Demography of a harvested population of wolves (*Canis lupus*) in west-central Alberta, Canada

N.F. Webb, J.R. Allen, and E.H. Merrill

Abstract: Wolves (*Canis lupus* L., 1758) are subject to liberal public harvests throughout most of their range in North America, yet detailed information on populations where sport harvest is the primary source of mortality are limited. We studied a harvested wolf population in west-central Alberta from 2003 to 2008. Demographic data were collected from visits to den sites, 84 collared wolves from 19 packs, and a harvest monitoring program that augmented mandatory reporting for registered traplines. Annual harvest rate of wolves was 0.34, with harvest on registered traplines (0.22 ± 0.03) being twice that of hunters (0.12 ± 0.04). Most wolves harvested (71%) were pre-reproductive. Probability of a pack breeding was 0.83 ± 0.01, litter size averaged 5.6 ±1.4, and these rates and stability of home ranges were unaffected by the number of wolves harvested. Natural mortality (0.04 ± 0.03) and dispersal rates (0.25 ± 0.04) were lower than reported for wolf populations in protected areas. Reproductive rates balanced total wolf mortality, indicating harvest was likely sustainable. We suggest that a high proportion of juveniles harvested and the spatial structure of the registered trapline system contributed to the sustainability of harvests.

Résumé : Les loups (*Canis lupus* L., 1758) sont soumis à des récoltes publiques permissives dans presque toute leur aire de répartition en Amérique du Nord, bien qu'il existe peu d'information détaillée sur les populations dont la principale cause de mortalité est la récolte sportive. Nous avons étudié une population de loups soumise à la récolte dans le centre ouest de l'Alberta de 2003 à 2008. Les données démographiques proviennent de visites aux sites de tanières, de 84 loups porteurs de colliers appartenant à 19 meutes et d'un programme de surveillance des récoltes qui a accru les déclarations obligatoires pour les lignes de piégeage enregistrées. Le taux annuel de récolte des loups est de 0,34 et la récolte est deux fois plus importante sur les lignes de piégeage enregistrées (0,22 ± 0,03) que par la chasse (0,12 ± 0,04). La plupart des loups récoltés (71 %) sont au stade pré-reproductif. La probabilité de reproduction d'une meute est de 0,83 ± 0,01 et la taille moyenne des portées est de 5,6 ± 1,4; ces taux et la stabilité des domaines vitaux ne sont pas affectés par le nombre de loups récoltés. La mortalité naturelle (0,04 ± 0,03) et les taux de dispersion (0,25 ± 0,04) sont inférieurs à ceux signalés chez les populations de loups des zones protégées. Les taux de reproduction compensent la mortalité totale des loups, ce qui indique que la récolte est vraisemblablement durable. Nous pensons que la forte proportion de jeunes dans les récoltes et la structure spatiale du système de lignes de piégeage enregistrées contribuent à la durabilité des récoltes.

[Traduit par la Rédaction]

Introduction

Across the majority of their range in North America, wolves (*Canis lupus* L., 1758) are subject to some of the most liberal harvests of any terrestrial species (Hayes and Gunson 1995; Haber 1996; Musiani and Paquet 2004). In portions of Alaska and Canada, regulations of wolf harvest permit year-round hunting, trapping with both foothold traps and neck snares, baiting, use of predator calls, and even use of snowmobiles or aircraft to follow and shoot wolves (Hayes and Gunson 1995; Stephenson et al. 1995; Musiani and Paquet 2004; Adams et al. 2008). Studies of the effect of harvest on the demography of wolves are not common (Ballard et al. 1987; Adams et al. 2008; Person and Russell 2008) and this lack of information has led to evaluations of potential regimes of wolf harvest in the lower 48 United States that rely primarily on data from protected and controlled populations (Creel and Rotella 2010). However, using information from protected or controlled populations to manage wolf harvests may be misleading because wolves may alter behaviour, social dynamics, hunting efficiency, or genetics when exploited with different methods (Haber 1996). Providing information on the effects of harvest on wolf populations is particularly timely for designing effective management of wolves in the lower 48 United States, where reestablished wolf populations will eventually be delisted from the Endangered Species Act and subject to public harvests.

Effects of public harvests on wolf populations may differ from control programs in several ways. First, timing of harvest may affect populations because wolves exhibit seasonal

Received 26 October 2010. Accepted 24 March 2011. Published at www.nrcresearchpress.com/cjz on 5 August 2011.

N.F. Webb.* Department of Biological Sciences, University of Alberta, Edmonton, AB T6G 2E9, Canada.
J.R. Allen. Fish and Wildlife Division, Alberta Sustainable Resource Development, Edmonton, AB T5K 2M4, Canada.
E.H. Merrill. Department of Biological Sciences, University of Alberta, Edmonton, AB T6G 2E9, Canada.

Corresponding author: N.F. Webb (e-mail: nathan.webb@gov.ab.ca).

*Present address: Fish and Wildlife Division, Alberta Sustainable Resource Development, 2nd Floor, Great West Life Building, 9920 – 108 Street, Edmonton, AB T5K 2M4, Canada.

patterns in reproduction and dispersal (Packard et al. 1983; Boyd and Pletscher 1999). Wolves in protected areas die throughout the year (Fuller 1989; Smith et al. 2006; 2010), whereas wolf-control efforts occur year-round or peak in spring and summer in areas with livestock depredation (Musiani et al. 2003; Fritts et al. 2003). In contrast, wolf populations are harvested for pelts during late fall and winter, immediately prior to and during the breeding season (Paquet and Carbyn 2003). Harvesting wolves during the breeding season could lead to pack instability and reproductive failure if a member of the breeding pair is removed (Haber 1996; Mech 2010), or if reduction in pack size reduces prey kill rates sufficiently to jeopardize pup survival (Brainerd et al. 2008). Alternatively, because most wolf dispersal occurs during winter and spring (Boyd and Pletscher 1999; Adams et al. 2008), winter harvests might result in compensatory declines in emigration, which could offset reductions in reproduction.

