PLOS ONE

RESEARCH ARTICLE

Implications of Harvest on the Boundaries of Protected Areas for Large Carnivore Viewing Opportunities

Bridget L. Borg[1,2]*, **Stephen M. Arthur**[2], **Nicholas A. Bromen**[2], **Kira A. Cassidy**[3], **Rick McIntyre**[3], **Douglas W. Smith**[3], **Laura R. Prugh**[1,4]

1 University of Alaska Fairbanks, Institute of Arctic Biology, 323 Murie Building, Fairbanks, Alaska 99775, United States of America, **2** National Park Service, Denali National Park and Preserve, P.O. Box 9, Denali Park, Alaska 99755, United States of America, **3** National Park Service, Yellowstone Center for Resources, Wolf Project, P.O. Box 168, Yellowstone National Park, Wyoming 82190, United States of America, **4** University of Washington, School of Environmental and Forest Sciences, Box 352100, Seattle Washington 98195, United States of America

* bridget_borg@nps.gov

CrossMark click for updates

Citation: Borg BL, Arthur SM, Bromen NA, Cassidy KA, McIntyre R, Smith DW, et al. (2016) Implications of Harvest on the Boundaries of Protected Areas for Large Carnivore Viewing Opportunities. PLoS ONE 11(4): e0153808. doi:10.1371/journal.pone.0153808

Editor: Danilo Russo, Università degli Studi di Napoli Federico II, ITALY

Received: September 16, 2015

Accepted: April 4, 2016

Published: April 28, 2016

Data Availability Statement: Data are available at the Integrated Natural Resource Application Portal https://irma.nps.gov/ Reference number: 2225028.

Funding: Funding was provided by the National Park Service and the US Geological Survey, National Science Foundation grant DEB-1245373, the Yellowstone Park Foundation, V. Gates, B. Graham, A. Graham, F. Yeager, and K. Yeager. National Park Service supported data collection, analysis, and preparation of the manuscript. Other funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Abstract

The desire to see free ranging large carnivores in their natural habitat is a driver of tourism in protected areas around the globe. However, large carnivores are wide-ranging and subject to human-caused mortality outside protected area boundaries. The impact of harvest (trapping or hunting) on wildlife viewing opportunities has been the subject of intense debate and speculation, but quantitative analyses have been lacking. We examined the effect of legal harvest of wolves (*Canis lupus*) along the boundaries of two North American National Parks, Denali (DNPP) and Yellowstone (YNP), on wolf viewing opportunities within the parks during peak tourist season. We used data on wolf sightings, pack sizes, den site locations, and harvest adjacent to DNPP from 1997–2013 and YNP from 2008–2013 to evaluate the relationship between harvest and wolf viewing opportunities. Although sightings were largely driven by wolf population size and proximity of den sites to roads, sightings in both parks were significantly reduced by harvest. Sightings in YNP increased by 45% following years with no harvest of a wolf from a pack, and sightings in DNPP were more than twice as likely during a period with a harvest buffer zone than in years without the buffer. These findings show that harvest of wolves adjacent to protected areas can reduce sightings within those areas despite minimal impacts on the size of protected wolf populations. Consumptive use of carnivores adjacent to protected areas may therefore reduce their potential for non-consumptive use, and these tradeoffs should be considered when developing regional wildlife management policies.

Competing Interests: The authors have declared that no competing interests exist.

Introduction

Large carnivore conservation relies heavily on sustaining populations within protected areas [1], and protection within these regions provides the majority of viewing opportunities for these species [2]. The desire to see iconic, free ranging large carnivores is a driver for wildlife tourism around the globe and may improve acceptability of their presence by the general public and contribute to conservation goals ([3] but see [4]). However, large predators are wide-ranging and seldom confined within the boundaries of protected areas, creating difficult trans-boundary management issues. Outside and even inside of protected areas, conflict with humans is the single most important cause of mortality for large carnivores [5–7]. Yet the link between human-caused mortality of carnivores adjacent to protected areas and viewing opportunities within a protected region has not been evaluated quantitatively.

In North America, gray wolves (*Canis lupus*) are emblematic of management issues occurring at the borders of protected areas. Protection of wolves in National Parks, such as Yellowstone National Park (YNP) and Denali National Park and Preserve (DNPP), provides the opportunity for thousands of visitors to see wolves each year, but these wide-ranging carnivores often travel across park boundaries onto other public or private lands. Mortality of individual wolves from frequently viewed packs due to hunting or trapping outside these parks has sparked widespread controversy and prompted concern regarding the impact of these losses on population and pack dynamics. Although harvest (hunting or trapping) occurring outside park boundaries may not have population-level effects, harvest of particular individuals can lead to the decline or dissolution of entire packs [8,9]. If the packs or individuals most susceptible to harvest are those that provide the majority of viewing opportunities to visitors of protected areas, then harvest may influence wolf sightings even if harvest levels are too low to reduce population size. Similar impacts of harvest may affect carnivore sightings in other regions as well. In Africa, for example, the desire to see lions (*Panthera leo)* and cheetahs (*Acinonyx jubatus*) in their natural habitat is the main reason tourists visit the continent's reserves, but these species are also the most vulnerable to threats such as human hunting adjacent to reserves [10].

The main objective of this study was to assess effects of harvest adjacent to protected areas on wildlife sightings, using wolves in Yellowstone National Park (YNP) and Denali National Park and Preserve (DNPP) as a case study. Agencies responsible for managing protected areas often have mandates to provide opportunities for visitor enjoyment. In the United States, the National Park Service is mandated to provide opportunities for visitor enjoyment of which wildlife viewing is an important component. Viewing large carnivores, particularly wolves and grizzly bears (*Ursus arctos*), is cited by visitors as one of the main reasons they come to YNP [11] and is a main indicator of a satisfying visitor experience in DNPP [12]. Additionally, in Alaska where wolves are among the most desired species for viewing [13], state wildlife management includes mandates to provide for multiple uses, including non-consumptive uses such as wildlife viewing [14]. In Montana, wildlife watching is listed by visitors and state residents as one of the primary activities in the state [15]. Wildlife viewing also brings an important socio-economic benefit to the states. Wolf watching activities in YNP following the reintroduction of wolves in 1995 brings an estimated $35 million annually to the states of Idaho, Montana and Wyoming [11]. Wildlife viewing is a driver of tourism for DNPP [16] and the state of Alaska [15,17] and wildlife viewing activities in Alaska supported over $2.7 billion dollars in economic activity in 2011 [17].At the same time, states are also mandated to provide for consumptive uses of wildlife, and harvest of wolves can provide significant economic benefits as well [18]. In 2011, statewide revenue in Montana from the purchase of wolf tags alone was over $400,000 [19] while hunting in Alaska supported over $1.3 billion dollars in economic activity [17].

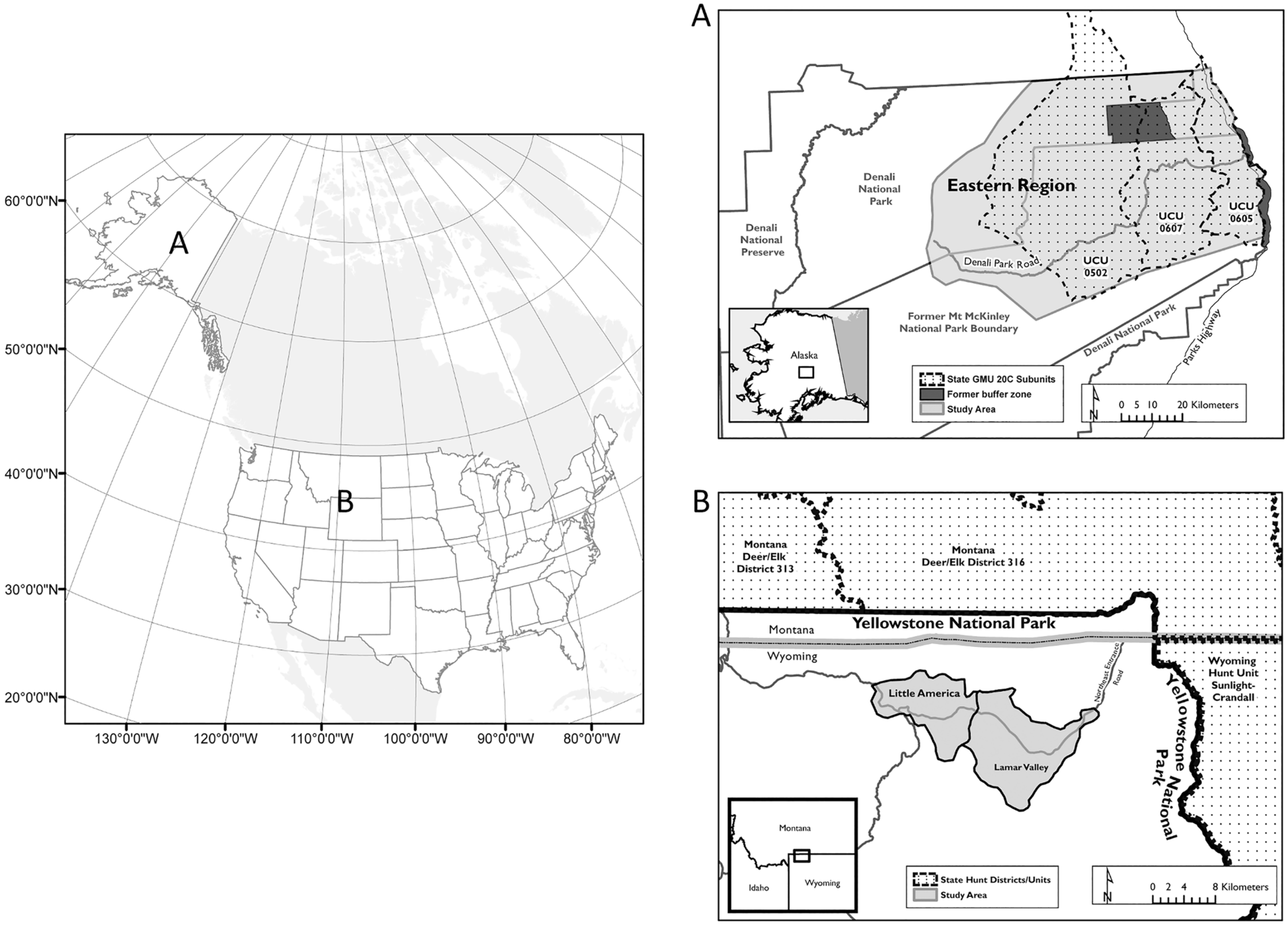


Fig 1. Map of study areas for monitoring wolf sightings in the United States: A) Denali National Park and Preserve study area with Uniform Coding Units (UCUs) within Game Management Unit 20C and former buffer zone where wolf hunting and trapping was prohibited from 2000 to 2010 shown and, B) Yellowstone National Park study area within the Northern Range with adjacent state hunt districts/units shown.

doi:10.1371/journal.pone.0153808.g001

As part of the delisting process for gray wolves in Montana, Wyoming and Idaho, each state has developed wolf management plans that include wolf hunting seasons (for details on state management: www.westerngraywolf.fws.gov), prompting concern that hunting may impact wolf viewing opportunities in YNP [20]. In DNPP, a buffer zone prohibiting the trapping and hunting of wolves was established in key regions bordering DNPP from 2000 to 2010 (Fig 1). The buffer was abolished in March 2010 and viewing rates in DNPP subsequently declined [21], raising concerns that harvest of wolves near park boundaries might have been responsible.

To examine the effect of harvest on wolf sightings, we first examined levels of wolf harvest adjacent to each park and the composition of harvested wolves to determine whether breeding and collared wolves were more or less susceptible to harvest. Concurrent analyses showed that breeding wolves were more likely to be near the Denali Park Road than non-breeding wolves [22], indicating that breeding wolves may contribute disproportionately to sightings. However, we anticipated that less experienced (younger, non-breeding) wolves would be more likely to be harvested than the generally more experienced breeding wolves ([22], but see [23–25]). If this was the case, we expected that harvested wolves may be relatively unimportant to sightings, thereby reducing the potential effect of harvest on viewing opportunities. However, in YNP, the presence of radio-collars on wolves, regardless of breeding status, may increase sighting opportunities for visitors because NPS staff routinely scans for signals from collared animals to assist in locating and viewing wolves. Therefore, if there was disproportional harvest of collared wolves (regardless of breeding status), harvest could decrease viewing opportunities, especially in YNP.

We analyzed data on wolf sightings, pack sizes, den site locations, and harvest adjacent to DNPP from 1997–2013 and YNP from 2008–2013 to evaluate the relationship between harvest of wolves and wolf viewing opportunities. We hypothesized that changes in wolf population size and den site proximity to park roads are the main drivers of wolf sightings and that additionally, the presence of harvest (or absence of the harvest buffer) would reduce wolf sightings. Alternatively, changes in wolf population size and den site proximity to park roads could be the main drivers of wolf sightings, and harvest could have comparably negligible effects.

