. Revel. 2010. Restoration of foothills rough fescue grassland following pipeline disturbance in Southwestern Alberta. Journal of Environmental Management 91:2763–2770.

Frantzen, M. A., J. B. Silk, J. W. Ferguson, R. K. Wayne, and M. H. Kohn. 1998. Empirical evaluation of preservation methods for faecal DNA. Molecular Ecology 7:1423–1428.

Fritts, S. H., and L. D. Mech. 1981. Dynamics, movements, and feeding ecology of a newly protected wolf population in northwestern Minnesota. Wildlife Monographs 80:1–79.

Fuller, T. K. 1989. Population dynamics of wolves in north-central Minnesota. Wildlife Monographs 105:1–41.

Fuller, T. K., L. D. Mech, and J. F. Cochrane. 2003. Wolf population dynamics. Pages 161–191 *in* L. D. Mech and L. Boitani, editors. Wolves: behavior, ecology, and concervation. The University of Chicago Press. Illinois, USA.

Gasaway, W. C., R. O. Stephenson, J. L. Davis, P. E. K. Shepherd, and O. E. Burris. 1983. Interrelationships of wolves, prey, and man in interior Alaska. Wildlife Monographs 84:1–50.

Gelman, A., J. Hwang, and A. Vehtari. 2014. Understanding predictive information criteria for Bayesian models. Statistics and Computing 24:997–1016.

Ginsberg, J. R., and E. J. Milner-Gulland. 1994. Sex-biased harvesting and population dynamics in ungulates: implications for conservation and sustainable use. Conservation Biology 8:157–166.

Grewal, S. K., P. J. Wilson, T. K. Kung, K. Shami, M. T. Theberge, J. B. Theberge, and B. N. White. 2004. A genetic assessment of the eastern wolf (*Canis lycaon*) in Algonquin Provincial Park. Journal of Mammalogy 85:625–632.

Gunson, J. R. 1991. Management plan for wolves in Alberta. Forestry, Lands and Wildlife, Fish and Wildlife Devision. Edmonton, Alberta, Canada.

Gunson, J. R. 1992. Historical and present management of wolves in Alberta. Wildlife Society Bulletin 20:330–339.

Haber, G. C. 1996. Biological, Conservation, and Ethical Implications of Exploiting and Controlling Wolves. Conservation Biology 10:1068–1081.

Haight, R. G., D. J. Mladenoff, and A. P. Wydeven. 1998. Modeling disjunct wolf populations in semi-wild landscapes. Conservation Biology 12:879–888.

Harper, E., W. J. Paul, L. D. Mech, and S. Weisberg. 2008. Effectiveness of lethal, directed wolf-depredation control in Minnesota. The Journal of Wildlife Management 72:778–784.

Hayes, R. D., A. M. Baer, and D. G. Larsen. 1991. Population dynamics and prey relationships of an exploited and recovering wolf population in the southern Yukon. Fish and Wildlife

Branch, Department of Renewable Resources, Final Report TR-91-1, Yukon Territory, Canada.

Hayes, R. D., and A. S. Harestad. 2000. Demography of a recovering wolf population in the Yukon. Canadian Journal of Zoology 78:36–48.

Hebblewhite, M. 2006. Linking predation risk and forage to ungulate population dynamics. Dissertation, University of Alberta. Edmonton, Canada.

Hebblewhite, M., and E. Merrill. 2008. Modelling wildlife-human relationships for social species with mixed-effects resource selection models. Journal of Applied Ecology 45:834–844.

Hooten, M. B., and N. T. Hobbs. 2015. A guide to Bayesian model selection for ecologists. Ecological Monographs 85:3–28.

Idaho Department of Fish and Game [IDFG] and Nez Perce Tribe. 2012. 2011 Idaho wolf monitoring progress report. Idaho Department of Fish and Game, Boise, Idaho, USA.

Idaho Department of Fish and Game [IDFG]. 2015. 2014 Idaho wolf monitoring progress Report. Idaho Department of Fish and Game, Boise, Idaho, USA.

Idaho Department of Fish and Game [IDFG]. 2016. 2015 Idaho wolf monitoring progress report. Idaho Department of Fish and Game. Idaho Department of Fish and Game, Boise, Idaho, USA.

Jędrzejewska, B., W. Jędrzejewski, A. N. Bunevich, L. Milkowski, and H. Okarma. 1996. Population dynamics of wolves Canis lupus in Bialowieza primeval forest (Poland and Belarus) in relation to hunting by humans, 1847-1993. Mammal Review 26:103–126.

Jędrzejewski, W., W. Branicki, C. Veit, I. MeĐugorac, M. Pilot, A. N. Bunevich, B. Jędrzejewska, K. Schmidt, J. Theuerkauf, H. Okarma, R. Gula, L. Szymura, and M. Förster. 2005. Genetic diversity and relatedness within packs in an intensely hunted population of wolves Canis lupus. Acta Theriologica 50:3–22.