Second, harvest often removes the most naïve and vulnerable segments of the population (Adams et al. 2008), whereas control programs may remove wolves more randomly. Transient individuals that are unfamiliar with an area or energetically stressed may be most susceptible to baits used in trapping (Mech 1970; Adams et al. 2008; Person and Russell 2008), and young wolves may be less able to identify and avoid harvest risks. If harvest is concentrated on pups and transients, breeding pairs would be left intact. This could promote higher social and territorial stability than in controlled populations where culling disrupts social behavior and results in frequent breeder turnover (Brainerd et al. 2008), or protected populations where interpack strife can be high (Mech et al. 1998). Indeed, Adams et al. (2008) showed that pups composed a higher proportion of the harvest than in the population. If young, naïve animals make up a large portion of the harvest, harvest mortality may be compensatory because naïve wolves exhibit the highest rates of natural mortality and dispersal (Boyd and Pletscher 1999; Hayes and Harestad 2000; Fuller et al. 2003; Smith et al. 2010). Under these circumstances, the wolf population might be expected to show strong pack stability, high pup production, and low natural mortality.

Additional information is needed on wolf demographic characteristics under a range of harvest rates to assess management options because wolf responses are likely to vary across environments and harvest approaches. Here we report on a wolf population in west-central Alberta, Canada, that has been trapped under a registered trapline system and hunted without quotas for ~10 months of the year since its recovery from a major poisoning program for rabies control during the 1950s (Alberta Forestry, Lands and Wildlife 1991; Gunson 1992). Our objectives were to (*i*) quantify harvest rates and composition of trapped and hunted wolves; (*ii*) evaluate the effect that harvest had on stability of home ranges, reproductive performance, natural mortality, and dispersal; and (*iii*) assess whether the reproductive capacity offset the combined effects of harvest and natural mortality to determine if harvest levels were sustainable.

Materials and methods

Study area

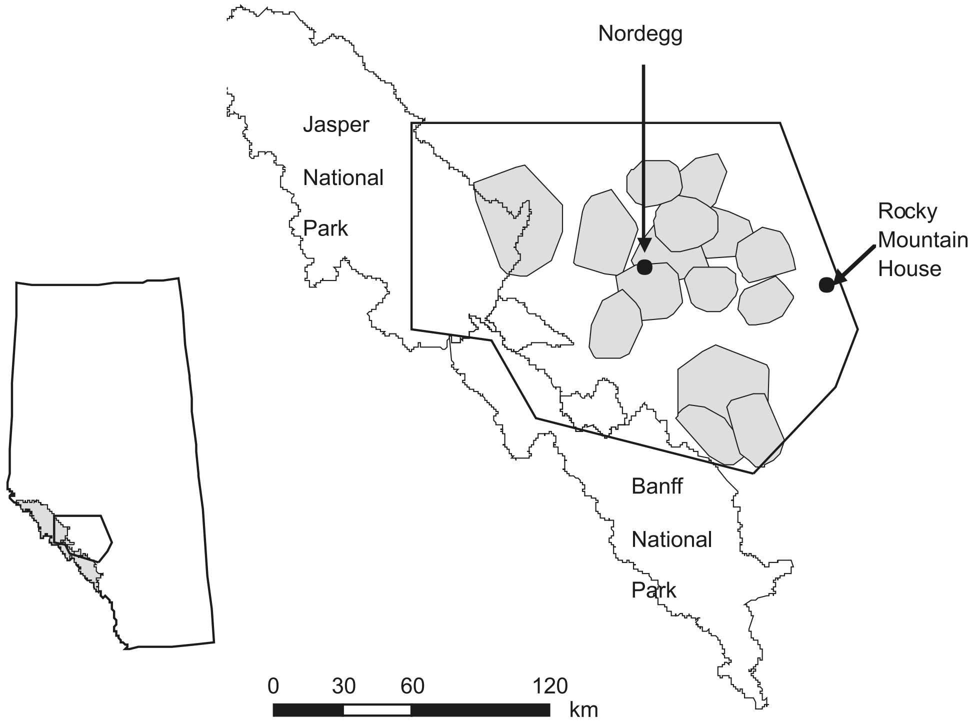
We captured and collared wolves in a 25 000 km^2 area west of Rocky Mountain House, about 200 km southwest of Edmonton, Alberta (52°27′N, 115°45′W) (Fig. 1). The dominant (>50%) land cover was conifer forest with abundant lodgepole pine (*Pinus contorta* Dougl. ex Loud.), white spruce (*Picea glauca* (Moench) Voss), and black spruce (*Picea mariana* (P. Mill.) B.S.P.) (Webb et al. 2008). Natural lowlands, subalpine meadows, and stands of quaking aspen (*Populus tremuloides* Michx.) and balsam poplar (*Populus balsamifera* L.) trees covered approximately 15% of the land. Permanent ice and snow covered much of the mountains in the west of the study area and accounted for approximately 25% of the total land cover. Terrain ruggedness and elevation increased from the eastern foothills into the Rocky Mountains in the west. Anthropogenic development existed predominately in the eastern foothills in the form of forestry cut blocks and an extensive network of oil and gas seismic lines, pipelines, well sites, and recreational trails. Prey for wolves included elk (*Cervus elaphus* L., 1758) (0.28 ± 0.17 animals/km^2; mean ± SE) moose (*Alces alces* (L., 1758)) (0.24 ± 0.04), feral horses (*Equus caballus* L., 1758) (0.10 ± 0.02), white-tailed deer (*Odocoileus virginianus* (Zimmermann, 1780)), and mule deer (*Odocoileus hemionus* (Rafinesque, 1817)) (0.61 ± 0.06). Aerial surveys and pellet counts indicated that total biomass of prey available to wolves declined in an east to west gradient, with higher prey densities occurring at lower elevations in the eastern foothills (Webb 2009).

Wolves were protected from harvest in Banff and Jasper national parks, but were still subject to human-caused mortality throughout the study area in the form of road and railway accidents. On provincial lands, wolves were subject to two types of public harvest. There was a 6-month trapping season (1 October – 31 March) for owners of registered fur management areas (RFMAs) on public lands, and for holders of resident trapping licenses on private land. RFMA holders were required to report the number of wolves trapped during the previous season when renewing their license each year; trappers that harvested wolves under the authority of a resident harvest license were not required to report the number of wolves killed. Wolves also were subject to a ~10-month hunting season from 25 August to 31 May over most of the area and to 15 June in the remaining area. Alberta residents were allowed to hunt wolves, without a license, on public lands during the wolf season, and on private lands or within 8 km of private lands year-round. Nonresidents of Alberta were permitted to hunt wolves during the hunting season by purchasing a wolf or coyote license. No quota existed on the number of wolves that could be taken by either hunting or trapping. Wolves harvested during hunting seasons were not required to be reported, and as such no official records on harvest were available for the study.