Methods

Study areas

Our study area encompassed two national parks in North America (Fig 1, Table 1). The DNPP study area encompassed 6,350 km^2 of the eastern region of the park and adjacent areas north of the Alaska Range (Fig 1). Elevation ranges from 150–3,000 m and contains habitat patches of boreal forest, high alpine, braided rivers, and willow-lined creeks. The diversity of habitat types supports populations of caribou (*Rangifer tarandus*), Dall's sheep (*Ovis dalli*), and moose (*Alces alces*) which constitute the main prey base for wolves in the region. The YNP study area encompassed approximately 1,000 km^2 of the Northern Range within and adjacent to the park (Fig 1). Elevation ranges from 1,500–2,400 m, with lower elevations characterized by large open meadows and shrub steppe vegetation and higher elevations characterized by coniferous

Table 1. Metrics summarizing wolf sighting datasets in Denali (Denali National Park and Preserve, Alaska, USA) and Yellowstone (Yellowstone National Park, Wyoming, USA). Table entries for wolf population size, road pack population size, number of road packs (packs whose home range overlapped park roads), and the annual probability of sighting are mean values, with the range among years in parentheses.

Metric	Denali	Yellowstone
Study Period	1997–2013	2008–2013
Length of road	88.5 km	42.3 km
Relevant Harvest Periods	Area closed to harvest adjacent to park: 2000–2010	Harvest Open: Idaho and Montana: 2009, 2011, 2012 Wyoming: 2012
Hunting Season	Mid-August to end of April or May	Varied by state
Hunting Limits	Bag limit range: 5 to 10 wolves	Varied by state
Trapping Season	November 1 to April 30	Varied by state
Trapping Limits	No bag limits	Varied by state
Wolf Population Size	40.8 (23–74)	45.7 (33–84)
Road Pack Population Size	32.8 (12–47)	27.4 (12–43)
Number of Road Packs	5.4 (3–9)	3.1 (2–5)
Annual Probability of Sighting	00.21 (0.04–0.45)	0.70 (0.45–0.85)

doi:10.1371/journal.pone.0153808.t001

forests [26]. Elk (*Cervus elaphus*) are the main prey for wolves in this region, but wolves also prey secondarily on mule deer (*Odocoileus hemionus*), white-tailed deer (*O. virginianus*), and bison (*Bison bison*).

Data collection

Population and pack counts. Biologists have radio-collared wolves in the DNPP study region since 1986 [27] and within YNP since the reintroduction of wolves in 1995 [28]. Each year, 6–22 wolves from 10–20 packs were fitted with radio collars in DNPP [29] and 10–20 wolves from 5–12 packs were collared in YNP ([28], see [29] for handling protocols). Wolf project staff in both YNP and DNPP used a combination of aerial and ground monitoring techniques to collect data on wolf locations, numbers of pack members, pack composition, active den site locations and use, breeding status of individual wolves and timing and suspected causes of mortality [27,30]. Capture and handling protocols were approved by the National Park Service Institutional Animal Care and Use Committee and were in accordance with recommendations from the American Society of Mammalogists [31]. Work was conducted under annual National Park Service permits, annual State of Alaska Department of Fish and Game scientific permits, and the University of Alaska permit (253217–3).

Harvest. All areas outside the DNPP boundary were open to hunting and trapping under state regulation, with the exception of a closed area established by the Alaska Board of Game in 2000, expanded in 2001 and 2002 (Fig 1), and abolished in 2010. Although the closed area was relatively small (75 km^2 in 2000, 233 km^2 from 2002–2010), it included areas that supported high seasonal densities of caribou and associated wolf activity [27]. In Game Management Units (GMU) 20A and 20C adjacent to the park's boundaries, the hunting season ranged from mid-August to the end of April or May with a bag limit ranging from 5–10 wolves, and the trapping season spanned November 1– April 30 with no bag limits for either unit. Subsistence and sport hunting and trapping were permitted in the Preserve and new park additions of DNPP, but all harvest was prohibited in the area of the original Mt. McKinley National Park (Fig 1). Outside YNP, wolves were hunted in 2009, 2011 and 2012 in Idaho and Montana, and in 2012 in Wyoming, with open seasons and limits that varied among hunting units within states. Wolves were not harvested in 2010 due to relisting under the Endangered Species Act. The numbers of wolves harvested from regions adjacent to park boundaries were obtained from state harvest records and mortality of collared wolves.

Harvest of collared and breeding wolves. To examine whether collared and breeding wolves were harvested disproportionately, we used chi-squared and Fisher exact tests to compare the proportion of collared and breeding wolves harvested in areas surrounding each park with their proportions in each park population. In DNPP, we used mortality records to determine the number of collared wolves that were shot or trapped in Uniform Coding Units (UCU) adjacent to DNPP (UCUs 605, 607, and 502) from 1996 to 2012 (Fig 1). We included all recorded wolf harvest within UCUs 605 and 607 in analyses because these UCUs were within the buffer zone or immediately adjacent to DNPP (Fig 1). UCU 502 extended north beyond DNPP and we therefore attempted to include only instances of wolves harvested in UCU 502 that occurred within the former buffer zone using information on the location of harvest. Instances of harvest with unknown locations within UCU 502 were included in the count of harvested wolves in the region. In YNP, we consulted with state agencies to estimate the number of collared and/or breeding wolves and the total number of wolves harvested outside of YNP that were from packs that lived predominantly in YNP. Harvested wolves that were uncollared were judged to have originated from YNP packs if the ages, colors, and sexes matched wolves recently missing from YNP.

We pooled data across years with wolf harvest (1996–2012 for DNPP and 2009, 2011, and 2012 for YNP). We calculated the proportion of collared wolves in the population as the number of individuals collared in or before year *t* that were still alive by August of year *t* divided by the fall population estimate. Similarly, we determined the proportion of breeders in the population as the number of collared individuals identified as breeders divided by the fall population estimate. We restricted our analysis to collared breeders because identification of uncollared breeders in the harvest was not always possible. We determined the proportion of collared or breeding wolves in the harvest as the number of collared/breeding wolves harvested divided by the number of wolves harvested in surrounding UCUs (DNPP) or from YNP packs.

Sighting data. Each study area is bisected by a road (Denali Park Road in DNPP and Northeast Entrance Road in YNP, Fig 1) providing visitor access to the region and wolf viewing opportunities. Traffic along the portion of the road where wolf observations were collected in DNPP was limited to 10,512 vehicle trips per summer season as per DNPP management plans [32]. Although there were slight variations, the traffic was essentially kept at a consistent level for the duration of the study period. According to traffic counts from the north and northeast entrance stations at YNP, traffic into the park gradually increased during the study period [33].

DNPP. We used data on wildlife sightings along the Denali Park Road collected during bus trips into the park from the Savage River entrance station at mile 15 (24.1 km) to Eielson Visitor Center at mile 66 (106.2 km) from 1997–2013. Data were collected by bus drivers as written observations or on panels installed on buses and by park staff as written observations or on handheld devices. Observers recorded all sightings of wolves during all westbound trips (see S1 Appendix for more details).

YNP. From 2008 to 2013, YNP staff (R. McIntyre) traveled through the Lamar Canyon and Little America region (Fig 1) every morning (from approximately 0430 or 0500 to 1100 or 1200 hours) and consistently recorded all direct sightings of wolves. These 6 years represent a sample of years with and without harvest, consistent monitoring of sightings, and a relatively stable wolf population. We reviewed the daily field notes and recorded the start and end time of each daily observation period and attributes of every wolf sighting (location and duration of sighting, number of wolves seen, pack affiliations) in June, July and August.

Annual probability of sightings metric. We calculated the annual probability of sighting metric in DNPP as the proportion of bus trips where at least one wolf was seen (S1 Table). In YNP, we calculated this metric as the number of days with direct sightings of wolves in Lamar Valley or Little America (Fig 1) divided by the number of days in the observation period (i.e. number of days in June, July and August), corrected for effort:

$$YNP\ P_{sighting} = \frac{S_t}{O_t} \times \frac{E_t}{E_{max}}$$

where S_t is the number of days with sightings in year *t*, O_t is the number of days in the observation period, E_t is the hours of effort in year *t*, and E_{max} is the maximum number of hours in the field from sampled years (S2 Table).

We predicted that the annual probability of sighting for a wolf was positively related to wolf population size and den site proximity to the roads and negatively related to the number of wolves or breeders harvested. We examined 2 metrics of population size: spring estimates of total wolf population size in each study area (TotalPop), and a metric that combined the estimated size of packs whose home range overlapped park roads (road packs) with distances from den sites to the nearest road (the Pack Near Road Index, or PNRI, Table 2). TotalPop represented a simple and potentially useful metric that could be calculated in spring prior to denning while PNRI was a metric that combined a spatially-explicit measure (den site distance from the

Table 2. Explanatory variables used to model annual probability of sighting rates in Denali National Park, Alaska, USA. Prediction column describes the predicted change in the response variable (annual probability of sighting) to an increase in the explanatory variable.

Variables	Description	Prediction
Wolf Population		
TotalPop	Spring estimates of total wolf population in each study area	Increase
PNRI	Pack Near Road Index. Metric combining the estimated size of road packs with distances of pack den sites to road	Increase
Wolf Harvest		
WolfHarv	Number of wolves harvested adjacent to park boundaries prior to sighting year	Decrease
BreedHarv	Binary, if a breeding wolf from a road pack was harvested in year prior to sighting year	Loss of breeding wolf: decrease
Buffer	Binary, presence or absence of hunting and trapping buffer zone	Presence of buffer zone: increase

doi:10.1371/journal.pone.0153808.t002

road) with a population measure (road pack size). We initially investigated a separate covariate for road pack size alone (S1 and S2 Figs, S6 Table) and found that the metric that combined road pack size and den distance (PNRI) explained more variance in sightings. We therefore used PNRI in our final model set.

TotalPop was obtained by compiling spring wolf pack counts for packs in each study area. We used ArcGIS 10.0 (Environmental Systems Research Institute, Redlands, CA) to assess home range overlap with park roads. PNRI was calculated using pack size and den site distance for road packs. Wolf management plan objectives require closing areas around known den sites to hikers [34]. Thus, den site locations and use were closely monitored for wolf packs in areas along the road corridors. We determined the distance of den sites to the nearest location on the road using the "near" tool in ArcGIS version 10.2 (ESRI 2011, ArcGIS Desktop: Release 10. Redlands, CA: Environmental Systems Research Institute). For all road packs in the sighting year, we divided the pack size by the distance from the pack's den or rendezvous site to the nearest road and defined the PNRI as the sum of these measures for all packs in the sighting year. In cases where there was more than one den or rendezvous site used by a single pack, we used the mean of the distances of multiple den or rendezvous sites as the value for that pack. Thus, an increase in pack sizes or numbers of packs, or a decrease in distances of pack activity centers from the road, would cause PNRI to increase.

For DNPP, we evaluated three metrics describing wolf harvest: number of wolves harvested in the region (WolfHarv), harvest of breeding wolves (BreedHarv) and the presence/absence of a wolf trapping buffer (Buffer) located outside of DNPP (Fig 1).WolfHarv was the number of wolves harvested in Uniform Coding Units (UCUs) 605 and 607 (Fig 1) in the regulatory year prior to the sighting year (July 1 of year t-1 to June 30 of year t). BreedHarv was a binary factor describing if a breeding wolf from a road pack was harvested prior to the sighting year. The trapping buffer was present from 2000–2010 and absent 1997–1999 and 2011–2013 (Table 1). In YNP, we obtained information on the number of wolves harvested outside of YNP from Yellowstone Wolf Project staff in collaboration with state wildlife agency professionals in Montana, Wyoming, and Idaho.

Effect of harvest on sightings

We evaluated factors that influenced annual wolf sightings in DNPP using a suite of generalized linear models and Akaike information criterion corrected for sample sizes and an estimate

Table 3. Candidate model set and model selection criteria evaluating factors potentially affecting probability of wolf sightings along Denali Park Road in Denali National Park and Preserve, Alaska, USA.

Model	K[a]	QAICc	ΔQAICc	Model Likelihood	QAICc Weight
PackNearRoad[b]+Buffer[c]+WolfHarv[d]	4	41.70	0.00	1.00	0.33
PackNearRoad+Buffer	3	42.15	0.44	0.80	0.27
PackNearRoad	2	43.42	1.71	0.43	0.14
PackNearRoad+WolfHarv	3	44.68	2.98	0.23	0.07
Buffer	2	45.92	4.22	0.12	0.04
TotalPop[e]+Buffer	3	45.95	4.25	0.12	0.04
PackNearRoad+Buffer+BreedHarv[f]	4	46.13	4.43	0.11	0.04
PackNearRoad+BreedHarv	3	46.55	4.85	0.09	0.03
TotalPop+Buffer+WolfHarv	4	47.84	6.14	0.05	0.02
TotalPop+Buffer+BreedHarv	4	47.92	6.21	0.04	0.01
TotalPop+BreedHarv	3	49.17	7.47	0.02	0.01
TotalPop	2	50.77	9.07	0.01	0.00
TotalPop+WolfHarv	3	54.10	12.40	0.00	0.00
WolfHarv	2	59.19	17.49	0.00	0.00

[a] Number of parameters in the model

[b] Pack Near Road Index

[c] Buffer is a factor indicating the presence/absence of a wolf hunting and trapping buffer

[d] WolfHarv is the number of wolves harvested in the prior year

[e] TotalPop is the population size

[f] BreedHarv is a factor indicating if breeders were or were not harvested from road packs in the prior year.

doi:10.1371/journal.pone.0153808.t003

of overdispersion (QAICc) to rank models [35]. We used the glm function in Program R (R Core Team 2013) to model wolf sightings using a binomial distribution with the response variable as the annual probability of wolf sightings, weighted by the number of trips per year to account for sample size. Predictor variables consisted of the 2 population and 3 harvest metrics described above (Table 2), and our model set consisted of 14 models selected a-priori that included 1–3 predictors per model (Table 3). We used the MuMIn package in R [36] for model selection and derived untransformed parameter estimates and associated standard errors from the top ranked model.