Jimenez, M. D., E. E. Bangs, D. K. Boyd, D. W. Smith, S. A. Becker, D. E. Ausband, S. P. Woodruff, E. H. Bradley, J. Holyan, and K. Laudon. 2017. Wolf dispersal in the rocky mountains, western United States: 1993-2008. The Journal of Wildlife Management DOI: 10.1002/jwmg.21238.

Kalinowski, S. T., A. P. Wagner, and M. L. Taper. 2006. ML-RELATE: A computer program for maximum likelihood estimation of relatedness and relationship. Molecular Ecology Notes 6:576–579.

Kéry, M. and M. Schaub. 2012. Bayesian population analysis using WinBUGS: a hierarchical perspective. Academic Press. Waltham, Massachusetts, USA.

Kéry, M. 2010. Introduction to Win BUGS for Ecologists. A Bayesian approach to regression, ANOVA, mixed models and related analyses. Academic Press. Burlington, Massachusetts, USA.

Kittle, A. M., M. Anderson, T. Avgar, J. A. Baker, G. S. Brown, J. Hagens, E. Iwachewski, S. Moffatt, A. Mosser, B. R. Patterson, D. E. B. Reid, A. R. Rodgers, J. Shuter, G. M. Street, I. D. Thompson, L. M. Vander Vennen, and J. M. Fryxell. 2015. Wolves adapt territory size, not pack size to local habitat quality. Journal of Animal Ecology 84:1177–1186.

Knowlton, F. F. 1972. Preliminary interpretations of coyote population mechanics with some management implications. The Journal of Wildlife Management 36:369–382.

Larivière, S., H. Jolicoeur, and M. Crete. 2000. Status and conservation of the gray wolf (*Canis lupus*) in wildlife reserves of Quebec. Biological Conservation 94:143–151.

Levins, R. 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. Bulletin of the Entomological Society of America 15:237–240.

Llaneza, L., J. V. Lopez-Bao, and V. Sazatornil. 2012. Insights into wolf presence in human-dominated landscapes: The relative role of food availability, humans and landscape attributes. Diversity and Distributions 18:459–469.

Mackenzie, D. I., J. D. Nichols, J. E. Hines, M. G. Knutson, and A. B. Franklin. 2003. Estimating occupancy, colonisation, and local extinction when a species is detected imperfectly. Ecology 84:2200–2207.

MacKenzie, D. I., J. D. Nichols, G. B. Lachman, S. Droege, J. Andrew Royle, and C. A. Langtimm. 2002. Estimating site occupancy rates when detection probabilities are less Than one. Ecology 83:2248–2255.

Mackenzie, D. I., J. D. Nichols, J. A. Royle, K. H. Pollock, L. L. Bailey, and J. E. Hines. 2006. Occupancy estimation and modeling: inferring patterns and dynamics of species occurrence. Academic Press. Burlington, Massachusetts, USA.

Mech, L. D., and L. Boitani. 2003. Wolf social ecology. Pages 1–34 *in* L. D. Mech and L. Boitani, editors. Wolves: behavior, ecology, and concervation. The University of Chicago Press. Illinois, USA.

Meier, T. J., J. W. Burch, J. D. Mech, and L. G. Adams. 1995. Pack structure and genetic relatedness among wolf packs in a naturally-regulated population. Pages 293–302 *in* L. N. Carbyn, S. H. Fritts, D. R. Seip, editors. Ecology and conservation of wolves in a changing world. Canadian Circumpolar Institude, Edmonton, Canada.

Montana Fish, Wildlife and Parks [MFWP]. 2010. Montana gray wolf conservation and management 2009 annual report. Montana Fish, Wildlife and Parks, Helena, Montana, USA.

Montana Fish, Wildlife and Parks [MFWP]. 2014. Montana gray wolf conservation and management 2013 annual report. Montana Fish, Wildlife and Parks, Helena, Montana, USA.

Montana Fish, Wildlife and Parks [MFWP]. 2015*a*. Montana gray wolf conservation and management 2015 annual report. Montana Fish, Wildlife and Parks, Helena, Montana, USA.

Montana Fish, Wildlife and Parks [MFWP]. 2015*b*. 2015 Montana Wolf Harvest Report. Montana Fish, Wildlife and Parks, Helena, Montana, USA.

Miller, C. R., P. Joyce, and L. P. Waits. 2002. Assessing allelic dropout and genotyping reliability using maximum likelihood. Genetics 160:357–249.

Miller, D. A., J. D. Nichols, B. T. McClintock, E. H. C. Grant, L. L. Bailey, and L. A. Weir. 2011. Improving occupancy estimation when two types of observational error occur : non-detection and species misidentification. Ecology 92:1422–1428.

Miller, D. A., J. D. Nichols, J. A. Gude, L. N. Rich, K. M. Podruzny, J. E. Hines, and M. S. Mitchell. 2013. Determining occurrence dynamics when false positives occur: Estimating the range dynamics of wolves from public survey data. Plos One 8:e65808.