Wolf capture and monitoring

We captured 84 wolves from 19 packs in 2003–2007 using helicopter netgunning during winter months and using modified foothold traps during summer (University of Alberta Animal Care Protocol Nos. 391305, 353112, and 411601). We physically restrained wolves captured with helicopter netgunning, whereas we either physically restrained or chemically immobilized wolves captured in traps. We fitted wolves with either Lotek (Lotek Engineering, Newmarket,

Fig. 1. Location of the study area and home ranges of 15 of the 19 wolf (*Canis lupus*) packs in the central east slopes of Alberta, Canada.



Ontario, Canada) LMRT-3 VHF collars (2003–2007), 3300Sw store-on-board GPS collars (2003–2007), or 4400S remote-downloadable GPS collars (2005–2007) weighing <600 g. We located wolves approximately bi-weekly during aerial telemetry flights and occasionally from the ground.

Home-range stability

Because we could not measure stability in pack membership across years, we used two measures that compare percent overlap of consecutive-year home ranges to reflect stability in intrapack dynamics (Haber 1996). We developed 95% minimum convex polygon (MCP) home ranges for each pack where we had 2 consecutive years of relocations from 1 April to 31 March (n = 10 packs) using data from all GPS-collared wolves in the pack. We calculated the proportion of home-range overlap for each wolf pack using the equation from Kernohan et al. (2001):

$$[1] \qquad O_{2,1} = \frac{A_{2,1}}{A_2}$$

where $O_{2,1}$ is the proportion of the home range of a wolf pack in year 2 that is overlapped by that pack's home range from year 1, $A_{2,1}$ is the area of overlap between the two home ranges, and A_2 is the area of the wolf pack's home range in year 2. Home-range overlap was also calculated following Millspaugh et al. (2004) as

$$[2] \qquad O = \frac{A_{1,2}}{(A_1 + A_2) - A_{1,2}}$$

where O is the overlap between home ranges, A_1 is the area of the wolf pack's home range in year 1, A_2 is the area of the wolf pack's home range in year 2, and $A_{1,2}$ is the area of overlap between the wolf pack's home range in year 1 and year 2. Linear regression was used to test for an influence of both total number of wolves harvested from the pack during the initial year and the proportion of the pack harvested during the initial year on home-range overlap in 2 consecutive years.

Wolf demography

Pack sizes

Numbers of wolves in each pack were counted during ground-based snow-tracking sessions and when packs were located using aerial telemetry. The pack size in fall was defined as the maximum number of wolves observed in a pack during October–March, plus the number of wolves that were known to be harvested from the pack prior to the date of the observation. The pack size in late winter was calculated by subtracting the number of wolves known to have dispersed or been harvested from each pack from the pack size in fall.

Mortality and harvest rates

A harvest-reporting program targeted towards trappers was implemented from fall 2003 to spring 2006. We obtained information on harvest date, location, sex, pelt color, and harvest method. Although we also received information from some hunters, the data were limited because hunters travelling from outside the area were too numerous to survey confidently. Therefore, estimates of hunter harvest were generated from the radio-collared sample. We received skulls from a sample of harvested wolves; these animals were aged based on cementum annuli of an extracted lower canine (Mattson's lab in Milltown, Montana, USA; Ballard et al. 1995). Uncollared, harvested wolves were assigned to packs based on weight of evidence using a combination of (*i*) the location where the wolf was killed in relation to pack home ranges; (*ii*) sizes of packs associated with wolves that were harvested and sizes of radio-marked packs; (*iii*) radio-collared wolves from marked packs that were harvested at the same time and location as uncollared wolves; (*iv*) GPS-collar locations that indicated packs were at trapper bait sites; and (*v*) trapper opinions. Pack-specific trapping and hunting rates were calculated as the estimated proportion of the pack size in fall that was removed during the subsequent trapping and hunting seasons, and as the estimated total number of wolves removed in each pack, each year, averaged across packs. We acknowledge that uncertainty in assigning harvested wolves to packs may have biased some results, and address this limitation in the Discussion.

We estimated cause-specific mortality rates of radio-collared wolves ≥6 months of age with a nonparametric cumulative incidence function estimator (Heisey and Patterson 2006) using R version 2.12.2 (R. Development Core Team 2011). We pooled data among years to determine annual rates. Wolves were entered into the analysis on the day that they were released with a radio collar. Cause of death was determined using reports from hunters and trappers, as well as by examination of the sites and carcasses of dead wolves. Because we worked closely with trappers and they reported the mortality of wolves, we assumed that radio collars that had been removed and left in the field ($n = 1$) were from wolves shot by hunters. The date of harvest from hunter and trapper reports was used as the date of mortality. When date of mortality was unknown, we assumed that death occurred at the midpoint between the date that the wolf was last known to be alive and the first date that its radio collar was detected on mortality mode. Wolves were censored from survival analyses during periods when they were unmarked and upon collar failure, collar removal, or dispersal from the study area (White and Garrott 1990).

Reproduction

Tunnels and chambers of dens were inspected to obtain pup counts for each radio-marked wolf pack from 2004 to 2006. Dens were visited in early May, when pups were approximately 3–5 weeks old (Person and Russell 2009). In four cases, dens included tunnel systems that were too small to enter and may have allowed pups to escape detection. Data from these dens were not included in estimates of mean litter size, but we could not determine the magnitude of the bias of this approach on estimates of litter size. We tested for an effect of the number of trapped wolves, number of wolves shot by hunters, total number of wolves harvested by humans, proportion of the pack in the fall that was killed by either hunters, trappers, or both, and pack size in late-winter (post-harvest season) on whether pups were produced using logistic regression, and on mean litter size using linear regression.

Dispersal

The midpoint between the last date that a wolf was known to be within its original home range and the first date that it was known to be outside its home range without returning was used as the date of dispersal. When contact was lost with radio-collared wolves, we included them in the analysis ($n = 3$) only when they appeared to be making predispersal movements, such as splitting from their original pack. Dispersal rates were calculated with a nonparametric cumulative incidence function estimator (Heisey and Patterson 2006) using R version 2.12.2 (R Development Core Team 2011). We pooled data among years to determine annual rates. Dispersers were categorized as (*i*) local dispersers if they remained within the boundaries of the study area and (*ii*) emigrants if they permanently left the study area. Wolves entered the analysis upon release with a radio collar and those that died were censored on the date of mortality. Direction of dispersal of wolves that were eventually killed was determined as the azimuth between the centre of the home range of the pack from which the wolf originated and the location where it was killed.