We used a variance partitioning procedure to quantify how much of the variation of the top-ranked model was explained by the pure effect of each explanatory variable and the interaction of the variables [37–39]. We compared estimates of population size between years with and without the buffer zone using a one-tailed t-test. We used nonparametric Mann-Whitney-Wilcoxon tests to compare PNRI and annual probability of sightings between these periods because these variables did not meet the assumptions of t-tests.

We lacked sufficient years of data in YNP to construct quantitative models of sightings including all covariates. Therefore, we visually examined patterns in the annual sighting metric in relation to TotalPop and PNRI. We compared annual probability of sightings in years with and without harvest of wolves from packs in the prior regulatory year using a one-tailed t-test.

Results

Harvest of collared and breeding wolves

DNPP. Wolves were harvested on state land adjacent to DNPP in 16 of the 17 years in our dataset (1996–2012). Across all 17 years, on average 5 (SD 3.5) wolves were harvested each year (S3 Table). Pooled across all years with harvest, neither the proportion of collared wolves in the harvest (0.25) nor the proportion of known (collared) breeding wolves in the harvest (0.16) were significantly different than expected given their frequency in the population (collared wolves in population: 0.29, $\chi 2 = 0.610$, df = 1, $P = 0.44$, collared breeders in population: 0.17, $\chi 2 = 0.072$ df = 1, $P = 0.79$).

YNP. In 2009, 4 park wolves were harvested from the study area. In 2011, 2 wolves ranging primarily within YNP but not considered members of a road pack were shot close to the park boundary. In 2012, 9 wolves that primarily lived within the Northern Range study area were harvested and a total 12 wolves that lived in the entire YNP were harvested. The proportion of collared wolves in the harvest (0.53) was greater than expected given the proportion of collared wolves in the Northern Range population (0.24, Fisher's exact test: $P = 0.03$). Similarly, in the entire YNP region, the proportion of collared wolves in the harvest (0.56) was greater than expected given the proportion of collared wolves in the YNP population (0.26, Fisher's exact test: $P = 0.01$, S4 and S5 Tables). The proportion of collared breeding wolves in the harvest (0.21) was not significantly different than the proportion of collared breeders in the Northern Range (0.17, 2-sided fisher's exact test, $P = 0.37$).

Annual Probability of Sighting

DNPP. We used sighting data from 2062 trips along the Denali Park Road from 1997–2013. One or more wolves were observed on 307 of the 2062 trips (S1 Table). Both the number of wolves denning near the road and wolf harvest influenced the mean probability of viewing wolves in DNPP. The top ranked model included the Pack Near Road Index (PNRI), the presence of the wolf harvest buffer, and the number of wolves harvested (Table 3). The number of wolves denning near the road was positively associated with the probability of viewing wolves (Table 4). The presence of the buffer was also positively associated with the probability of viewing wolves. The number of wolves harvested in the prior year was negatively associated with the probability of viewing a wolf, although the effect was not significant as the confidence intervals overlapped zero (Table 4).

The pure effects of PNRI, the presence of the buffer, and the number of wolves harvested in the prior year explained 53%, 42.3%, and 15.1%, respectively, of the variation in the top-ranked model. The combined effect of the variables PNRI, buffer presence, and the number of wolves harvested in the prior year explained the largest proportion of variation in the top-ranked model (61.7%).

The annual probability of sighting appeared to roughly follow the trend of the annual PNRI and spring population size, with peaks in sightings coinciding with peaks in either PNRI or total population size (Fig 2, see S1 Fig for figure with road pack size). Population size, PNRI

Table 4. Model-averaged parameter estimates for annual probability of sighting model evaluating factors potentially affecting probability of wolf sightings along Denali Park Road in Denali National Park and Preserve, Alaska.

	β	SE	95% CL	
			Lower	Upper
(Intercept)	-2.70	0.488	-3.660	-1.748
PNRI[a]	22.84	8.455	6.264	39.408
Buffer (Presence)[b]	0.96	0.448	0.082	1.838
WolfHarv[c]	-0.10	0.057	-0.211	0.013

[a] PNRI is the Pack Near Road Index

[b] Buffer is the presence of a wolf hunting and trapping buffer

[c] WolfHarv is the number of wolves harvested in surrounding regions.

doi:10.1371/journal.pone.0153808.t004

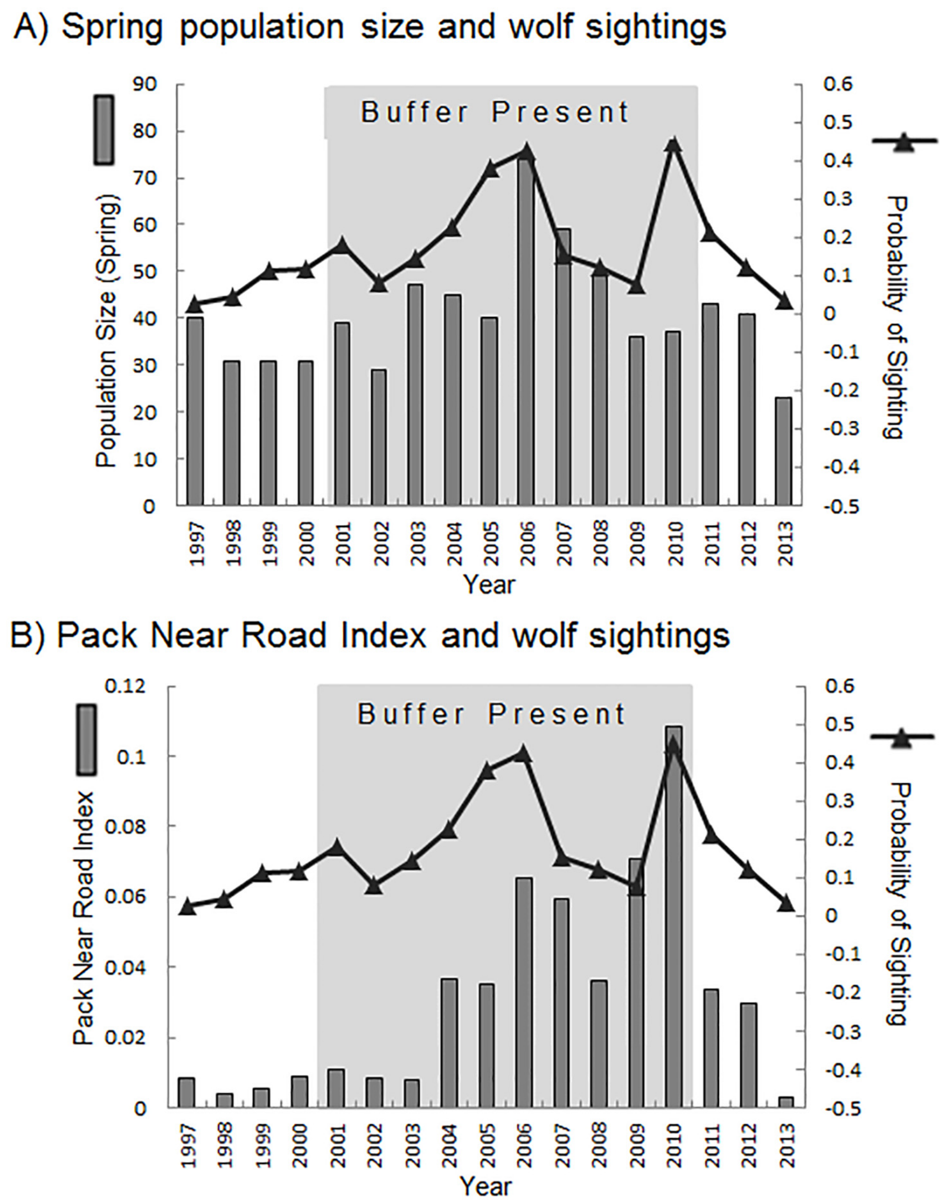


Fig 2. Probability of wolf sighting along the Denali Park Road from 1997 to 2012 (black triangles) in relation to A) spring population size (gray bars) and B) the Pack Near Road Index (number of wolves in road packs divided by den distances from the road, gray bars) in Denali National Park and Preserve, Alaska, USA. Shaded areas indicate the time period (2000–2010) when a harvest buffer zone adjacent to the park was in effect.

doi:10.1371/journal.pone.0153808.g002

and the probability of sighting were significantly higher in years when the buffer zone was in place (Table 5, Fig 3).

YNP. We used sighting data from 552 days in YNP from 2008–2013. One or more wolves were observed during 436 of the 552 days (S2 Table). There were 2 years of sighting data following harvest from YNP road packs (2010 and 2013) and 4 years with no prior road pack harvest (2008, 2009, 2011 and 2012). The annual probability of sighting metric for YNP appeared to roughly mirror spring population size and PNRI, but sightings were lower in years following

Table 5. Comparisons of the annual probability of wolf sighting, wolf population, and Pack Near Road Index (PNRI) for years following the presence (2001–2010) and absence (1997–2000, 2011–2013) of a hunting and trapping buffer adjacent to Denali National Park and Preserve, AK, USA. Table entries are the mean values (SE), test statistics (*t* for t-test and *W* for Mann-Whitney-Wilcoxon test), and associated probability for each metric.

	Buffer	No Buffer	Test Stat	*P*-value
Population	45.5 (4.11)	34.3 (2.73)	$t_{15} = -2.27$	0.039
Sightings	0.22 (0.045)	0.10 (0.025)	$W = 57$	0.033
PNRI	0.04 (0.010)	0.01 (0.005)	$W = 60$	0.014

doi:10.1371/journal.pone.0153808.t005

harvest of wolves from road packs than in years with similar population size (Fig 4, see S2 Fig for figure with road pack size). The mean probability of sighting was lower following years with harvest of road pack wolves (0.54 ± 0.127 SE) than in years without harvest of a road pack wolf (0.78 ± 0.084 SE, $t_4 = 2.88$, $P = 0.02$, Fig 4). If we consider 2012 as a post-harvest year (based on the harvest of 2 non-road pack wolves in 2011), the mean probability of sighting was not significantly different between years following harvest (0.64 ± 0.040 SE) and years without harvest (0.76 ± 0.086 SE, $t_4 = 0.92$, $P = 0.21$).

Discussion

This study provides the first quantitative evidence that harvest of wildlife adjacent to protected areas can reduce wildlife sighting opportunities. Harvest of wolves was associated with reduced sightings in both Denali and Yellowstone National Parks. The probability of viewing a wolf was 45% greater in YNP following years with no harvest of a wolf from a road pack, and sightings in DNPP were more than twice as high in years with the presence of a wolf harvest buffer (Fig 4). There was a trend indicating that sightings decreased as the number of wolves harvested adjacent to DNPP increased, although the relationship was weak. These findings imply a tradeoff between harvest (i.e., consumptive use) of large carnivores and the non-consumptive viewing opportunities and associated economic benefits. Additionally, we found that population size, pack size and den site location were strong drivers of sighting opportunities for wolves within these protected areas. These findings suggest that harvest is likely to have particularly strong effects on sightings when harvest reduces population size or affects breeding behavior within protected regions.

Human-caused mortality of large carnivores adjacent to protected areas can lead to population declines within the protected region [40–42] which our research indicates has the largest potential to decrease viewing opportunities. Although harvest of wolves in our study systems may not have occurred at rates generally considered sufficient to reduce population size (reviewed in [43]), harvest may influence sightings through other mechanisms. Behavioral avoidance of humans by wolves following exposure to hunting or trapping could reduce sightings. Although wolves show preference for linear travel corridors [44] and roads with low levels of traffic [8,45], wolves will avoid of high levels of human activity [46–48]. The presence of hunters is known to affect large carnivore behavior and movements [49]. However, the direct link between exposure to harvest and subsequent behavioral avoidance leading to reduction in sightings was not explicitly tested in our analysis and warrants further investigation. Monitoring behavior of large carnivores that survive negative encounters with humans is needed to determine the strength of these anti-predatory responses.