Mills, L. S. 2012. Conservation of wildlife populations: demography, genetics, and management. Second edition. Wiley-Blackwell. West Sussex, UK.

Milner, J. M., E. B. Nilsen, and H. P. Andreassen. 2007. Demographic side effects of selective hunting in ungulates and carnivores. Conservation Biology 21:36–47.

Natural Regions Committee. 2006. Natural regions and subregions of Alberta. Compiled by D.J. Downing and W.W. Pettapiece. Government of Alberta. Pub. No. I/005. Edmonton, Alberta, Canada.

Novaro, A. J., M. C. Funes, and R. S. Walker. 2005. An empirical test of source-sink dynamics induced by hunting. Journal of Applied Ecology 42:910–920.

Peakall, R., and P. E. Smouse, 2006. GENALEX 6: genetic analysis in Excel. Population genetic software for teaching and research. Molecular Ecology 6:288–295.

Peakall, R., and P. E. Smouse. 2012. GenALEx 6.5: Genetic analysis in Excel. Population genetic software for teaching and research-an update. Bioinformatics 28:2537–2539.

Hanski, I. 1991. Single-species metapopulation dynamics: concepts, models and observations. Biological Journal of the Linnean Society 42:17–38.

Person, D. K., and A. L. Russell. 2008. Correlates of mortality in an exploited wolf population. The Journal of Wildlife Management 72:1540–1549.

Peterson, R. O., J. D. Woolington, and T. N. Bailey. 1984. Wolves of the Kenai Peninsula, Alaska. Wildlife Monographs 88:1–52.

Plummer, M. 2013. JAGS Version 3.4.0 user manual. 1–41.

Pritchard, J. K., M. Stephens, and P. Donnelly. 2000. Inference of population structure using multilocus genotype data. Genetics 155:945–959.

Proffitt, K. M., J. A. Gude, K. L. Hamlin, R. A. Garrott, J. A. Cunningham, and J. L. Grigg. 2011. Elk distribution and spatial overlap with livestock during the brucellosis transmission risk period. Journal of Applied Ecology 48:471–478.

R Core Team. 2016. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rich, L. N., R. E. Russell, E. M. Glenn, M. S. Mitchell, J. A. Gude, K. M. Podruzny, C. A. Sime, K. Laudon, D. E. Ausband, and J. D. Nichols. 2013. Estimating occupancy and predicting numbers of gray wolf packs in montana using hunter surveys. Journal of Wildlife Management 77:1280–1289.

Robichaud, C. B., and M. S. Boyce. 2010. Spatial and temporal patterns of wolf harvest on registered traplines in Alberta, Canada. Journal of Wildlife Management 74:635–643.

Rothman, R. J., and L. D. Mech. 1979. Scent-marking in lone wolves and newly formed pairs. Animal Behaviour 27:750–760.

Royle, J. A., and M. Kéry. 2007. A Bayesian state-space formulation of dynamic occupancy models. Ecology 88:1813–1823.

Royle, J. A., and W. A. Link. 2006. Generalized site occupancy models allowing for flase positive and false negative errors. Ecology 87:835–841.

Royle, J. A., and J. D. Nichols. 2003. Estimating abundance from repeated presence–absence data or point counts. Ecology 84:777–790.

Rutledge, L. Y., B. R. Patterson, K. J. Mills, K. M. Loveless, D. L. Murray, and B. N. White. 2010. Protection from harvesting restores the natural social structure of eastern wolf packs. Biological Conservation 143:332–339.

Smith, D. W., P. J. White, D. R. Stahler, A. Wydeven, and D. E. Hallac. 2016. Managing wolves in the Yellowstone area: Balancing goals across jurisdictional boundaries. Wildlife Society Bulletin 40:436–445.

Stahler, D. R., D. W. Smith, and R. Landis. 2002. The acceptance of a new breeding male into a wild wolf pack. Canadian Journal of Zoology 80:360-365.

Stansbury, C. R., D. E. Ausband, P. Zager, C. M. Mack, C. R. Miller, M. W. Pennell, and L. P. Waits. 2014. A long-term population monitoring approach for a wide-ranging carnivore: Noninvasive genetic sampling of gray wolf rendezvous sites in Idaho, USA. Journal of Wildlife Management 78:1040–1049.

Stansbury, C. R., D. E. Ausband, P. Zager, C. M. Mack, and L. P. Waits. 2016. Identifying gray wolf packs and dispersers using noninvasive genetic samples. The Journal of Wildlife Management 80:1408–1419.

Stenglein, J. L., M. De Barba, D. E. Ausband, and L. P. Waits. 2010*a*. Impacts of sampling location within a faeces on DNA quality in two carnivore species. Molecular Ecology Resources 10:109–114.

Stenglein, J. L., L. P. Waits, D. E. Ausband, P. Zager, and C. M. Mack. 2010*b*. Efficient, noninvasive genetic sampling for monitoring reintroduced wolves. Journal of Wildlife Management 74:1050–1058.