Harvest sustainability

We assessed the effects of harvest on the current wolf population in terms of net recruitment (NR):

$$[3] \qquad \mathrm{NR} = WP_{\mathrm{p}}LS_{\mathrm{p}} - WNM_{\mathrm{A}}$$

where W was number of packs, P_{p} was the probability a pack produced pups, L was the litter size, S_{p} was survival rate of pups, N was pack size in the fall, and M_{A} was adult mortality. We used mean estimates of P_{p}, L, and N derived from data of 29 pack-years. M_{A} was the total annual mortality rate of wolves ≥6 months of age. We used an estimate of 0.66 ± 0.19 for S_{p} based on survival estimates of juveniles (<6 months of age) across wolf range provided by Fuller et al. (2003). We calculated variability around NR using Monte Carlo simulations ($n = 1000$) by randomly drawing from a normal distribution based on the observed mean and σ^2, and assuming variables were uncorrelated. Variability in P_{p} was based on the binomial distribution as $s^2 = P_{\mathrm{p}}(1 - P_{\mathrm{p}})/(n - 1)$. Although we never observed a pack disbanding, we also included variability in the number of packs assuming a normal distribution and a standard deviation that was 10% of the mean. We considered evidence for current levels of harvest being sustainable if the upper 95% confidence limit of NR was ≥0.

To investigate the influence of variation in demographic rates on net recruitment, we also calculated NR using the upper and lower 95% confidence limit for each parameter in eq. 3 while maintaining variability in the other parameters. We plotted the high and low NR values for each parameter, and visually inspected the graph to determine which contributed the most variation to NR.

Results

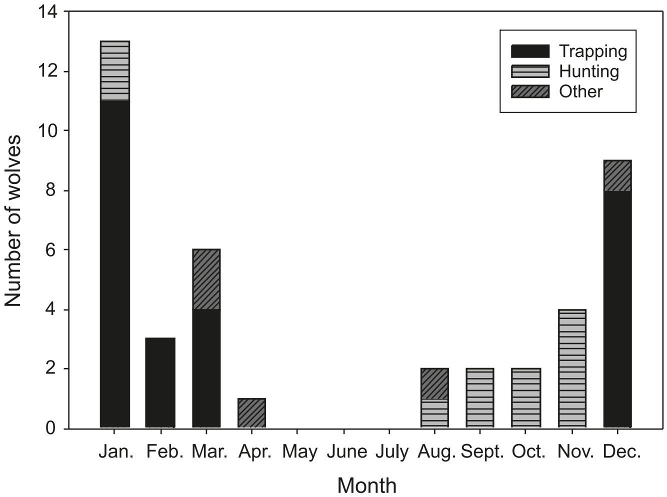
Home-range stability

The proportion of the 2nd-year home ranges that overlapped the 1st-year home range was 0.79 ± 0.13 (range: 0.61–1.0; eq. 1). The proportion of home-range overlap across 2 years was 0.67 ± 0.20 (range: 0.44–1.0; eq. 2). No linear correlation existed between the number of wolves harvested ($P > 0.38$) or proportion of the pack harvested in the first year ($P > 0.26$) and either measure of home-range stability.

Reproduction

We documented 81 pups at 17 occupied den sites from 13 packs in 2004–2006 (2004: $n = 1$; 2005: $n = 7$; 2006: $n = 9$). In no cases did we locate >1 litter/pack in 1 year, despite visiting all known den sites for each pack each year. Pups were produced in 24 (0.83 ± 0.01) of 29 pack-years. Litter

Fig. 2. Month and cause of mortality for 42 radio-collared wolves (*Canis lupus*) that died in 2003–2008 in the central east slopes of Alberta, Canada.



sizes averaged 5.6 ± 1.4 pups/pack (range = 4–7 pups/pack). In one case of reproductive failure, a pregnant female was harvested from the pack by a trapper in mid-March. In a second case, 8 wolves from the same pack, including the alpha female, were harvested over the fall and winter. No den site was found in the home range of this pack the following spring. Causes for the remaining reproductive failures were unknown, but either harvest rates during the preceding fall or winter were very low (0.11, $n = 1$), or no wolves were harvested from those packs ($n = 2$). No relationship existed between the number of pups produced and the number or proportion of wolves in a pack that were harvested ($P > 0.19$, $n = 23$), or between the number of wolves or proportion of wolves in a pack that were harvested and litter size ($P > 0.12$, $n = 11$).

Mortality

The mean fall pack size of collared wolf packs was 7.76 ± 2.80 wolves. A total of 42, nonemigrating radio-collared wolves died during the study. Of these, 26 (62%) were trapped, 11 (26%) were shot by hunters, 4 (10%) died of natural or unknown causes, and 1 (2%) was hit by a vehicle (Fig. 2). Harvest mortality occurred between November and March, with the majority of the hunted wolves taken during the big-game hunting season in the fall (Fig. 2). Seasonal patterns of natural mortality and relationships of natural mortality to harvest mortality could not be determined because of a low number of collared wolves ($n = 4$) dying of natural causes.

Based on all wolves harvested (radio-collared and uncollared) from radio-marked packs, at least 60% ± 9.8% of all packs had at least 1 wolf killed by trappers, 18% ± 19% (0%–50%) of the wolves in each pack were trapped, and 1.44 ± 1.73 wolves/pack were killed by trappers each year (range: 0–7). Based on a ratio of shot to trapped wolves of 0.42 ± 0.08 in the sample of collared animals, a total of 2.0 ± 1.2 wolves/pack were harvested each year. Age composition of harvested wolves ($n = 52$) was 55% pups and 16% yearlings. If we assume pup survival was 0.66 (Fuller et al. 2003), then pups would be an estimated 40% of the fall population, which at our sample sizes indicated the proportion harvested was not different from that in the population ($\chi^2_{[1]} = 1.54$, $P = 0.18$).

Table 1. Cause-specific annual mortality rates of radio-collared wolves (*Canis lupus*) monitored between 2003 and 2008 in the central east slopes of Alberta, Canada.

Cause	*n*	Mortality rate	95% confidence interval
Trapping	26	0.218	0.152 to 0.283
Hunting	11	0.121	0.049 to 0.192
Other	5	0.043	–0.010 to 0.097
Total	42	0.382	0.286 – 0.478

Note: Other causes of annual mortality rates include natural, hit by vehicle, and unknown.