Selection for behavioral traits may be another method by which harvest of carnivores could decrease sightings. In our study systems, a small number of wolves may contribute to a large number of wolf sighting opportunities. Harvest can selectively target 'bold' individuals [50, 51], thereby removing bold individuals and over time, the trait, from populations. Indeed,

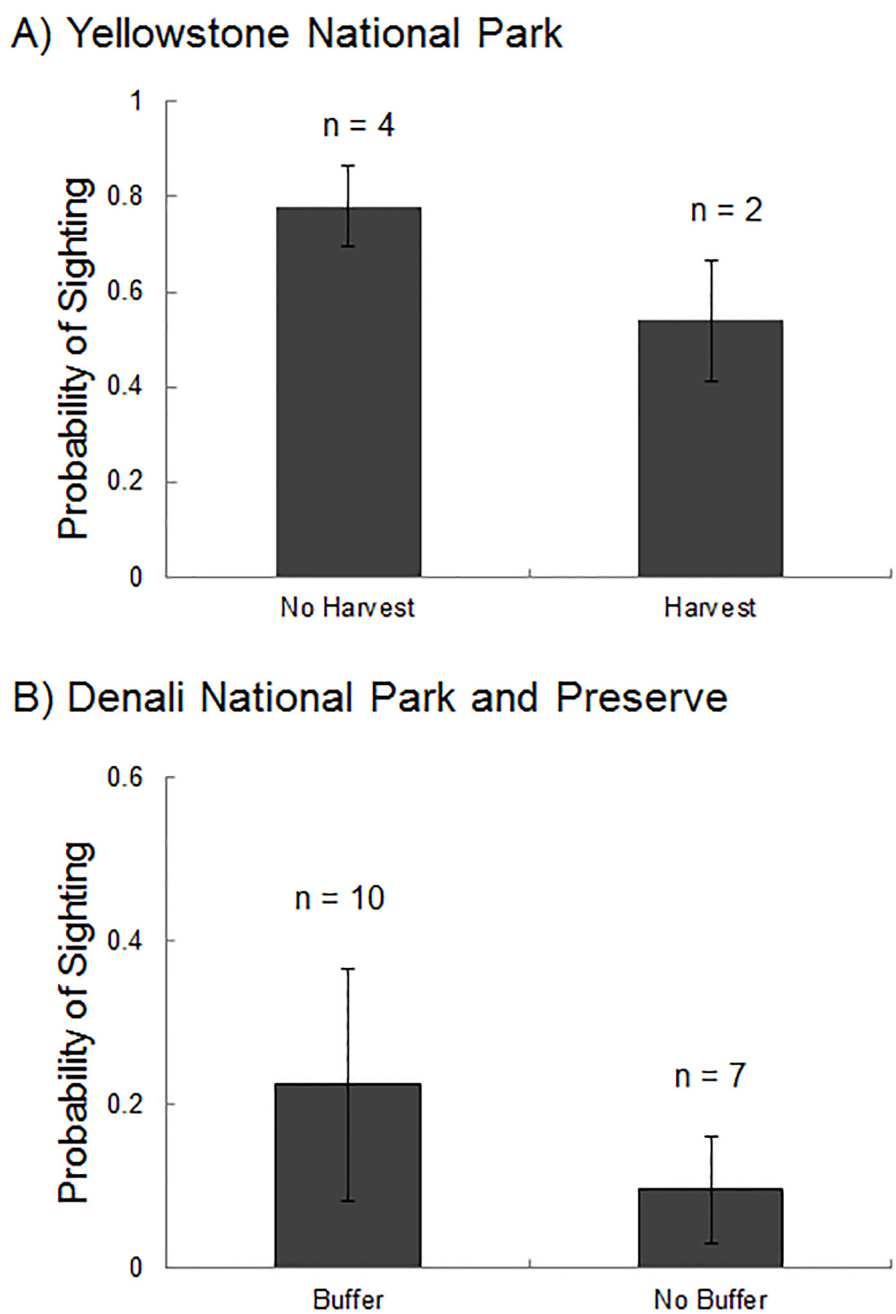


Fig 3. Mean probability of sighting for wolves A) in Lamar Valley and Little America following years with and without harvest of pack wolves, Yellowstone National Park, Wyoming, USA and B) along the Denali Park Road following years with and without the presence of a buffer zone prohibiting the trapping and hunting of wolves outside of Denali National Park and Preserve, Alaska, USA. Standard error bars and sample sizes (number of years) are shown.

doi:10.1371/journal.pone.0153808.g003

phenotypic changes driven by human harvest can outpace selection of traits driven by other forces [52]. As large carnivores that are less wary may contribute disproportionately to viewing opportunities, sightings could decrease if harvest selects these individuals.

We hypothesized that harvest of breeding wolves would disproportionately influence sightings, because these individuals play an important role in pack continuity and reproduction [9,

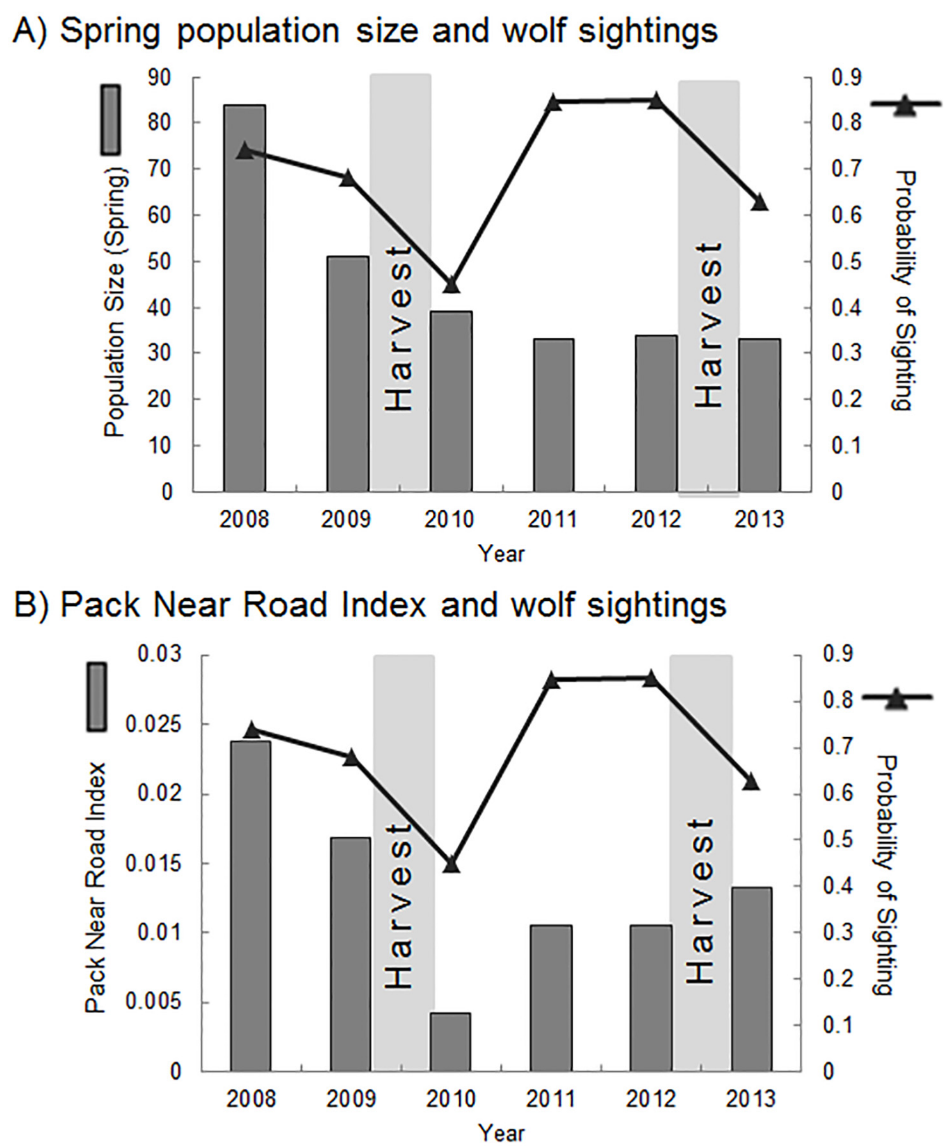


Fig 4. Probability of wolf sighting in Little America and Lamar Valley from 2008–2012 (black triangles) in relation to A) spring population size and B) Pack Near Road Index (number of wolves in road packs divided by den distances from the road) in Yellowstone National Park, Wyoming, USA. Shaded areas indicate years following harvest of wolves from packs. Two non-pack wolves were harvested prior to 2012.

doi:10.1371/journal.pone.0153808.g004

53] and were more likely to be near the road than non-breeding wolves [22]. Although harvest reduced sightings, the breeding status of harvested wolves was not identified as an important factor in our analyses (Table 1). Instead, our results suggest that harvest of wolves from road packs may have a larger influence on sightings than harvest of other wolves. Sightings were not reduced in YNP following the harvest of 2 wolves that were not members of road packs. These wolves resided in the park but likely contributed little to sightings as they did not live along the road corridor. However, we caution that our results from YNP were based on a limited sample size. We recommend continued monitoring of carnivore sightings and increased emphasis on identifying age, reproductive status and social group affiliation for carnivores harvested adjacent to protected areas to increase our understanding of these influences on sightings.

Collared wolves made up over half of the harvest adjacent to YNP but were only approximately a quarter of wolves in the YNP population, whereas collared wolves were harvested in proportion to their occurrence in the DNPP population. A major difference between these parks is that harvest near YNP is through hunting whereas harvest near DNPP is primarily through trapping. Although both harvest methods have the potential to act as selective forces on behavioral traits (i.e. bold or unwary individuals), hunting involves more active selection by humans whereas trapping passively selects wolves. This distinction could explain why there was disproportional harvest of collared wolves adjacent to YNP and not adjacent to DNPP if hunters targeted collared wolves. It is important to note that results from YNP were based on three years of data, and longer term analysis could yield different results. Still, the disproportional harvest of collared individuals may be a mechanism by which sightings decrease following harvest, as the presence of collared individuals aids in locating individuals (R. McIntyre, pers. obs.) or understanding behavioral patterns [54] thereby creating viewing opportunities.

In both parks, the number of identified breeders that were harvested was not different than expected given their proportion in the population. We expected that breeders would be less likely to be harvested, particularly when trapping was the primary source of harvest, as in DNPP [23]. It is possible that the benefit of experience and age in avoiding trapping may be offset in protected regions by habituation to human activity and use of linear travel corridors during the summer months [8]. Given that the primary source of harvest was hunting, the result in YNP is consistent with previous findings [23–25].

The presence of the trapping and hunting buffer zone was associated with increased wolf sightings in DNPP. Both the wolf population size and PNRI, which were strongly associated with increased wolf sightings, were also greater during the period when the buffer zone was in place. Thus, the presence of the buffer may have influenced local population size and the likelihood that wolves would den near the park road. Alternatively, the increase in sightings may have been a result of coincidental peaks in population size or PNRI as a result of variables not measured or explicitly included in our models. Two variables generally considered to be strong drivers of wolf population dynamics are prey density and snow conditions, which influence prey vulnerability to wolf predation [27]. However, during the period of the study, prey densities were relatively consistent [55–57]. Similarly, although snow conditions varied among years, there has been no statistically significant trend in the annual snowfall data for park headquarters over the past 20 years [58]. Traffic levels, managed at a consistent level during the study period, likely did not influence annual trends in sightings. Similarly in YNP, there was a decrease in sightings during years with harvest that did not appear to be explained by a change in wolf population size or change in the size of packs near the road (Figs 3 and 4). Although our sample size was low, the decrease was statistically significant. Neither climatic conditions nor prey base were thought to significantly alter wolf population dynamics in YNP during the study period. The elk population was stable during the study time period, and although snow depth in winter 2010–2011 was above average, the other winters were within the average range for snowfall and temperature [59]. Although there was an increase in visitation in YNP during the study period, there was no indication that annual wolf sighting trends were influenced by this pattern in visitation [33].

The opportunity to view free ranging large carnivores is an important driver for wildlife tourism worldwide, and the National Park Service mission in particular emphasizes the preservation of wildlife resources in their natural condition for the non-consumptive benefit and enjoyment of the public. Thus, factors that influence sightings of iconic wildlife such as wolves are important to track and understand. Here, we have shown that consumptive use of a large carnivore reduces opportunities for non-consumptive use in protected areas. Limiting harvest of large carnivores along the boundaries of protected areas may provide a strategy to increase sighting opportunities for visitors to these areas and the associated economic benefits to adjacent communities. However, there are associated costs of limiting harvest, given the revenue generated from hunting [17, 19, 60] and the potential of harvest to reduce threats to livestock and increase land owner's acceptance of large carnivores [61, 62]. Cross boundary movements will continue to make large carnivore management an on-going source of debate. Wolf viewing and harvest opportunities are 2 of the many issues surrounding cross boundary wolf management. There are many stakeholders, including state and federal management agencies, private land owners, trappers, hunters, non-profit agencies, environmental advocates, and the general public Effective management in areas where cross boundary movements are common requires knowledge of complex system dynamics, in addition to understanding and defining the objectives of stakeholders, and quantifying the associated costs and benefits of management actions.