Stenglein, J. L., L. P. Waits, D. E. Ausband, P. Zager, and C. M. Mack. 2011. Estimating gray wolf pack size and family relationships using noninvasive genetic sampling at rendezvous sites. Journal of Mammalogy 92:784–795.

Su, Y.S. and M. Yajima. 2015. R2jags: A Package for Running JAGS from R. R package version 0.03-06. <http://CRAN.R-project.org/package=R2jags>.

U.S. Fish and Wildlife Service [USFWS]. 2009. Endangered and threatened wildlife and plants; final rule to identify the northern Rocky Mountain population of gray wolf as a distinct population segment and to revise the list of Endangered and Threatened wildlife. Federal Register 74:15123–15188.

U.S. Fish and Wildlife Service [USFWS], Idaho Department of Fish and Game, Montana Fish, Wildlife & Parks, Wyoming Game and Fish Department, Nez Perce Tribe, National Park Service, Blackfeet Nation, Confederated Salish and Kootenai Tribes, Wind River Tribes, Confederated Colville Tribes, Spokane Tribe of Indians, Washington Department of Fish and Wildlife, Oregon Department of Fish and Wildlife, Utah Department of Natural Resources, and USDA Wildlife Services. 2016. Northern Rocky Mountain wolf recovery program 2015 interagency annual report. Northern Rocky Mountain Wolf Recovery Program 2015 Interagency Annual Report. M.D. Jimenez and S.A. Becker, eds. USFWS, Ecological Services, 585 Shepard Way, Helena, Montana, USA.

Vehtari, A., A. Gelman, and J. Gabry. 2016. Practical Bayesian model evaluation using leave-one-out cross-validation and WAIC. Statistics and Computing DOI 10.1007/s11222-016-9696-4.

Watanabe S. 2010. Asymptotic equivalence of Bayes cross validation and widely applicable information criterion in singular learning theory. J. ournal of Machine Learning Research 11:3571–3594.

Weaver, J. L., and S. H. Fritts. 1979. Comparison of coyote and wolf scat diameters. Journal of Wildlife Management 43:786–788.

Webb, N. F. 2009. Density, demography, and functional responses of a harvested wolf population in west-central Alberta, Canada. Dissertaion, University of Alberta, Canada.

Webb, N. F., J. R. Allen, and E. H. Merrill. 2011. Demography of a harvested population of wolves (*Canis lupus*) in west-central Alberta , Canada. Canadian Journal of Zoology 89:744–752.

Webb, N., E. Merrill, and J. Allen. 2009. Density, demography, and functional response of a harvested wolf population in West-Central Albeta, Canada. University of Alberta, Edmonton, Canada.

Whittington, J., C. C. St. Clair, and G. Mercer. 2005. Spatial responses of wolves to roads and trails in mountain valleys. Ecological Applications 15:543–553.

Williams, B. K., J. D. Nichols, M. J. Conroy. 2002. The use of models in conservation and management. Pages 223 – 242 *in* Analysis and management of animal populations. Academic Press. San Diego, California, USA.

Zuur, A. F., E. N. Ieno, and C. S. Elphick. 2010. A protocol for data exploration to avoid common statistical problems. Methods in Ecology and Evolution 1:3–14.

Figure 1. Study area of southwestern Alberta, Canada 2012–2014.