Radio-collared wolves were monitored for a mean of 363 days (range 3–1465 days) before collar failure, collar removal, loss of telemetry contact owing to emigration, death of the wolf, or the termination of monitoring. Wolves were killed by trappers as soon as 3 days after collaring. The annual rate of adult mortality was 0.38 ± 0.05 and the annual rate of total harvest was 0.34, indicating that harvest was the major cause of mortality (Table 1). Estimates of trapping mortality (0.22 ± 0.03) based on radio-collared animals did not differ from the rate of trapping mortality (0.18 ± 0.19, $P > 0.10$) derived from the harvest-reporting program.

Harvest sustainability

At the reported mortality and reproductive rates, net recruitment (eq. 3) was 2.5 wolves/year with the 95% confidence interval (–56.1 to 61.1) encompassing zero, indicating that reproduction was sufficient to offset the combined natural and harvest mortalities. Net recruitment was most sensitive to variability in pack size, followed closely by pup survival and litter size (Fig. 3). Observed variation in rates of adult mortality and the proportion of packs producing litters had relatively little effect on net recruitment.

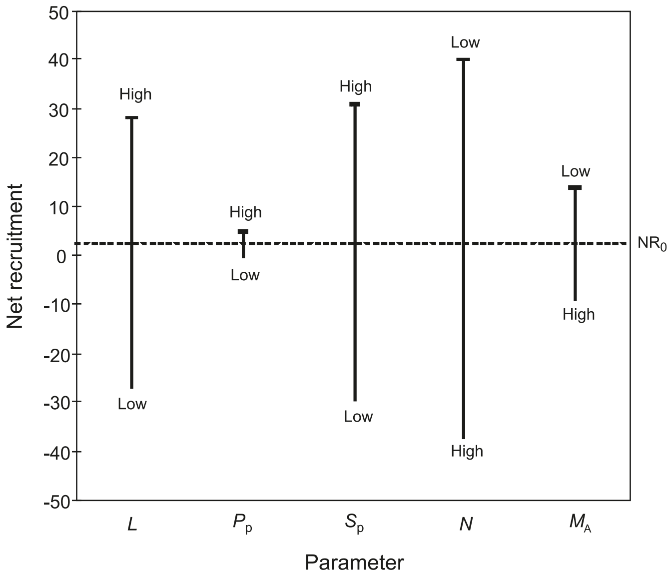
Dispersal

Wolves left their natal packs at a rate of 0.25 ± 0.04, with about equal rates of local dispersal ($n = 11$) within the study area and emigration ($n = 10$) outside the study area (Table 2). Fourteen (82%) of the 17 wolves for which we could determine month of dispersal left their natal pack between October and March and 6 of these (35%) dispersed during the breeding season (between January and February). Of the locally dispersing wolves, 5 joined existing packs, and 6 were killed by humans prior to joining a pack. Six emigrating wolves and 8 wolves that dispersed locally lived through ≥1 breeding season after dispersal. Of 7 emigrants with known fates, all 7 dispersed northwards. One other wolf appeared to travel initially in a southeasterly direction prior to the loss of radio contact, while the other 2 emigrants traveled northwest prior to loss of their signals.

Discussion

The harvest rate of wolves in our study area was three times the value of 0.10 reported by Adams et al. (2008) in

Fig. 3. Influence of variation in demographic parameters on net recruitment of wolves (*Canis lupus*) in the central east slopes of Alberta, Canada. NR_o is mean net recruitment, P_p is the probability a pack producing pups, L is litter size, S_p is survival rate of pups, N is fall pack size, and M_A is adult mortality.



Gates of the Arctic National Park and Preserve in Alaska, and higher than the legal harvest (0.23) but lower than the combined legal and illegal harvest (0.42) in southeast Alaska (Person and Russell 2008). We cannot compare legal to illegal harvest because currently there is no quota on wolf harvest by resident hunters and trappers. The relatively high harvest rate in our study was attributed primarily to trapping. High trapping levels are consistent with an active trapping community. Prevalence of dense forests and wolves' tendency to avoid well-traveled trails and roads (Thurber et al. 1994) probably contributed to poor success of hunters. However, the rate of hunting mortality that we report is conservative because hunters are not required to report harvest, and collared wolves whose fate was censored owing to collar failure (n = 7) could have been related to unreported hunter kills. Nonetheless, the combined harvest rate was high and likely related to the lack of quotas, the proximity of the study area to major population centres, and relatively easy access for both hunters and trappers (Person and Russell 2008). Estimates of trapping rates based on radio-collared wolves were substantially more precise than those derived from the harvest-reporting program, indicating that maintaining a sample of radio-collared wolves may be a more effective approach to monitor wolf mortality.

Pre-reproductive wolves were more vulnerable to harvest, composing 71% of the harvest. Therefore, although we could not directly measure the number of breeding wolves lost from each pack, it appeared that harvest left most breeding pairs intact, which lent itself to stability of wolf home ranges. This also resulted in reproductive performance that was comparable to unharvested wolf populations (Fuller et al. 2003). In fact, the proportion of packs producing litters (0.83) was nearly twice as high as the value of 0.47 reported by Brainerd et al. (2008) for packs from which breeding members were killed. Harvest did not appear to alter litter size, with mean litter size 4–6 weeks after birth similar to litter size of wolves across their range (6 pups; Paquet and Carbyn 2003). However, because inherent uncertainty existed in assigning harvested wolves to packs, some effects of harvesting on pup production or litter size may not have been apparent. We found no evidence of multiple breeding, which has been documented in some socially disrupted wolf populations (Harrington et al. 1982; Peterson et al. 1984; Fuller et al. 2003; Smith et al. 2006).

Table 2. Annual dispersal rates and 95% confidence intervals for 84 radio-collared wolves (*Canis lupus*) ≥6 months old monitored from 2003 to 2008 in the central east slopes of Alberta, Canada.

Type	n	Dispersal rate	95% confidence interval
Local dispersal	11	0.116	0.056 to 0.175
Emigration	10	0.132	0.072 to 0.193
Total	22	0.248	0.166 to 0.330

In reviewing North American wolf studies, Adams et al. (2008) reported a threshold of 29% human-caused mortality below which there was little evidence for declines in natural mortality, but found reduced natural mortality above this level (Berg and Kuehn 1982; Peterson et al. 1984; Ballard et al. 1987, 1997; Hayes et al. 1991; Person and Russell 2008). At a harvest rate of 0.34, natural mortality in this study (<0.05 or 9.5% of all mortalities) is more consistent with this assessment than the conclusions of Creel and Rotella (2010), who indicated that human-caused mortality of wolves may not result in declines in natural mortality. Although declines in natural mortality have been reported under high harvests, the reasons for reduced natural mortality have not been well documented. In the 19 packs monitored, there were no observed cases of disease or intraspecific killing, which can be important factors contributing to self-regulation of wolf populations in the absence of human exploitation (Mech et al. 1998). Because intraspecific strife among packs often results in the death of breeding wolves (Mech et al. 1998; Smith et al. 2006), it is possible that moderate levels of trapping which remove primarily juveniles may actually promote stability within packs compared with unexploited populations. In contrast, infrastructure (roads and trails) associated with increasing industrial development in the area may lead to increased harvest rates over time, particularly by hunters, because high human access has been related to wolf mortality (Person and Russell 2008). If this alters the age structure of the harvest or the ratio of residents to transients harvested, it may alter the compensatory nature of harvest mortality.