Supporting Information

S1 Appendix. Recording Wildlife Sightings in Denali National Park and Preserve.
(DOCX)

S1 Fig. Wolves in road packs and the probability of wolf sightings along the Denali Park Road, Alaska, USA. Cumulative count of wolves in road packs in the eastern region of Denali National Park and Preserve (grey bars) and the probability of wolf sightings along the Denali Park Road (black triangles) from 1997 to 2012. Shading indicates years with a harvest buffer zone adjacent to the park in effect.
(TIF)

S2 Fig. Wolves in road packs and the probability of wolf sightings in Yellowstone National Park, Wyoming, USA. Cumulative count of wolves in road packs in the Northern Range of Yellowstone National Park (grey bars) and probability of wolf sightings in Little America and Lamar Valley (black triangles) from 2008–2012. Hashed bars indicate years preceded by harvest of wolves from road packs. Light gray shading indicates years preceded by harvest of non-pack wolves.
(TIF)

S1 Table. Annual probability of sighting index for Denali National Park and Preserve, Alaska, USA. Sample size (in number of trips), number of trips with wolf sightings, and annual probability of sighting index for wolves along the Denali Park Road from 1997 to 2013.
(DOCX)

S2 Table. Annual probability of sighting index for Yellowstone National Park, Wyoming, USA. Sample size (in number of days within the observation period), number of days with wolf sightings, relative effort for each year (calculated as hours of effort in the given year divided by the maximum number of hours in the field from sampled years), and annual probability of sighting index for wolves in the Lamar Valley and Little America region of Yellowstone National Park from 2008 to 2013.
(DOCX)

S3 Table. Summary of wolf harvest for the Eastern Region of Denali National Park and Preserve, Alaska, USA. Population size estimates, number of collared wolves, number of collared breeding wolves, and their proportions in the population and harvest included. Population size, number of collared wolves, and number of collared breeders were pre-hunt numbers.
(DOCX)

S4 Table. Summary of wolf harvest for Northern Range packs (including Mollie's pack) in Yellowstone National Park, Wyoming, USA. Population size estimates, number of collared wolves, number of collared breeding wolves, and their proportions in the population and harvest for Northern Range packs (including Mollie's pack) included. Population size, number of collared wolves, and number of collared breeders were pre-hunt numbers.
(DOCX)

S5 Table. Summary of wolf harvest for wolf packs in Yellowstone National Park, Wyoming, USA. Population size estimates, number of collared wolves, number of collared breeding wolves, and their proportions in the population and harvest included. Population size and number of collared wolves were pre-hunt numbers.
(DOCX)

S6 Table. Model selection table evaluating factors potentially affecting probability of wolf sightings in Denali National Park and Preserve, Alaska, USA (including the factor RoadPop). Candidate model set includes the factor RoadPop. K is the number of parameters in the model, PNRI is the Pack Near Road Index, TotalPop is the wolf population size, RoadPop is the number of wolves in packs that overlap the Denali Park Road, Buffer is a factor indicating the presence/absence of a harvest buffer, WolfHarv is the number of wolves harvested in the prior year and BreedHarv is a binary factor describing if breeders were or were not harvested from road packs in the prior year.
(DOCX)

Acknowledgments

L. D. Mech, L. Adams, J. Burch, B. Dale and T. Meier pioneered the long term study wolf study in Denali National Park and Preserve and collected data from 1986 to 2012. J. Drain, R. Rausch diligently reviewed and summarized YNP sighting data. S. Brainerd, G. Hilderbrand, M. Lindberg provided valuable comments on earlier versions of this manuscript. Any use of trade, firm or product names is for descriptive purposes only and does not imply endorsement by the United States Government.

Author Contributions

Conceived and designed the experiments: BB LP. Performed the experiments: BB RM. Analyzed the data: BB NB KC LP. Contributed reagents/materials/analysis tools: BB SA NB KC RM DS LP. Wrote the paper: BB SA NB KC RM DS LP.

References

1. Brashares JS, Arcese P, Sam MK. Human demography and reserve size predict wildlife extinction in West Africa. Proc R Soc B Biol Sci. 2001;268.
2. Walpole MJ, Thouless CR. Increasing the value of wildlife through non-consumptive use? Deconstructing the myths of ecotoursim and community-based tourism in the tropics. In: Woodroffe R, Thirgood S, Rabinowitz A, editors. People and Wildlife, Conflict or Co-existence? New York, New York: Cambridge University Press; 2005. pp. 122–139.
3. Frank LG, Woodroffe R, Ogada MO. People and predators in Laikipai District, Kenya. In: Woodroffe R, Thirgood S, Rabinowitz A, editors. People and Wildlife, Conflict or Co-existence? New York, New York: Cambridge University Press; 2005. pp. 286–304.
4. Dickman AJ, Macdonald EA, Macdonald DW. A review of financial instruments to pay for predator conservation and encourage human–carnivore coexistence. Proc Natl Acad Sci. 2011; 108: 13937–13944. doi: 10.1073/pnas.1012972108 PMID: 21873181
5. Woodroffe R, Ginsberg JR. Edge effects and the extinction of populations inside protected areas. Science. 1998; 280: 2126–2129. PMID: 9641920

6. Balme GA, Slotow R, Hunter LTB. Edge effects and the impact of non-protected areas in carnivore conservation: leopards in the Phinda-Mkhuze Complex, South Africa. Anim Conserv. 2010; 13: 315–323.
7. Murray DL, Smith DW, Bangs EE, Mack C, Oakleaf JK, Fontaine J, et al. Death from anthropogenic causes is partially compensatory in recovering wolf populations. Biol Conserv. 2010; 143: 2514–2524.
8. Thurber JM, Peterson RO, Drummer TD, Thomasma SA. Gray wolf response to refuge boundaries and roads in Alaska. Wildl Soc Bull. 1994; 22: 61–68.
9. Borg BL, Brainerd SM, Meier TJ, Prugh LR. Impacts of breeder loss on social structure, reproduction and population growth in a social canid. J Anim Ecol. 2015; 84: 177–187. doi: 10.1111/1365-2656.12256 PMID: 25041127
10. Ray JC, Hunter L, Zigouris J. Setting conservation and research priorities for larger African carnivores. Bronyx, NY; 2005. Report No.: 24.
11. Duffield JW, Neher CJ, Patterson DA. Wolf recovery in Yellowstone: park visitor attitudes, expenditures, and economic impacts. Yellowstone Sci. 2008; 16: 20–25.
12. Manning RE, Hallo JC. The Denali park road experience: Indicators and standards of quality. Park Sci. 2010; 27: 33–41.
13. Shea L, Tankersley N. Alaska's tourism potential. Alaska's Wildl. 1991; 23: 6–41.
14. Alaska Department of Fish and Game. Our wealth maintained: a strategy for conserving Alaska's diverse wildlife and fish resources. Wildlife Action Plan. Juneau (AK): Alaska Department of Fish and Game; 2006. p. 824.
15. U.S. Department of the Interior, U.S. Fish and Wildlife Service, U.S. Department of Commerce, U.S. Census Bureau. National Survey of Fishing, Hunting, and Wildlife-Associated Recreation. 2011.
16. Stynes DJ, Ackerman A. Impacts of visitor spending on the local ecomony: Denali National Park and Preserve. Final report. East Lansing (MI): Michigan State University; 2010.
17. ECONorthwest. The Economic Importance of Alaska's Wildlife in 2011. Summary report. Portland (OR); 2012. Contract No. IHP-12-052.
18. National Research Council. Wolves, Bears, and Their Prey in Alaska. Washington, DC; 1997.
19. Montana Fish Wildlife and Parks. 2011 Montana Wolf Hunting Season Report. 2011.
20. Schweber N. "Famous" Wolf Is Killed Outside Yellowstone. The New York Times. New York, New York; 2012 Dec 8.
21. Wolf Viewing Project -Denali National Park and Preserve [Internet]. 2014. Available: http://www.nps.gov/dena/naturescience/wolfviewing.htm
22. Borg BL. Effects of harvest on wolf social structure, population dynamics and viewing opportunites in National Parks [dissertation]. Fairbanks (AK): University of Fairbanks; 2015.
23. Adams LG, Stephenson RO, Dale BW, Ahgook RT, Demma DJ. Population dynamics and harvest characteristics of wolves in the Central Brooks Range, Alaska. Wildl Monogr. 2008; 170: 1–25.
24. Peterson RO, Woolington JD, Bailey TN. Wolves of the Kenai Peninsula, Alaska. Wildl Monogr. 1984; 3–52.
25. Ballard WB, Whitman JS, Gardner CL. Ecology of an exploited wolf population in South-Central Alaska. Wildl Monogr. 1987; 1–54.
26. Houston DB. The northern Yellowstone elk: ecology and management. New York (NY): MacMillan; 1982.
27. Mech LD, Adams LG, Meier TJ, Burch JW, Dale BW. The Wolves of Denali. Minneapolis (MN): University of Minnesota Press; 1998.
28. Bangs EE, Fritts SH. Reintroducing the gray wolf to Central Idaho and Yellowstone National Park. Wildl Soc Bull. 1996; 24: 402–413.
29. Meier TJ, Burch JW, Wilder D, Cook M. Wolf monitoring protocols for Denali National Park and Preserve, Yukon-Charley Rivers National Preserve and Wrangell-St. Elias National Park and Preserve, Alaska. Protocol-2167760. Fort Collins (CO); 2009.
30. Smith DW, Stahler DR, Stahler E, Metz M, Quimby K, McIntyre R, et al. Yellowstone Wolf Project Annual Report 2012. Yellowstone National Park (WY); 2012.
31. Sikes RS, Gannon WL, The Animal Care and Use Committee of the American Society of Mammalogists. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. J Mammal. 2011; 92: 235–253.
32. National Park Service. General Management Plan, Denali National Park and Preserve, Alaska. NPS D-96-A. Denver Service Center (CO); 1986.

33. National Park Service. National Park Service Visitor Use Statistics [Internet]. 2016 [cited 3 Jan 2016]. Available: https://irma.nps.gov/Stats/Reports/Park/YELL Service.
34. National Park Service. Wolf-human conflict management plan, Denali National Park and Preserve. Denali National Park and Preserve (AK); 2007. p. 85.
35. Burnham KP, Anderson DR. Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach. 2nd ed. New York (NY): Springer Verlag; 2002.
36. Barton K. MuMIn: Multi-Model Inference. R package version 1.12.1. 2014.
37. Legendre P. Spatial autocorrelation: trouble or new paradigm? Ecology. 1993; 74: 1659–1673.
38. Legendre P, Legendre L. Numerical Ecology. Amsterdam: Elsevier Science; 1998.
39. Muñoz AR, Real R, Barbosa AM, Vargas JM. Modelling the distribution of Bonelli's eagle in Spain: implications for conservation planning. Divers Distrib. 2005; 11: 477–486. doi: 10.1111/j.1366-9516.2005.00188.x
40. Woodroffe R, Ginsberg JR. Edge effects and the extinction of populations inside protected areas. Science. 1998; 280: 2126–2129. PMID: 9641920
41. Croes BM, Funston PJ, Rasmussen G, Buij R, Saleh A, Tumenta PN, et al. The impact of trophy hunting on lions (Panthera leo) and other large carnivores in the Benoue Complex, northern Cameroon. Biol Conserv. 2011; 144: 3064–3072.
42. Packer C, Brink H, Kissui BM, Maliti H, Kushnir H, Caro T. Effects of trophy hunting on lion and leopard population in Tanzania. Conserv Biol. 2011; 25: 142–153. doi: 10.1111/j.1523-1739.2010.01576.x PMID: 20825444
43. Fuller TK, Mech LD, Cochrane JF. Wolf population dynamics. In: Mech LD, Boitani L, editors. Wolves: Behavior, Ecology and Conservation. Chicago and London: University of Chicago Press; 2003. pp. 161–191.
44. James ARC, Stuart-Smith AK. Distribution of caribou and wolves in relation to linear corridors. J Wildl Manage. 2000; 64: 154–159.
45. Ciucci P, Masi M, Boitani L. Winter habitat and travel route selection by wolves in the northern Apennines, Italy. Ecography. 2003; 26: 223–235.
46. Theuerkauf J, J□drzejewski W, Schmidt K, Gula R. Spatiotemporal segregation of wolves from humans in the Bialowieza Forest (Poland). J Wildl Manage. 2003; 67: 706–716.
47. Whittington J, St. Clair CC, Mercer G. Spatial responses of wolves to roads and trails in mountain valleys. Ecol Appl. 2005; 15: 543–553.
48. Hebblewhite M, Merrill E. Modelling wildlife-human relationships for social species with mixed-effects resource selection models. J Appl Ecol. 2008; 45: 834–844.
49. Ruth TK, Buotte PC, Quigley HB, Smith DW, Murphy KM, Haroldson M a, et al. Large-carnivore response to recreational big-game hunting along the Yellowstone National Park and Absaroka-Beartooth Wilderness boundary. Wildl Soc Bull. 2003; 31: 1150–1161.
50. Ciuti S, Muhly TB, Paton DG, McDevitt a. D, Musiani M, Boyce MS. Human selection of elk behavioural traits in a landscape of fear. Proc R Soc B Biol Sci. 2012; 279: 4407–4416.
51. Madden JR, Whiteside MA. Selection on behavioural traits during "unselective" harvest. Anim Behav. 2014; 87: 129–136.
52. Darimont CT, Carlson SM, Kinnison MT, Paquet PC, Reimchen TE, Wilmers CC. Human predators outpace other agents of trait change in the wild. Proc Natl Acad Sci U S A. 2009; 106: 952–954. doi: 10.1073/pnas.0809235106 PMID: 19139415
53. Brainerd SM, Andrén H, Bangs EE, Bradley EH, Fontaine J a., Hall W, et al. The effects of breeder loss on wolves. J Wildl Manage. The Wildlife Society; 2008; 72: 89–98.
54. Stander PE. Tourism and the Conservation of Desert Lions in Namibia. Research report. Desert Lion Conservation; 2008.
55. Adams LG, Roffler G. Dynamics of the Denali Caribou Herd, Denali National Park, Alaska: Progress Report. Anchorage (AK); 2009.
56. Owen PA, Meier TJ. 2008 Aerial Moose Survey, Denali National Park and Preserve. Final report. Denali Park (AK); 2009.
57. Schmidt JH, Rattenbury KL. Reducing effort while improving inference: Estimating Dall's sheep abundance and composition in small areas. J Wildl Manage. 2013; 77: 1048–1058.
58. Western Regional Climate Center. Cooperative Climatological Data Summaries [Internet]. 2015 [cited 5 Mar 2015]. Available: http://www.wrcc.dri.edu/climatedata/climsum/
59. NOAA. National Oceanographic and Atmospheric Association National Climatic Data Center website [Internet]. 2015 [cited 5 Feb 2014]. Available: http://www.ncdc.noaa.gov/

60. Loveridge AJ, Searle AW, Murindagomo F, Macdonald DW. The impact of sport-hunting on the population dynamics of an African lion population in a protected area. Biol Conserv. 2007; 134: 548–558.