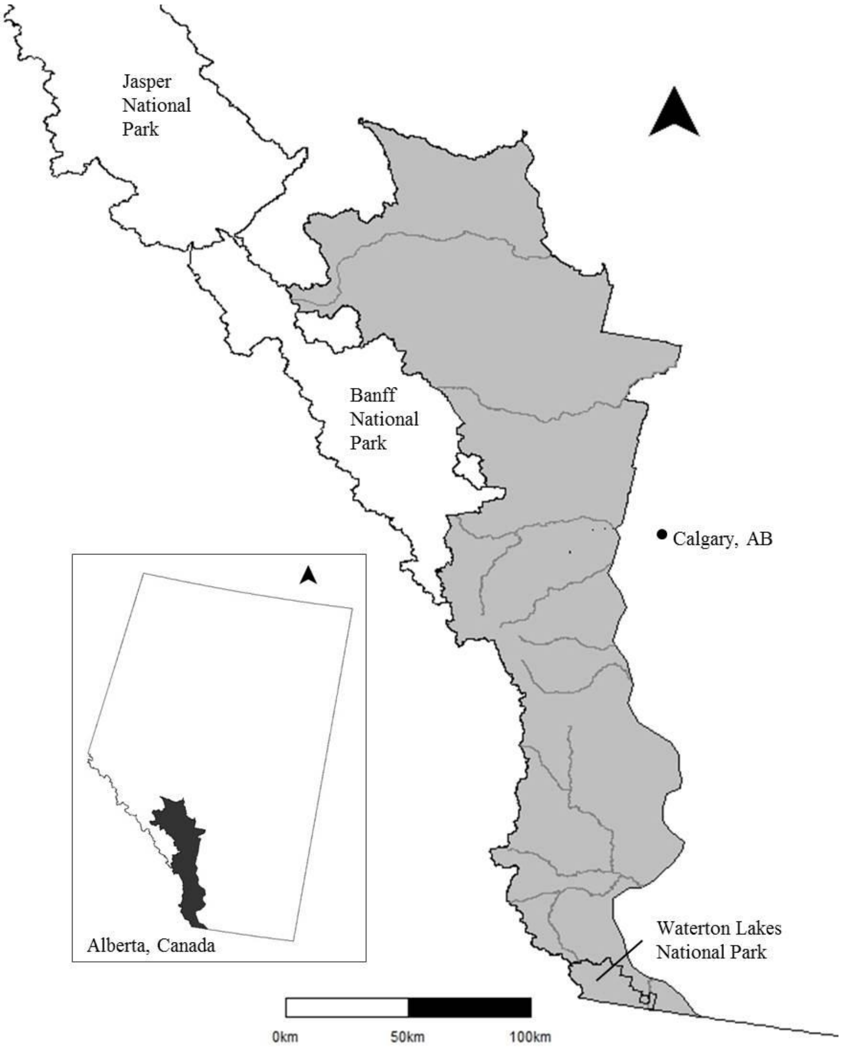

Figure 2. Distribution of the probability sample units were occupied by wolf packs in southwestern Alberta, Canada, 2012–2014. Occupancy estimates were based on a model that included the effects of forest cover on the probability of occupancy and intensity of wolf harvest on detection probabilities.

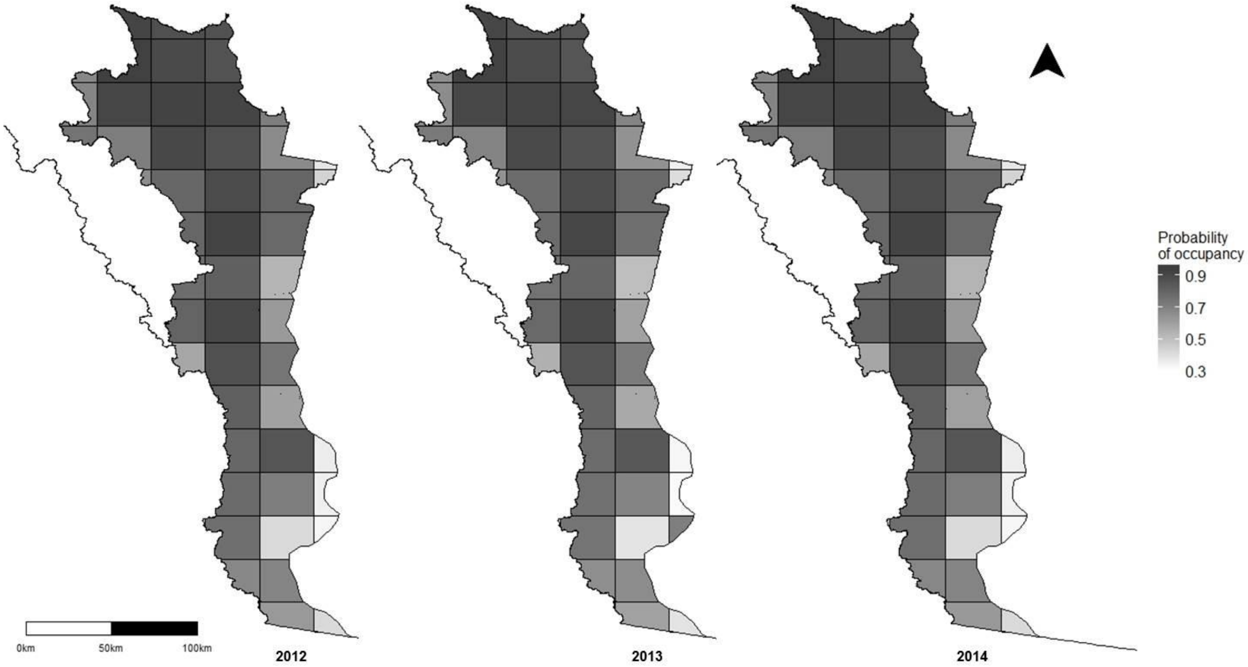

Table 1. Mean (standard error) values for covariates included in occupancy analysis of wolf packs in southwestern Alberta (2012–2014), and predicted relationships between covariates and the probability a wolf pack occupied a sample unit ($\boldsymbol{\psi}$) and was detected (p) by either noninvasive genetic or hunter surveys.