In addition to reduced natural mortality, dispersal (0.25) in this population was lower than reported for colonizing or expanding wolf populations (0.48: Boyd and Pletscher 1999; 0.50: Kojola et al. 2006), for an unharvested population in central Minnesota (0.35: Fuller 1989), and for exploited populations in Alaska (0.33: Peterson et al. 1984; 0.44: Adams et al. 2008). When wolves are harvested, reduced dispersal may result from lower competition, but trapping, in particular, also may remove the age classes most likely to disperse (Packard and Mech 1980; Shields 1987; Gese and Mech 1991; Adams et al. 2008). Prey densities in this area were moderate (Webb 2009), but in areas of low prey availability where a wider range of age classes disperse (Fuller et al. 2003), harvest may not result in reduced dispersal rates.

Spatial distribution of harvest across wolf packs likely contributed to the dynamics that we observed, but the influence of spatially structured harvests is not well understood for wolves. Forty percent of packs in our study were untrapped each year, and successful dispersers from these and other lightly harvested packs likely reduced local variation in wolf density in surrounding areas with high harvest (Sirén et al. 2004; Novaro et al. 2005). All 5 wolves that dispersed locally and joined packs were accepted into packs that experienced harvest during the previous season, providing some evidence that harvest may facilitate successful dispersal. Furthermore, in the 4 packs where wolf removal was particularly high (≥0.33), trappers were less successful in the following year (in 3 of 4 packs, harvest rates were <0.10), even though pack sizes in the fall were similar. A similar pattern has been reported for the trapline system at the provincial level in Alberta (Robichaud and Boyce 2010). A lag in trapping intensity within individual packs might allow recovery from years of intense harvests, preventing social breakdown at the pack level if mostly nonbreeding wolves are harvested. Most trappers in west-central Alberta use neck snares to trap wolves at established bait sites, which adult wolves may learn to avoid. When different trapping techniques, such as foot-hold traps, are used, or when trapping techniques are varied, a higher percentage of breeding wolves may be killed and packs may be less stable.

Under the current harvest regime and with the observed demographic rates, the wolf population in our study appeared stable. However, several factors add uncertainty to our estimate of net recruitment. First, our approach to estimate pack sizes may have been biased low because some wolves may have been missed during ground or aerial counts. Our estimates of adult mortality may also have been low because we censored wolves whose collars failed, rather than treating them as mortalities. If true pack sizes were larger or adult mortality rates higher than those we recorded, our estimate of net recruitment may be too high. Our results also indicate that pup survival has a substantial impact on net recruitment. Although we did not measure pup survival and these rates vary widely, pup survival is typically high in the absence of disease outbreaks and in areas with high prey availability (Mech et al. 1998; Fuller et al. 2003). However, if pup survival was lower than the estimate we used, it is possible that wolf mortalities exceeded recruitment. More generally, high variation in parameter estimates could have masked a true net recruitment <0 (Patterson and Murray 2008). Finally, our analysis focused only on comparing the current reproductive potential and as such provided only a snap shot of potential population growth. We did not use a matrix modeling approach because we had little information on either density dependence (Patterson and Murray 2008), or covariation in vital rates (Coulson et al. 2005), which can have important effects on model outcomes.

Although our estimate of net recruitment is accompanied by some uncertainty, harvest under a trapline system and the presence of an abundant, multispecies prey base likely contributed to the moderate density (Webb 2009) and apparent resiliency of the wolf population that we studied. Results of this study suggest that under the current harvest regime, primarily juvenile wolves are removed, breeding pairs are left largely intact, and spatial harvest patterns may contribute to a local source–sink dynamic within the area. If industrial development and associated access increase in this area, as is expected during the next decade, harvest pressure by hunters may increase and more breeding wolves are likely to be killed. Even if limits were imposed, illegal take may occur, making access management important (Person and Russell 2008). Implementation of mandatory registration of hunter kills, combined with web-based surveys of hunters as occurs with other game species, may provide a means of obtaining the information needed for managing wolves for the diverse public interested in wolves in this area.

As wildlife agencies in the United States formulate wolf management plans, our results suggest that wolf populations can remain viable under certain harvest regimes even when season lengths and quotas are liberal. Because registered traplines limit the number of trappers and disperse trapping pressure more evenly across the landscape than an open-access system, the number of packs that are harvested at unsustainable rates is minimized. Alternatively, where wolves are managed in a system of open access, trapping efforts can be directed more readily to areas where depredation on domestic or native ungulates is a problem. An open-access system to managing wolves may require strict harvest limits, particularly in areas where human access is high and wolves are naïve. Large-scale planning for spatially structured harvest of wolves could provide for concentrated harvest of wolves in areas of expected conflicts while maintaining overall viability of populations as has been indicated for other species in both marine and terrestrial systems (Joshi and Gadgil 1991; Hall 1998; Novaro et al. 2005). In any case, initial harvest systems are likely to result in more disruptive effects because wolves would be naïve and more susceptible to hunting and trapping than we observed in Alberta.

Acknowledgements

We thank those organizations that contributed funding or in-kind support for this research, including the Alberta Conservation Association, Alberta Cooperative Conservation Research Unit, Alberta Fish and Game Association, Alberta Professional Outfitters Society, Alberta Sustainable Resource Development, Alberta Trappers Association, Foundation for North American Wild Sheep – Alberta Chapter, Foundation for North American Wild Sheep – International, the Natural Sciences and Engineering Research Council of Canada (Collaborative Research Grant No. 261091-02), Parks Canada, Red Deer River Naturalists, Rocky Mountain Elk Foundation, Safari Club International – Northern Alberta Chapter, Yellowstone to Yukon/Wilburforce Foundation, Sundance Forest Industries, Sundre Forest Products, Weyerhaeuser Company, and the University of Alberta. Mark Boyce and Kyle Knopff provided helpful reviews of an earlier version of the manuscript. Special thanks go to the numerous field assistants who made this research possible.