61. Treves A. Hunting for large carnivore conservation. J Appl Ecol. 2009; 46: 1350–1356.

62. Mech LD. Considerations for Developing Wolf harvesting regulations in the contiguous United States. J Wildl Manage. 2010; 74: 1421–1424.

Journal of Animal Ecology

British Ecological Society

Journal of Animal Ecology 2015, **84,** 177–187 doi: 10.1111/1365-2656.12256

Impacts of breeder loss on social structure, reproduction and population growth in a social canid

Bridget L. Borg[1,2]*, Scott M. Brainerd[1,3], Thomas J. Meier[2]† and Laura R. Prugh[1]

[1]*University of Alaska Fairbanks, Institute of Arctic Biology, 323 Murie Building, Fairbanks, AK 99775, USA;* [2]*National Park Service, Denali National Park and Preserve, P.O. Box 9, Denali Park, AK 99755, USA; and* [3]*Alaska Department of Fish & Game, Division of Wildlife Conservation, 1300 College Rd, Fairbanks, AK 99701, USA*

Summary

1. The importance of individuals to the dynamics of populations may depend on reproductive status, especially for species with complex social structure. Loss of reproductive individuals in socially complex species could disproportionately affect population dynamics by destabilizing social structure and reducing population growth. Alternatively, compensatory mechanisms such as rapid replacement of breeders may result in little disruption. The impact of breeder loss on the population dynamics of social species remains poorly understood.

2. We evaluated the effect of breeder loss on social stability, recruitment and population growth of grey wolves (*Canis lupus*) in Denali National Park and Preserve, Alaska using a 26-year dataset of 387 radiocollared wolves. Harvest of breeding wolves is a highly contentious conservation and management issue worldwide, with unknown population-level consequences.

3. Breeder loss preceded 77% of cases (n = 53) of pack dissolution from 1986 to 2012. Packs were more likely to dissolve if a female or both breeders were lost and pack size was small. Harvest of breeders increased the probability of pack dissolution, likely because the timing of harvest coincided with the breeding season of wolves. Rates of denning and successful recruitment were uniformly high for packs that did not experience breeder loss; however, packs that lost breeders exhibited lower denning and recruitment rates. Breeder mortality and pack dissolution had no significant effects on immediate or longer term population dynamics.

4. Our results indicate the importance of breeding individuals is context dependent. The impact of breeder loss on social group persistence, reproduction and population growth may be greatest when average group sizes are small and mortality occurs during the breeding season. This study highlights the importance of reproductive individuals in maintaining group cohesion in social species, but at the population level socially complex species may be resilient to disruption and harvest through strong compensatory mechanisms.

Key-words: *Canis lupus*, den fidelity, gray wolf, grey wolf, harvest mortality, hunting pack dynamics, reproductive heterogeneity, social organization, social species, trapping

Introduction

Many species have evolved complex social systems in which only a few individuals within a social group reproduce. For example, reproduction among subordinates can be suppressed or delayed in eusocial animals (e.g. Wilson 1971), a number of bird species (Arnold & Owens 1998), and in social carnivores (Kleiman 1977; MacDonald 1983). The importance of specific individuals may be especially variable for social species that exhibit reproductive suppression of subordinates, because this suppression creates skewed heterogeneity in the reproductive value of individuals (e.g. Stahler *et al*. 2013). Population models are particularly sensitive to variation in reproductive performance among individuals or age classes (Kendall *et al*. 2011; Lindberg, Sedinger & Lebreton 2013). However, the impact of reproductive individuals on the population dynamics of species with complex social structure remains poorly understood. Mortality of reproductive individuals may disproportionately affect population growth, unless other reproductively viable individuals are able to take their place with little disruption. In this study, we examine the

*Correspondence author. E-mail: bridget_borg@nps.gov
†Deceased

effects of mortality of reproductive individuals ("breeders") on grey wolf (*Canis lupus*) social structure, reproduction, and population growth using a 26-year data set from Denali National Park and Preserve (DNPP) in interior Alaska.

As long-lived canids with a family-based social system (Mech 2000), grey wolf pack and population dynamics may be highly sensitive to the fate of breeders. Breeders and/or dominant individuals play an important role in pup survival (Brainerd *et al.* 2008), hunting behaviour and efficiency (Sand *et al.* 2006; MacNulty *et al.* 2011) and interpack competitions (Cassidy 2013). However, early models of wolf population dynamics ignored this source of individual variation (Soule 1980, 1987; Keith 1983; Fuller 1989; Boyce 1990) and generally failed to predict dynamics accurately (Fuller, Mech & Cochrane 2003). More recent models have accounted for wolf social structure (Haight & Mech 1997; Vucetich, Peterson & Waite 1997; Haight, Mlandenoff & Wydeven 1998; Cochrane & Fitts 2000; Haight *et al.* 2002; Fuller, Mech & Cochrane 2003), but we still lack an adequate understanding of how the loss of breeding individuals affects pack and population dynamics. Better understanding of how social structure relates to population viability and the fitness of wolves has been identified as a priority for wolf management and conservation (Stenglein *et al.* 2011).

There is growing recognition of the importance of explicitly considering sources of heterogeneity in harvest management of vertebrates (Lindberg, Sedinger & Lebreton 2013), because harvest of individuals with high reproductive value can have a greater effect on population dynamics than harvest of individuals with low reproductive value (Kokko 2001; Hauser, Cooch & Lebreton 2006). Understanding the consequences of breeder mortality on wolf population dynamics is increasingly important as wolves recolonize areas of North America and Europe (Wabakken *et al.* 2001; USFWS 2007; Wydeven *et al.* 2009). Wolves have recently been delisted from the Endangered Species Act (ESA) in several of the United States and are currently subject to hunting and trapping in regions of the United States and Europe. Scientists, policy makers and the public continue to debate what constitutes a sustainable level of harvest for these wolf populations. Progress in resolving this debate is hindered in part because the effect of breeder loss on the population dynamics of social species such as wolves remains largely unknown.

Wolf populations have typically been viewed as highly resilient to harvest (reviewed in Fuller, Mech & Cochrane 2003; Adams *et al.* 2008), but recent studies suggest wolf populations may be less resistant to harvest impacts than previously thought (Smith *et al.* 2010; Creel & Rotella 2010; Sparkman, Waits & Murray 2011; but see Gude *et al.* 2012). We hypothesize that the level of sustainable wolf harvest may depend on the breeding status of harvested wolves and the timing of harvest. For example, removal of a breeding female, especially if timed during the breeding season, may induce reproductive failure for the pack that year (Brainerd *et al.* 2008; Stahler *et al.* 2013). If individuals of high reproductive value, such as breeding wolves, are selectively harvested or disproportionately vulnerable to harvest, the level of harvest that can occur without population level impacts may be lower than commonly accepted thresholds (Lindberg, Sedinger & Lebreton 2013).

In a previous analysis of breeder loss in wolves, Brainerd *et al.* (2008) found that pack fate (i.e. whether a pack persisted or dissolved) depended on pack size prior to breeder loss and whether one or both breeders died. However, the effect of breeder loss on population growth was not assessed. Additionally, the importance of other factors that could moderate the effects of breeder loss on pack maintenance or population growth, such as the timing and cause of mortality, remains unknown.

We evaluated the impacts of anthropogenic and natural mortality of breeders on wolf pack maintenance, reproduction and population growth using data on 387 radiocollared wolves in 70 packs. We hypothesized that the sex of breeder lost, pack size prior to loss and the timing of loss would influence pack fate, denning behaviour, pup recruitment and population growth. Anticipating high overlap between anthropogenic mortality and the breeding season, we also expected cause of death to affect pack fate. We hypothesized that loss of breeders and packs could reduce population growth primarily by reducing the reproductive capacity of the population (Mech *et al.* 1998; Fuller, Mech & Cochrane 2003). Alternatively, breeders could be replaced with negligible impact or even a positive effect on population growth. Pack dissolution may create opportunities for existing packs to usurp old territories, allow new pairs to set up territories where packs have dissolved, or packs may subdivide existing wolf territories with the effect of increasing wolf densities locally (Ballard & Stephenson 1982; Meier *et al.* 1995; Mech *et al.* 1998; Mech & Boitani 2003).

Materials and methods

STUDY AREA

The study area encompassed *c.* 17 270 km^2 of wolf habitat primarily north and west of the Alaska Range in and adjacent to DNPP (Fig. 1). The eastern region of DNPP contains habitat patches of high alpine, open gravel river bars, and willow-lined creeks. The western region of the park is more homogenous, dominated by relatively flat, lowland black spruce (*Picea mariana*) forest and long meandering rivers and wetlands. The diversity of habitat types in the eastern region of the DNPP supports caribou (*Rangifer tarandus*), Dall's sheep (*Ovis dalli*), and moose (*Alces alces*) populations. The western lowlands support lower densities of ungulates (primarily moose), and salmon are an important food source for wolves in this region (Mech *et al.* 1998; Adams & Roffler 2009; Owen & Meier 2009; Adams *et al.* 2010).

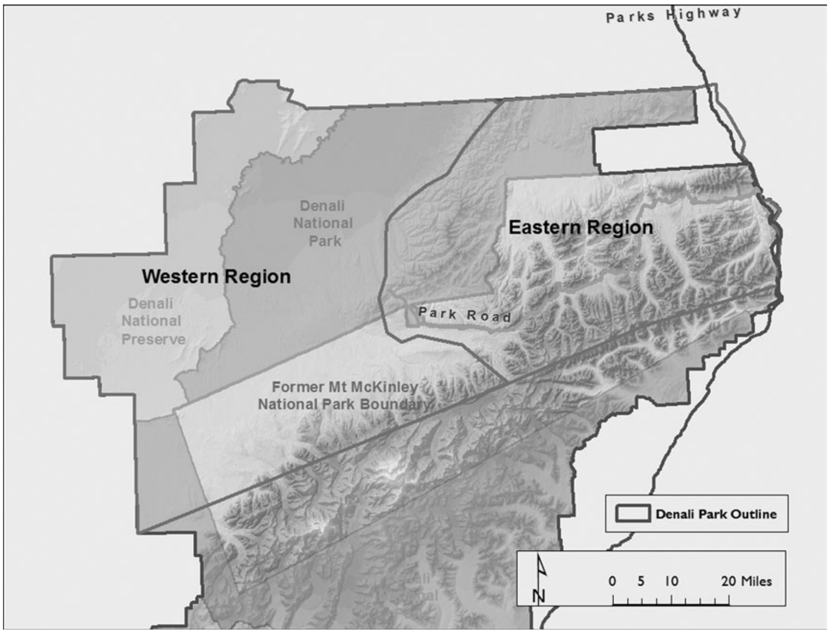


Fig. 1. Map of study area and geographical regions for long term monitoring of grey wolf packs in Denali National Park and Preserve, Alaska, USA.

DATA COLLECTION

Wolf population monitoring efforts in DNPP and use of radiotelemetry for tracking and monitoring packs began in 1986 (Mech *et al.* 1998). From 1986 to 2012, 387 individual wolves were radiocollared with very high frequency (VHF) collars (Meier 2011). From 2003 to 2012, 30 of the VHF collars were equipped with GPS (Telonics, Mesa, CA, USA) which provided daily locations uploaded through the Argos satellite system (Meier *et al.* 2009). Wolves were immobilized by darting from helicopters and collared following protocols described in Meier *et al.* (2009).

Researchers gathered annual wolf population and composition data in early and late winter (November–December and February–March respectively). Radiocollared wolves were located by VHF signal from fixed-wing aircraft. Approximately 10–20 wolf packs were monitored annually in the study area and efforts were made to maintain collars on two or more individuals in each pack whose home range was mostly within DNPP boundaries. Wolf location, number of pack members, pelt colours and estimated age classes (if distinguishable) were recorded. Observers also recorded detailed information on mortality, den site location/use and pack affiliation (Mech *et al.* 1998; Meier *et al.* 2009).