	Annual mean (SE)			Predicted relationship	
Model Covariate	2012	2013	2014	$\boldsymbol{\psi}$	p
Forest cover (%)	0.45 (0.32)	0.45 (0.23)	0.45 (0.32)	+	
Mean ruggedness (TPI)	4.39 (2.90)	4.39 (2.90)	4.39 (2.90)	–	
Wolves harvested[a]	2.23 (2.65)	2.35 (2.50)	0.47 (0.64)	–/+	–
Wolves harvested previous year[a]	2.12 (2.08)	2.23 (2.65)	2.35 (2.50)	–	–
Reported cattle density (no. cattle/km^{2b})	18.93 (31.41)	20.12 (32.00)	16.61 (24.40)	–/+	
Rendezvous sites surveyed[c]	8.40 (20.40)	6.02 (10.76)	6.40 (10.72)		+
Hunter effort (hunter days/km^2)[d]	0.54 (0.80)	0.94 (0.68)	0.96 (0.64)		+
Proportion of sample unit in study area	0.60 (0.32)	0.60 (0.32)	0.60 (0.32)		+

[a] Reported number of wolves harvested per sample unit. Values were then area-weighted and categorized as low medium, or high density.

[b] Reported cattle density was categorized as low, medium, or high density.

[c] Number of predicted rendezvous sites surveyed for noninvasive genetic observations of wolves.

[d] Number of reported days spent hunting by big game hunters, area-weighted by size of sample unit.

Table 2. Model type, parameters, and annual estimates (95% Bayesian Credible Intervals) used to test changes in abundance and distribution of wolf packs in southwestern Alberta (2012–2014), where the probabilities a sample unit was occupied, became colonization, and remained occupied (i.e, survival) by a wolf pack were estimated over time (2012–2014). We tested the probability a wolf pack was detected when not present (FP = false-positive detection) by estimating the probabilities of detecting (*p*11), falsely detecting (p10), and detecting with certainty (b) a wolf pack in each sample unit for both single-season and dynamic occupancy models.

			Estimate (95% CRI)		
Model	FP[a]	Parameter[b]	2012	2013	2014
Single	No				
		Occupancy	0.68 (0.46 – 0.89)	0.70 (0.54 – 0.84)	0.71 (0.55 – 0.86)
		Detection, gen.	0.59 (0.29 – 0.86)	0.49 (0.25 – 0.74)	0.55 (0.31 – 0.78)
		Detection, hunt	0.28 (0.12 – 0.37)	0.27 (0.21 – 0.34)	0.26 (0.20 – 0.32)
Single	Yes				
		Occupancy	0.67 (0.45 – 0.90)	0.68 (0.52 – 0.83)	0.70 (0.54 – 0.85)
		Detection (p_{11})	0.30 (0.22 – 0.39)	0.29 (0.23 – 0.35)	0.28 (0.22 – 0.34)
		Detection (p_{10})	0.01 (0.00 – 0.01)	0.00 (0.00 – 0.03)	0.00 (0.00 – 0.01)
		Detection (b)	0.57 (0.42 – 0.72)	0.56 (0.45 – 0.66)	0.62 (0.51 – 0.72)
Dynamic	No				
		Occupancy	0.88 (0.64 – 0.99)	0.64 (0.46 – 0.81)	0.68 (0.53 – 0.83)
		Colonization	0.31 (0.01 – 0.99)	0.17 (0.01 – 0.52)	–
		Survival	0.70 (0.48 – 0.92)	0.97 (0.87 – 0.99)	–

		Detection, gen.	0.51 (0.23 – 0.80)	0.60 (0.30 – 0.87)	0.63 (0.37 – 0.85)
		Detection, hunt	0.11 (0.06 – 0.16)	0.16 (0.11 – 0.21)	0.15 (0.11 – 0.20)
Dynamic	Yes				
		Occupancy	0.64 (0.44 – 0.83)	0.63 (0.47 – 0.78)	0.69 (0.55 – 0.82)
		Colonization	0.20 (0.01 – 0.55)	0.26 (0.03 – 0.53)	–
		Survival	0.87 (0.62 – 0.99)	0.94 (0.80 – 0.99)	–
		Detection (p_{11})	0.30 (0.22 – 0.39)	0.30 (0.24 – 0.37)	0.28 (0.22 – 0.33)
		Detection (p_{10})	0.00 (0.00 – 0.01)	0.02 (0.00 – 0.06)	0.00 (0.00 – 0.01)
		Detection (b)	0.57 (0.42 – 0.72)	0.58 (0.47 – 0.69)	0.62 (0.51 – 0.72)

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[a] Indicates whether we accounted for potential false-positive detections in the data.

[b] We estimated detection probability separately for different survey methods when we assumed false-positive detections did not occur. Different survey methods included: gen. = noninvasive genetic surveys for wolves, and hunt = hunter observations of live wolves made during the ungulate hunting season.

Table 3. Single-season occupancy models tested to estimate abundance and distribution of wolf packs in southwestern Alberta where $\boldsymbol{\psi}$ = occupancy, *p* = detection probability, Watanabe-Akaike information criteria (WAIC), standard error (SE) of WAIC value, and change in (Δ) WAIC. We evaluated covariate effects on detection probability and then used the most supported parameterization of detection probability to evaluate covariate effects on occupancy probability. We considered models within 10 ΔWAIC values of the top model for inference.