References

Adams, L.G., Stephenson, R.O., Dale, B.W., Ahgook, R.T., and Demma, D.J. 2008. Population dynamics and harvest characteristics of wolves in the central Brooks Range, Alaska. Wildl. Monogr. No. 170.

Alberta Forestry, Lands, and Wildlife. 1991. Management plan for wolves in Alberta. Wildl. Manage. Planning Ser. No. 4. Alberta Forestry, Lands, and Wildlife, Edmonton.

Ballard, W. B., Whitman, J. S., and Gardner C. L. 1987. Ecology of an exploited wolf population in south-central Alaska. Wildl. Monogr. No. 98.

Ballard, W.B., Matson, G.M., and Krausman, P.R. 1995. Comparison of two methods to age gray wolf teeth. *In* Ecology and conservation of wolves in a changing world. *Edited by* L.N. Carbyn, S.H. Fritts, and D.R. Seip. Occas. Publ. No. 35. Canadian Circumpolar Institute, Edmonton, Alta. pp. 455–460.

Ballard, W. B., Ayres, L. A., Krausman, P. R., Reed, D. J., and Fancy, S. G. 1997. Ecology of wolves in relation to a migratory caribou herd in northwest Alaska. Wildl. Monogr. No. 135.

Berg, W.E., and Kuehn, D.W. 1982. Ecology of wolves in north-central Minnesota. *In* Wolves of the world: perspectives of behavior, ecology, and conservation. *Edited by* F.H. Harrington, and P.C. Pacquet. Noyes Publishers, Park Ridge, N.J. pp. 4–11.

Boyd, D.K., and Pletscher, D.H. 1999. Characteristics of dispersal in a colonizing wolf population in the central Rocky Mountains. J. Wildl. Manage. **63**(4): 1094–1108. doi:10.2307/3802828.

Brainerd, S.M., Andrén, H., Bangs, E.E., Bradley, E.H., Fontaine, J.A., Hall, W., Iliopoulos, Y., Jiminez, M.D., Jozwiak, E.A., Liberg, O., Mack, C.M., Meier, T.J., Niemeyer, C.C., Pedersen, H.C., Sand, H., Schultz, R.N., Smith, D.W., Wabakken, P., and Wydeven, A.D. 2008. The effects of breeder loss on wolves. J. Wildl. Manage. **72**(1): 89–98. doi:10.2193/2006-305.

Coulson, T., Gaillard, J.M., and Festa-Bianchet, M. 2005. Decomposing the variation in population growth into contributions from multiple demographic rates. J. Anim. Ecol. **74**(4): 789–801. doi:10.1111/j.1365-2656.2005.00975.x.

Creel, S., and Rotella, J.J. 2010. Meta-analysis of relationships between human offtake, total mortality and population dynamics of gray wolves (*Canis lupus*). PLoS ONE, **5**(9): e12918. doi:10.1371/journal.pone.0012918. PMID:20927363.

Fritts, S.H., Stephenson, R.O., Hayes, R.D., and Boitani, L. 2003. Wolves and humans. *In* Wolves: behavior, ecology, and conservation. *Edited by* L.D. Mech and L. Boitani. The University of Chicago Press, Chicago. pp. 289–316.

Fuller, T.K. 1989. Population dynamics of wolves in north-central Minnesota. Wildl. Monogr. No. 105.

Fuller, T.K., Mech, L.D., and Cochrane, J.F. 2003. Wolf population dynamics. *In* Wolves: behavior, ecology, and conservation. *Edited by* L.D. Mech and L. Boitani. The University of Chicago Press, Chicago. pp. 161–191.

Gese, E.M., and Mech, L.D. 1991. Dispersal of wolves (*Canis lupus*) in northeastern Minnesota, 1969–1989. Can. J. Zool. **69**(12): 2946–2955. doi:10.1139/z91-415.

Gunson, J.R. 1992. Historical and present management of wolves in Alberta. Wildl. Soc. Bull. **20**: 330–339.

Haber, G.C. 1996. Biological, conservation, and ethical implications of exploiting and controlling wolves. Conserv. Biol. **10**(4): 1068–1081. doi:10.1046/j.1523-1739.1996.10041068.x.

Hall, S.J. 1998. Closed areas for fisheries management—the case consolidates. Trends Ecol. Evol. **13**(8): 297–298. doi:10.1016/S0169-5347(98)01399-8. PMID:21238313.

Harrington, F.H., Paquet, P.C., Ryon, J., and Fentress, J.C. 1982. Monogamy in wolves: a review of the evidence. *In* Wolves of the world: perspectives of behavior, ecology, and conservation. *Edited by* F.H. Harrington and P.C. Paquet. Noyes Publishers, Park Ridge, N.J. pp. 209–222.

Hayes, R.D., and Gunson, J.R. 1995. Status and management of wolves in Canada. *In* Ecology and conservation of wolves in a changing world. *Edited by* L.N. Carbyn, S.H. Fritts, and D.R. Seip. Occas. Publ. No. 35. Canadian Circumpolar Institute, Edmonton, Alta. pp. 21–33.

Hayes, R.D., and Harestad, A.S. 2000. Demography of a recovering wolf population in the Yukon. Can. J. Zool. **78**(1): 36–48. doi:10.1139/cjz-78-1-36.

Hayes, R.D., Baer, A.M., and Larsen, D.G. 1991. Population dynamics and prey relationships of an exploited and recovering wolf population in the southern Yukon. Final Rep. No. TR-91-1. Fish and Wildlife Branch, Department of Renewable Resources, Whitehorse, Y.T.

Heisey, D.M., and Patterson, B.R. 2006. A review of methods to estimate cause-specific mortality in the presence of competing risks. J. Wildl. Manage. **70**(6): 1544–1555. doi:10.2193/0022-541X(2006)70[1544:AROMTE]2.0.CO;2.

Joshi, N.V., and Gadgil, M. 1991. On the role of refugia in promoting prudent use of biological resources. Theor. Popul. Biol. **40**(2): 211–229. doi:10.1016/0040-5809(91)90053-I.

Kernohan, B.J., Gitzen, R.A., and Millspaugh, J.J. 2001. Analysis of animal space use and movements. *In* Radio tracking and animal populations. *Edited by* J.J. Millspaugh and J.M. Marzluff. Academic Press, San Diego, Calif. pp. 126–168.