Wolf mortalities were noted during aerial tracking and observation and through weekly GPS data checks. Cause of death was determined through a field necropsy or by wildlife veterinary staff at the University of Alaska Fairbanks (UAF) or the Alaska Department of Fish and Game (ADF&G). When carcasses were too decomposed to determine cause of death or both laboratory and field evidence were inconclusive, cause of death was recorded as "unknown natural".

All areas outside of the DNPP boundary were open to hunting and trapping under state regulation, with open seasons and bag limits (i.e. the number of wolves that could be harvested per person) managed by ADF&G. In Game Management Units (GMU) 20A and 20C adjacent to the park's boundaries, the hunting season was August 10–April 30 from regulatory year 1996–1997 through 2005–2006 and extended until May 31 starting in 2006–2007. The bag limit was 10 wolves until 2001–2002 and was then decreased to five wolves per season. The wolf trapping season spanned November 1 to April 30 in GMUs 20A and 20C, with no bag limits for either unit. Subsistence and sport hunting and trapping were permitted in the Preserve and new park additions of DNPP, but all hunting and trapping was prohibited in the area of the original Mt. McKinley National Park (Fig. 1).

PACK SIZE AND PACK FATE

We examined the size and fate of all packs monitored in DNPP from 1986 to 2012. Pack size during spring and fall was defined as the maximum count observed during surveys within each season. We defined pack formation as occurring the season (spring or fall) and year of the first pack count recorded for the associated pack name. We defined pack dissolution as the reduction of a pack of ≥3 wolves to zero or one wolf the subsequent season. Because the exact fate of remaining pack members was often unknown (i.e. they may have died, dispersed or remained present but undetected), the concept of pack persistence in this study is analogous to "apparent survival" in capture–mark–recapture studies (Lebreton *et al.* 1992). Pack life span was calculated as the number of years from pack formation (or from the start of monitoring) to pack dissolution.

For analyses of breeder loss effects on pack maintenance and reproduction, we included only established packs that were monitored or known to exist for ≥1 year. Packs were considered to have dissolved following breeder loss if the dissolution occurred the season following or during the same season as the breeder loss. In the absence of collars, observers used colour composition and number of associated individuals or distinguishing features to determine if individuals or groups found within the former territory were original pack members, neighbouring pack members or previously unknown wolves. Pack dissolution rate for the population was calculated as the number of packs dissolving in a year divided by the total number of packs monitored.

BREEDER LOSS

Biologists generally targeted dominant members of packs for collaring by observing the behaviour of pack members during aerial tracking and collaring operations (Meier *et al.* 2009), but subordinate wolves were sometimes collared. The breeding status of individuals was determined through observation of leadership behaviour, attendance at den sites, observation of nursing pups (for females) during aerial tracking, and/or through testes and nipple measurements during collaring (Mech 1999, 2000; Peterson *et al.* 2002; Meier *et al.* 2009). However, breeding status or dominance status was not recorded for all wolves in the data set.

We used a heuristic method to identify likely breeders from the dataset of all collared wolves in DNPP from 1986 to 2012. We censored wolves from our dataset that were: (i) <2 years old when they died, (ii) dispersing or had dispersed out of the study area at the time of death, (iii) classified as pups or yearlings when captured, unless these were later classified as "alpha", "breeder" or "paired" in the capture or aerial tracking data, or (iv) had an unknown fate due to collar failure or dispersal. We performed additional review to corroborate our method of breeder classification in two ways: (i) we compared wolves identified as breeders by our method to a subset of breeders from 1986 to 1993 identified and used for analysis by Brainerd *et al.* (2008), and (ii) classification of individuals monitored from 1995 to 2012 was verified by reviewing capture, mortality and aerial tracking information from the corresponding time period.

We classified breeder mortality as occurring in one of four equal length seasons. Season breakpoints were determined primarily based on wolf breeding cycles in interior Alaska. Wolves in DNPP typically come into oestrus in March (Mech *et al.* 1998) and give birth in early May following a 2 month gestation (Hayssen & van Tienhoven 1993). There is a prolonged period of proestrus in grey wolves of about 6 weeks (Asa & Valdespino 1998) during which the mated pair spends time together coordinating their activity, and this period appears important for the formation and maintenance of the pair bond (Mech & Knick 1978; Rothman & Mech 1979). We therefore defined spring as February–April (breeding season), summer as May–July (pup-rearing season), fall as August–October, and winter as November–January. Cause of mortality was classified as natural (including intraspecific strife, starvation, accident and unknown natural causes) or anthropogenic (trapped, shot, vehicle strikes or capture-related mortality). We evaluated the proportion of natural and anthropogenic mortalities of identified breeders that occurred within each season to assess seasonal patterns in cause of mortality.

For analysis of the probability of pack maintenance, we censored cases of breeder loss where (i) pack persistence was unknown following the loss of the breeder, (ii) pack size prior to the loss of the breeder was unknown, (iii) packs were monitored or existed for less than a year after wolves were collared, or (iv) groups were identified as pairs rather than reproductive packs.

RECRUITMENT AND DEN FIDELITY

We examined cases of pack denning and recruitment from 1997 to 2012 for packs in the eastern region of DNPP (Fig. 1). Data on den site use and reproduction prior to 1997 were not accessible and therefore excluded from analysis. We collated locations from collared wolves by pack and created minimum convex polygons that bounded the territory for each wolf pack by year using the program ArcGIS 10.0 (Esri, Redwoods, CA, USA). Packs were designated as belonging to the eastern or western region when the centre of the pack territory was located within the corresponding geographical region. DNPP wolf management plan objectives require closing areas around known den sites to hikers (National Park Service 2007). Thus, den site locations and use were closely monitored for wolf packs in the eastern region, which includes the areas of higher potential backcountry recreational use in DNPP. This close monitoring provided more accurate data on denning status and presence of pups in fall (recruitment) in the eastern region than in the western region.

Wolf packs were recorded as having successfully reproduced using one of three methods: (i) one or more visual observations of attendance at known or suspected den sites during the denning season (April through mid-August), (ii) clusters of GPS points at a known or suspected den locations, or (iii) detection of pups during aerial tracking flights. Denning status was assumed to be an indication of reproduction. Early denning behaviour that failed to produce surviving pups may have been missed and classified as no known denning or unknown denning status.

Den site fidelity was recorded for each pack each year; packs that used the same den in year $n + 1$ as in year n had fidelity, whereas packs that changed locations between years did not. Den site tenure was defined as the number of consecutive years that a pack used the same den site.

Recruitment was categorized as successful or failed based on: (i) visual observations of pups during the summer or early fall counts when pups were easily distinguished from adults, or (ii) an increase in estimated pack sizes from spring to fall. We censored cases with increases in pack size of one or two individuals without corresponding visual observation of pups, because these cases could be explained by possible immigration or adoption of individuals. Recruitment was recorded as failed when packs either did not den or pups were never observed and pack size did not increase as described. We censored cases of newly formed pairs (those that formed after or during the breeding season) in our analysis because newly formed pairs have a lower probability of successful reproduction and recruitment (Mech *et al.* 1998). We evaluated denning and recruitment for packs that experienced breeder mortalities that occurred during the breeding season, pup-rearing season or the prior winter. Cases where packs dissolved or were maintained following breeder loss were both included.

STATISTICAL ANALYSES

Factors affecting pack maintenance following breeder loss

We hypothesized that pack maintenance would depend on the sex of breeder lost (male, female or both), pack size prior to breeder loss, season of breeder loss and cause of mortality (anthropogenic or natural). We used the glm function in Program R (R Core Team 2013) to create generalized linear models with all four main effects and all nested models with no interaction or higher order terms ($n = 15$ models). We used Akaike information criterion corrected for small sample sizes (AIC_c) to rank models, and we calculated pseudo-R^2 to estimate explained variance (Veall & Zimmerman 1992). We used the modavg function in R package AICcmodavg (Mazerolle 2013) to obtain model-averaged parameter estimates for factors that were included in models with $\Delta AIC < 2$ (Burnham & Anderson 2002). For ease of interpretation of parameter estimates, we transformed the parameter estimates (β) into odds ratios such that the odds ratio was equal to e^{β}.

Effect of breeder loss on recruitment and den site fidelity

We used chi-squared tests of independence to test the hypotheses that breeder loss (loss of a male, female or both breeders) would (i) reduce rates of denning, (ii) reduce successful recruitment and (iii) reduce den site fidelity.

Effect of breeder loss on population growth

The annual population growth rate, or finite rate of increase (λ), for year n was calculated as the spring population size in year $n + 1$ divided by the spring population size in year n. Breeder mortality rate was calculated as the number of breeder mortalities from May 1 in year n to April 30 in year n + 1, divided by two times the number of packs monitored in year n (to correspond to the estimated number of breeders in the population). If a different number of packs were observed during the spring and fall population counts, the larger number of packs was used as the number of packs monitored during the year.

We examined the relationships between the breeder mortality rate and λ and between the pack dissolution rate and λ using linear regression. To examine the immediate and longer term effects of breeder loss on population growth, relationships were modelled with and without a 1-year time lag (i.e. effect of breeder mortality or pack dissolution in year n on the population growth rate in $n + 1$). We censored the first 3 years of the study (1986–1988) due to the low number of packs that were tracked during those years.

Results

PACK FATE AND BREEDER LOSS

From 1986 to 2012, wolves from 70 packs were monitored in DNPP (Table S1). Eight packs were censored because the pack fate was unknown due to limited monitoring, and nine packs continued to be monitored at the end of the study period in 2012. Of the remaining 53 packs, there were 41 cases (77%) where breeder mortality preceded or coincided with the end of the pack, and 12 cases (23%) where either there was no breeder mortality prior to the end of the pack or breeder mortality was not documented.

We identified 163 cases of breeder mortality from 1986 to 2012. Our heuristic method correctly identified 27 of the 31 (87%) collared breeder mortalities from 1986 to 1993 identified by Brainerd *et al.* (2008). The four breeders that were missed by our selection were all individuals that were captured as pups ($n = 2$) or yearlings ($n = 2$) and later became breeders in their own pack ($n = 2$) or dispersed and became breeders in another pack ($n = 2$). Some breeders that were collared as pups or yearlings and later became breeders may be missing in our data set if there was no corresponding note in the capture, mortality or aerial tracking data to indicate that the individual was a breeder.

After censoring (see Methods), we used 94 cases of breeder loss for our analysis of factors affecting pack fate (Table 1). We found that packs dissolved the season following breeder loss in 31 cases (33%) and remained intact following breeder loss in 63 cases (67%). Roughly equal proportions of yearly breeder mortality occurred in spring, fall and winter, with 29·8%, 29·8%, and 30·9% of mortalities occurring in these seasons respectively. The remaining 9·5% of mortalities occurred during summer. Anthropogenic mortality represented 11% and 14% of total mortality during summer and fall, respectively, while in spring and winter anthropogenic mortality represented 39% and 34% of total mortality (Fig. 2). Harvest (trapping or hunting) was the source of 21 of 26 (81%) of anthropogenic mortalities; the other five cases (19%) were capture related.

Sex of lost breeders and pack size were the most important predictors of pack persistence following breeder mortality (Table 2). A pack was 14·9 times more likely to persist if only the male was lost and 3·4 times more likely to persist if only the female was lost compared to cases where both breeders were lost (Table 3). The odds of a

Table 1. Cases of grey wolf pack persistence and dissolution following breeder mortality in Denali National Park, Alaska, USA, 1986–2012

Breeder mortality	Pack persist	Pack dissolve
Both	5	11
Female	27	14
Male	31	6
All breeder mortality	63	31

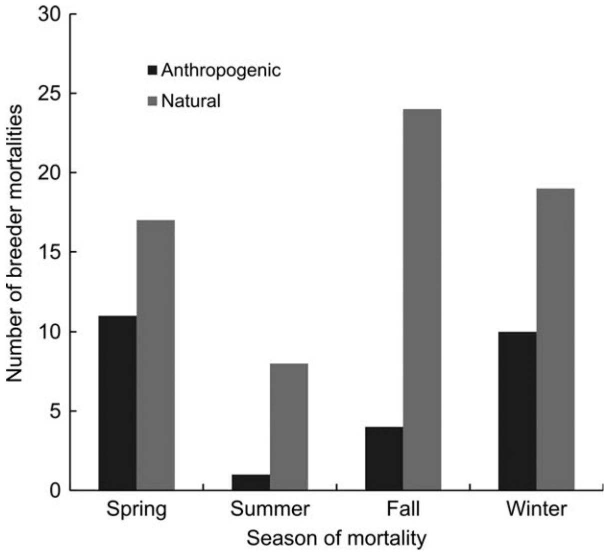


Fig. 2. Total number of mortalities of breeding grey wolves by season and type of mortality in Denali National Park, Alaska, USA, 1986–2012 ($n = 94$). Spring = February–April, Summer = May–July, Fall = August–October, Winter = November–January. Anthropogenic mortality includes hunting, trapping and capture-related deaths; natural mortality includes intraspecific strife, starvation, injuries and accidents.