Parameter of interest	Model[a]		WAIC	SE	ΔWAIC
Occupancy	$\boldsymbol{\psi}$ (forest)	*p* (harvest)	232.8	1050.7	0
Occupancy	$\boldsymbol{\psi}$ (forest + harvest)	*p* (harvest)	449.4	993.2	216.6
Occupancy	$\boldsymbol{\psi}$ (lag-harvest)	*p* (harvest)	921.5	1336.8	688.7
Occupancy	$\boldsymbol{\psi}$ (harvest)	*p* (harvest)	1307.1	1188.4	1074.3
Occupancy	$\boldsymbol{\psi}$ (ruggedness)	*p* (harvest)	1313.8	1031.0	1081.0
Occupancy	$\boldsymbol{\psi}$ (livestock)	*p* (harvest)	2301.7	1733.4	2068.9
Occupancy	$\boldsymbol{\psi}$ (harvest + livestock)	*p* (harvest)	3310.6	1377.1	3077.8
Detection	$\boldsymbol{\psi}$ (.)	*p* (harvest)	442.9	1470.7	0
Detection	$\boldsymbol{\psi}$ (.)	*p* (hunter effort)	447.3	1477.6	4.4
Detection	$\boldsymbol{\psi}$ (.)	*p* (.)	520.9	1458.5	78
Detection	$\boldsymbol{\psi}$ (.)	*p* (lag-harvest)	588.3	1501.9	145.4
Detection	$\boldsymbol{\psi}$ (.)	*p* (rend. effort + hunter effort)	619.6	1502.3	176.7
Detection	$\boldsymbol{\psi}$ (.)	*p* (rend. effort)	755.4	1527.3	312.5

[a] Forest = percent forest cover; ruggedness = mean Terrain Ruggedness Index (TRI); harvest = density of reported number of wolves harvested in current year (wolves/km^2), categorized as low, medium, or high density; lag-harvest = density of reported number of wolves harvested in previous year (wolves/km^2), categorized as low, medium, or high density; livestock = density of reported livestock per year (reported cattle/km^2), categorized as low, medium, or high density; rendezvous effort = number of rendezvous sites surveyed per sample unit; hunter effort = hunter survey effort per sample unit (hunter days/km^2).

[b,c] Rendezvous effort and hunter effort were tested on respective detection parameters only.

Table 4. Results from surveys of wolf rendezvous sites and hunters for observations of wolf packs in southwestern Alberta, Canada, where the total number of predicted and active wolf rendezvous sites surveyed, unique genotypes identified from genetic samples, online responses from ungulate hunters, and observations of ≥ 2 live wolves made by hunters are reported, 2012–2014.

Year	No. sites surveyed	No. active sites detected	No. samples collected	No. unique genotypes detected	No. hunter responses[a]	No. hunter observations ≥ 2 wolves
2012	420	3	439	45	2227	189
2013	301	2	441	37	2844	372
2014	321	10	829	76	3256	408

[a] Included hunters that responded NO to question: did you hunt in the study area?.

Table 5. Estimates for the mean probabilities (95% Bayesian Credible Interval) a sample unit was occupied by a wolf pack and a wolf pack was detected through rendezvous site surveys and hunter surveys in southwestern Alberta, 2012–2014.

	Estimated probability (95% CRI)		
Year	Occupancy	Rendezvous detection	Hunter detection
2012	0.74 (0.56 – 0.89)	0.61 (0.31 – 0.86)	0.30 (0.21 – 0.40)
2013	0.72 (0.57 – 0.86)	0.53 (0.27 – 0.77)	0.27 (0.21 – 0.33)
2014	0.74 (0.59 – 0.89)	0.56 (0.32 – 0.78)	0.25 (0.19 – 0.31)

Table 6. Parameter estimates (95% Bayesian Credible Interval) for occupancy analysis of wolf packs in southwestern Alberta, 2012–2014. The model included 2 survey methods: rendezvous site surveys (Rend.) for noninvasive wolf DNA and surveys for observations of wolves made by hunters during the ungulate hunting season. We estimated annual probabilities of occupancy and detection within a single model.