Kojola, I., Aspi, J., Hakala, A., Heikkinen, S., Ilmoni, C., and Ronkainen, S. 2006. Dispersal in an expanding wolf population in Finland. J. Mammal. **87**(2): 281–286. doi:10.1644/05-MAMM-A-061R2.1.

Mech, L.D. 1970. The wolf: the ecology and behavior of an endangered species. Natural History Press, Garden City, N.Y.

Mech, D.L. 2010. Consideration for developing wolf harvesting regulations in the contiguous United States. J. Wildl. Manage. **74**(7): 1421–1424. doi:10.2193/2009-540.

Mech, L.D., Adams, L.G., Meier, T.J., Burch, J.W., and Dale, D.W. 1998. The wolves of Denali. University of Minnesota Press, Minneapolis.

Millspaugh, J.S.J., Gitzen, R.A., Kernohan, B.J., Larson, J.A., and Clay, C.L. 2004. Comparability of three analytical techniques to assess joint space use. Wildl. Soc. Bull. **32**(1): 148–157. doi:10.2193/0091-7648(2004)32[148:COTATT]2.0.CO;2.

Musiani, M., and Paquet, P.C. 2004. The practices of wolf persecution, protection, and restoration in Canada and the United States. Bioscience, **54**(1): 50–60. doi:10.1641/0006-3568(2004)054[0050:TPOWPP]2.0.CO;2.

Musiani, M., Mamo, C., Boitani, L., Callaghan, C., Gates, C.C., Mattei, L., Visalberghi, E., Breck, S., and Volpi, G. 2003. Wolf depredation trends and the use of fladry barriers to protect livestock in western North America. Conserv. Biol. **17**(6): 1538–1547. doi:10.1111/j.1523-1739.2003.00063.x.

Novaro, A.J., Funes, M.C., and Walker, R.S. 2005. An empirical test of source–sink dynamics induced by hunting. J. Appl. Ecol. **42**(5): 910–920. doi:10.1111/j.1365-2664.2005.01067.x.

Packard, J.M., and Mech, L.D. 1980. Population regulation in wolves. *In* Biosocial mechanisms of population regulation. *Edited by* M.N. Cohen, R.S. Malpass, and H.G. Klein. Yale University Press, New Haven, Conn. pp. 135–150.

Packard, J.M., Mech, L.D., and Seal, U.S. 1983. Social influences on reproduction in wolves. *In* Wolves in Canada and Alaska: their status, biology, and management. *Edited by* L.N. Carbyn. Rep. Ser. No. 45. Canadian Wildlife Service, Edmonton, Alta. pp. 78–85.

Paquet, P.C., and Carbyn, L.N. 2003. Gray wolf. *In* Wild mammals of North America: biology, management, and conservation. *Edited by* G.A. Feldhamer, B.C. Thompson, and J.A. Chapman. Johns Hopkins University Press, Baltimore, Md. pp. 482–510.

Patterson, B.R., and Murray, D.L. 2008. Flawed population viability analysis can result in misleading population assessment: a case study for wolves in Algonquin park, Canada. Biol. Conserv. **141**(3): 669–680. doi:10.1016/j.biocon.2007.12.010.

Person, D.K., and Russell, A.L. 2008. Correlates of mortality in an exploited wolf population. J. Wildl. Manage. **72**: 1540–1549.

Person, D.K., and Russell, A.L. 2009. Reproduction and den site selection by wolves in a disturbed landscape. Northwest Sci. **83**(3): 211–224. doi:10.3955/046.083.0305.

Peterson, R.O., Woolington, J.D., and Bailey, T.N. 1984. Wolves of the Kenai Peninsula, Alaska. Wildl. Monogr. No. 88.

R Development Core Team. 2011. R version 2.12.2. The R Foundation for Statistical Computing, Vienna, Austria. Available from http://www.r-project.org/ [accessed 8 March 2011].

Robichaud, C.B., and Boyce, M.S. 2010. Spatial and temporal patterns of wolf harvest on registered traplines in Alberta, Canada. J. Wildl. Manage. **74**(4): 635–643. doi:10.2193/2009-260.

Shields, W.M. 1987. Dispersal and mating systems: investigating their causal connections. *In* Mammalian dispersal patterns: the effects of social structure and population genetics. *Edited by* B.D. Chepko-Sade and Z.T. Halpin. University of Chicago Press, Chicago. pp. 3–26.

Sirén, A., Hambck, P., and Machoa, J. 2004. Including spatial heterogeneity and animal dispersal when evaluating hunting: a model analysis and an empirical assessment in an Amazonian community. Conserv. Biol. **18**(5): 1315–1329. doi:10.1111/j.1523-1739.2004.00024.x.

Smith, D.W., Stahler, D.R., and Guernsey, D.S. 2006. Yellowstone wolf project: annual report, 2005. National Park Service, Yellowstone Center for Resources, Yellowstone National Park, Wyo.

Smith, D.W., Bangs, E.E., Oakleaf, J.K., Mack, C., Fontaine, J., Boyd, D., Jimenez, M., Pletscher, D.H., Niemeyer, C.C., Meier, T.J., Stahler, D.R., Holyan, J., Asher, V.J., and Murray, D.L. 2010. Survival of colonizing wolves in the northern Rocky Mountains of the United States, 1982–2004. J. Wildl. Manage. **74**(4): 620–634. doi:10.2193/2008-584.

Stephenson, R.O., Ballard, W.B., Smith, C.A., and Richardson, K. 1995. Wolf biology and management in Alaska, 1981–1992. *In* Ecology and conservation of wolves in a changing world. *Edited by* L.N. Carbyn, S.H. Fritts, and D.R. Seip. Occas. Publs. No. 35. Canadian Circumpolar Institute, Edmonton, Alta. pp. 43–54.

Thurber, J.M., Peterson, R.O., Drummer, T.D., and Thomasma, S.A. 1994. Gray wolf response to refuge boundaries and roads in Alaska. Wildl. Soc. Bull. **22**: 61–68.

Webb, N.F. 2009. Density, demography, and functional response of a harvested wolf population in west-central Alberta, Canada. Ph.D. dissertation, University of Alberta, Edmonton.

Webb, N.F., Hebblewhite, M., and Merrill, E.H. 2008. Statistical methods for identifying wolf kill sites using global positioning system locations. J. Wildl. Manage. **72**(3): 798–807. doi:10.2193/2006-566.

White, G.C., and Garrott, R.A. 1990. Analysis of wildlife radio-tracking data. Academic Press, San Diego, Calif.