		Coefficient (95 % CRI)		
Parameter	Variable	2012	2013	2014
Occupancy[a]	Intercept	1.29 (0.20 – 2.71)	1.15 (0.25 – 2.56)	1.30 (0.34 – 2.90)
	Forest cover	1.29 (0.46 – 2.30)	1.29 (0.46 – 2.30)	1.29 (0.46 – 2.30)
Detection[b]				
Rend. surveys	Intercept	0.19 (-1.14 – 1.60)	-0.17 (-1.29 – 0.95)	0.16 (-0.84 – 1.21)
	Medium harvest[c]	0.23 (-0.21 – 0.67)	0.23 (-0.21 – 0.67)	0.23 (-0.21 – 0.67)
	High harvest[c]	0.48 (-0.05 – 1.01)	0.48 (-0.05 – 1.01)	0.48 (-0.05 – 1.01)
Hunter surveys	Intercept	-1.15 (-1.66 – -0.67)	-1.32 (-1.79 – -0.89)	-1.21 (-1.57 – -0.87)
	Medium harvest[c]	0.23 (-0.21 – -0.67)	0.23 (-0.21 – 0.67)	0.23 (-0.21 – 0.67)
	High harvest[c]	0.48 (-0.05 – -1.01)	0.48 (-0.05 – 1.01)	0.48 (-0.05 – 1.01)

[a] Probability a wolf pack occupied a sample unit.

[b] Probability a wolf pack was detected in an occupied sample unit.

[c] Effect of medium and high harvest of wolves were compared to the effect of low harvest of wolves.

APPENDIX A. Sampling location data and genetic criteria used to classify wolves in central Idaho (2008–2014) and southwestern Alberta (2013–2014). Individuals were classifications as either a resident, neighbor, short-distance immigrant (SDI), or long-distance immigrant (LDI) based on sampling location (Location), pairwise relatedness estimates (Relatedness), genetic cluster analyses (Assignment), and first-generation migrant tests (Migrant test). These criteria were also used to identify an individual's most likely origin when possible. The number of individuals classified in each category are reported for wolves in central Idaho (No. Idaho) and southwestern Alberta (No. Alberta), as well as the identification number of each individual (UI ID).

Classification	Location	Relatedness[a]	Assignment[b]	Migrant test[c]	Likely origin	No. Idaho	No. Alberta[d]	UI ID[e]
Resident	Sampled with focal pack	$r \geq 0.5$	$q \geq 0.7$	$P > 0.01$ and highest probability with focal pack	Born to focal pack	285	85	
Neighbor	Not sampled with other wolves; Sampled on periphery of study area	$r < 0.5$	$q < 0.5$	$P \leq 0.01$ with focal pack and highest probability with a different local pack	Born to neighboring pack	3	0	115, 116, 209
SDI	Sampled with focal pack and/or within territory of focal pack	$r \geq 0.5$ with different local pack	$q \geq 0.7$ with different local pack	$P \leq 0.01$ with focal pack and highest probability with a different local pack	Born to different local pack	7	3	52, 61, 63, 299, 301, 371, 558, 1075, 1093
SDI	Sampled with focal	$r < 0.5$	$q < 0.5$	$P \leq 0.01$ with focal pack and	Born to neighboring pack	1	1	80, 642

	pack			highest probability with a different local pack				
SDI	Sampled with focal pack and/or within territory of focal pack	$r < 0.5$ with most of pack	$0.5 < q < 0.7$ w/ local pack	$P \leq 0.01$ with focal pack and highest probability with a different local pack or no other likely natal pack identified	Born to neighboring pack	2	0	398, 706
LDI	Sampled with focal pack and/or within territory of focal pack	$r \geq 0.5$ with pack in different study area	$q \geq 0.7$ with pack in different study area	$P > 0.01$ with pack in different study area highest probability	Born to pack in different study area	3	0	204, 279, 354
LDI	Sampled with focal pack and/or within territory of focal pack	$r < 0.5$	$q < 0.5$	$P \leq 0.01$ with focal pack and no likely alternative natal pack identified highest probability with focal pack	Unknown origin but genetically different from all packs in all study areas	3	1	207, 1058
LDI	Sampled with focal pack and/or within territory of focal pack	$r < 0.5$	$q < 0.5$	$P \leq 0.01$ with focal pack and highest probability with pack in different study area	Born to neighboring pack in different study area	9	1	106, 107, 179, 180, 203, 329, 990, 157, 158,

								1078
LDI	Sampled with focal pack and/or within territory of focal pack	$r < 0.5$	$q < 0.5$	$0.01 < P < 0.1$ and highest probability with a focal pack in a different study area	Unknown origin but genetically different from all packs in study area where it was sampled	6	0	82, 120, 121, 174, 208, 330
LDI	Sampled with focal pack and/or within territory of focal pack	$r < 0.5$	$0.5 < q < 0.7$ with pack in different study area	$P \leq 0.01$ with focal pack and highest probability with a different pack in diff. study area or no other likely natal pack identified	Born to neighboring pack in different study area	2	0	175, 173

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[a] Pairwise relatedness between an individual and others it was sampled with (r-value).

[b] Assignment probability to the pack an individual was sampled with (q-value).

[c] Probability the pack an individual was sampled with is the natal pack of that individual.

[d] Three individuals (UI ID: 630, 632, 1074) did not fit into the short-distance immigrant categories but due to sampling locations and genetic ties to other individuals that were classifiable as short-distance immigrants we included them in regression analyses.

[e] Identification numbers for residents were not included due to the large number of resident wolves detected.