Table 2. Candidate model set and model selection criteria evaluating factors potentially affecting grey wolf pack maintenance following breeder mortality in Denali National Park, Alaska, USA, 1986–2012. M-Z Pseudo-R^2 estimates the amount of deviance in the data explained by each model

Model	# Parameters	AICc	ΔAICc	Model likelihood	AICc weight	M-Z Pseudo-R^2
PP[a] + Sex[b]	4	103·44	0·00	1·00	0·49	0·33
PP + Sex + Mort[c]	5	104·84	1·40	0·50	0·24	0·34
PP + Season[d] + Sex	7	105·41	1·97	0·37	0·18	0·39
PP + Season + Sex + Mort[e]	8	107·64	4·20	0·12	0·06	0·39
Sex	3	111·59	8·14	0·02	0·01	0·18
Season + Sex	6	113·60	10·16	0·01	0·00	0·25
Sex + Mort	4	113·61	10·17	0·01	0·00	0·18
PP + Season	5	114·74	11·30	0·00	0·00	0·25
PP	2	115·44	12·00	0·00	0·00	0·13
Season + Sex + Mort	7	115·93	12·49	0·00	0·00	0·25
PP + Season + Mort	6	117·02	13·58	0·00	0·00	0·25
PP + Mort	3	117·22	13·78	0·00	0·00	0·14
Season	4	121·43	17·99	0·00	0·00	0·09
Mort	2	123·29	19·85	0·00	0·00	0·00
Season + Mort	5	123·48	20·04	0·00	0·00	0·10

[a]Pack size prior to breeder loss.
[b]Sex of breeder loss.
[c]Cause of mortality: natural or anthropogenic.
[d]Season of breeder loss: spring, summer, fall or winter.
[e]Global model.

pack dissolving decreased with pack size (Fig. 3). The probability of pack maintenance was <0·5 if both breeders were lost in packs with ≤11 members or a female was lost in packs with <6 members.

Cause and season of mortality were included in the top-ranked models (ΔAIC_c <2). The model-averaged odds ratios indicated the probability of pack persistence was 1·6 times higher when breeders were lost due to natural causes rather than anthropogenic mortality, and mortality that occurred in spring or winter decreased the probability of pack maintenance, whereas mortalities that occurred during the summer increased the probability of pack persistence relative to mortalities that occurred in the fall (Table 3).

Table 3. Parameter estimates for factors included in the top-ranked models (ΔAIC_c <2) predicting the probability of pack maintenance following breeder mortality in Denali National Park, Alaska, USA, 1986–2012. See Table 2 for all models. PackPrior is the pack size prior to breeder loss

Parameter	β (Model averaged)	SE	95% CL Lower	95% CL Upper	Odds ratio (Model averaged)
(Intercept)	−2·42	1·07	−4·52	−0·33	0·09
PackPrior	0·24	0·08	0·07	0·4	1·27
Sex (F)[a]	1·22	0·71	−0·17	2·61	3·39
Sex (M)[a]	2·7	0·77	1·19	4·22	14·88
Cause mortality (Natural)[b]	0·48	0·62	−0·73	1·69	1·62
Season (Spring)[c]	−1·12	0·73	−2·54	0·31	0·33
Season (Summer)[c]	0·18	1·00	−1·79	2·14	1·20
Season (Winter)[c]	−1·16	0·71	−2·56	0·24	0·31

[a]β and odds ratio estimates relative to mortality of both breeders.
[b]β and odds ratio estimates relative to anthropogenic cause of mortality.
[c]β and odds ratio estimates relative to mortalities that occur in fall.

BREEDER LOSS AND POPULATION GROWTH

Breeder loss did not affect population growth in the current year, λ_n, or the following year, λ_{n+1} (λ_n: $\beta = -0{\cdot}64$,

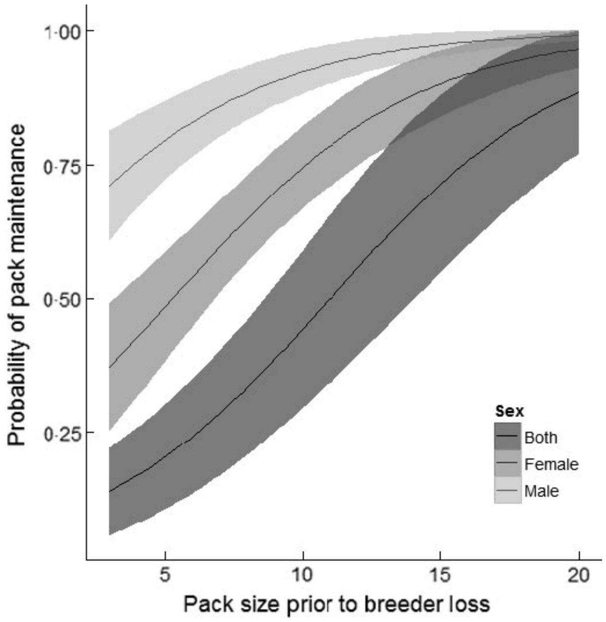


Fig. 3. Effect of pack size prior to breeder loss and sex of breeder(s) lost on the probability of grey wolf packs remaining intact in Denali National Park, Alaska, USA, 1986–2012. Shaded areas show 95% confidence intervals around predicted probabilities.

$F_{1,21}$ = 1·87, P = 0·19, R^2 = 0·08, n = 23, Fig. 4a; λ_{n+1}: β = 0·23, $F_{1,20}$ = 0·23, P = 0·63, R^2 = 0·01, n = 22, Fig. 4b). Pack dissolution had a marginal negative effect on population growth in the current year but no effect the following year (λ_n: β = −0·81, $F_{1,21}$ = 3·10, P = 0·09, R^2 = 0·13, n = 23, Fig. 4c; λ_{n+1}: β = 0·71, $F_{1,20}$ = 2·11, P = 0·16, R^2 = 0·10, n = 22, Fig. 4d).

RECRUITMENT AND DEN FIDELITY

We determined pack denning status in 79 cases from 1997 to 2012. Packs denned in 72 cases (91%) and successfully reared pups in 63 of the 72 cases (88%; Table 4). For packs that did not lose breeders, rates of denning (96%, n = 54) and successful recruitment (94%, n = 52) were uniformly high. Packs that experienced breeder loss had significantly lower denning and recruitment rates than packs that did not experience breeder loss (denning: 80%, χ^2 = 3·896, d.f. = 1, P = 0·049, n = 79, recruitment: 70%, χ^2 = 5·697, d.f. = 1, P = 0·017, n = 72).

Breeder loss did not significantly affect den site fidelity (χ^2 = 1·90, d.f. = 1, P = 0·17, n = 48). Packs used the same den site in consecutive years in 20 of 37 cases (54%) when no breeder loss occurred between breeding seasons and in 10 of 16 cases (63%) following breeder loss when the pack continued following the breeder loss (Table 4). Packs used the same den for an average of three consecutive years (range = 1–13 years, n = 10 packs).

Discussion

Our results show that the mortality of breeding individuals in social groups can often lead to social group dissolution, but population growth can be resilient to the effects of breeder mortality. Although breeder loss preceded or coincided with most documented cases of wolf pack dissolution, packs remained intact in approximately two of every three cases of breeder loss (Table 1). Population growth rates were largely unaffected by breeder loss and pack dissolution despite reduced reproductive rates, indicating that

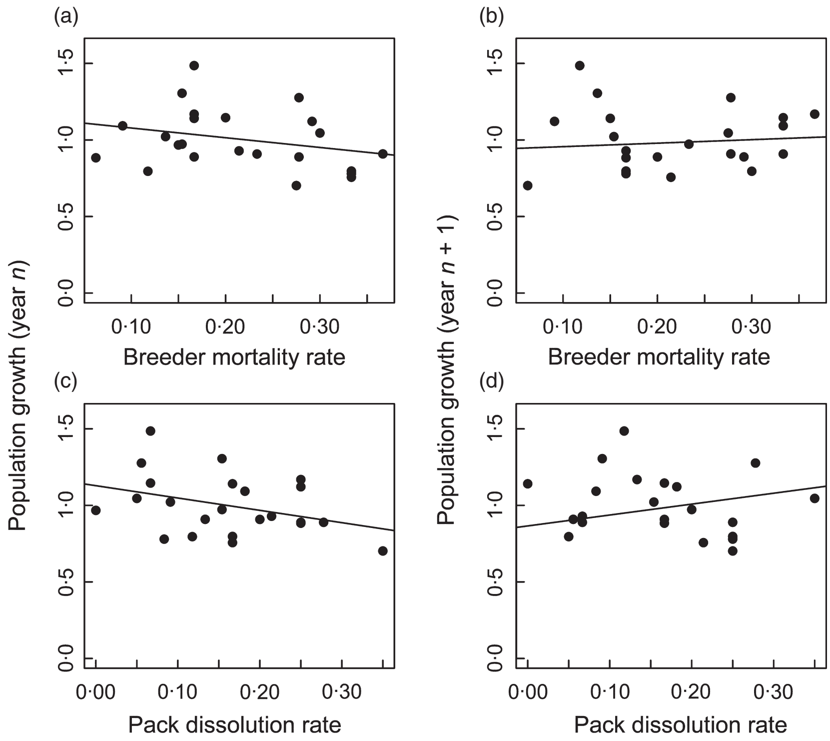


Fig. 4. Effect of breeder mortality and pack dissolution on annual population growth of grey wolves in Denali National Park, Alaska, USA, 1986–2012 with and without a time lag. Effect of breeder mortality rate in year n on population growth rate in (a) year n and (b) year n + 1. Effect of pack dissolution rate in year n on population growth rate in (c) year n and (d) year n + 1. Non-significant regression lines are displayed.

Table 4. Cases of pack denning (reproduction), successful recruitment and den site fidelity in relation to breeder mortality for grey wolf packs in Denali National Park, Alaska, USA, 1997–2012

Breeder mortality	Denning	No denning	Recruitment	No recruitment	Den fidelity[a]	New den	No denning
Both sexes	2	3	2	0	2	0	4[b]
Female	10	0	6	4	4	1	0
Male	8	2	6	2	4	1	2
Total							
Breeder mortality	20	5	14	6	10	2	6
No breeder mortality	52	2	49	3	20	16	1

[a]Den fidelity data are a subset of denning data for which we have information on denning in the prior year.
[b]Includes two cases of pack dissolution following breeder mortality.

strong compensatory mechanisms can reduce the negative impacts of breeder loss in socially complex species such as wolves.

While the effects of breeder loss on wolf population dynamics in DNPP appear to be minor in general, our findings indicate the availability of replacement breeders and timing of mortality can moderate the consequences of breeder loss. The importance of the cause and timing of mortality indicates the value of reproductive individuals in social species may be context-dependent and characterized by strong seasonal heterogeneity. Our results suggest that reproductive value of individuals increases as they approach parturition such that mortality of breeders during this time can destabilize social groups and lead to reproductive failure. The effects of variable reproductive value among age classes can alter population dynamics (Francis *et al.* 1992), and our results imply that seasonal variation in addition to reproductive status can affect social and population dynamics.

Although direct causes of pack dissolution were generally not known, dissolution followed or coincided with the loss of one or both breeders in at least 77% of the cases. This rate was likely underestimated because not all breeders were collared, and thus not all breeder mortality events were observed. Breeders may thus contribute disproportionately to the social stability of groups (Mech & Boitani 2003) in addition to having high reproductive values. The importance of breeders in this socially structured species highlights the need to explicitly consider the effects of harvest of these individuals, especially when harvest overlaps the breeding season.

Anthropogenic mortality has been shown to impact social structure in grey wolves, such that harvested populations tend to have smaller packs (Ballard, Whitman & Gardner 1987) and harvest may reduce genetic relatedness (Rutledge *et al.* 2010 but see Lehman *et al.* 1992). We found that packs were less likely to be maintained when breeders were killed by humans than when mortality resulted from natural causes. Although this finding supports previous research, it is still surprising given that the cause of mortality should not necessarily affect pack fate per se. We suspect the timing of anthropogenic mortality in relation to breeding season may partially account for the observed effects on pack fate. Anthropogenic harvest mortalities were concentrated in spring breeding and winter pre-breeding seasons (Fig. 2). Mortalities during spring in particular leave little time for replacement of breeders and may have a disproportionate effect on pack persistence. Our results indicate that harvest of breeding wolves has the potential to impact pack persistence and reproduction, and these impacts are likely to be greatest when pack sizes are small (<6) and harvest overlaps the breeding season.

The role of individual breeders in maintaining pack cohesion appears moderated by the availability of replacement breeders as indicated by the effect of pack size. Consistent with the findings of Brainerd *et al.* (2008), our analysis indicates that large packs are more likely to persist following breeder mortality than small packs (Fig. 3). Large packs are more likely to have multiple breeders, unrelated adoptees or reproductively viable related individuals present as replacement breeders (Meier *et al.* 1995; Mech & Boitani 2003), whereas small packs are more likely to have young of only the previous year (Mech 1999). Heterogeneity in the reproductive value of individuals in social groups may therefore depend on group size, such that the reproductive value of a single breeder in a small group is higher than the reproductive value of individual breeders in large groups.

The availability of replacement breeders may increase with the overall size of the population as well as pack size. Brainerd *et al.* (2008) found that breeder replacement in wolf packs occurred more quickly in saturated versus recolonizing populations. Thus the effects of breeder loss on pack fate could be moderated by the availability of replacement breeders not only within the pack, but in the population and surrounding areas. The wolf population in DNPP is generally considered to be a saturated population at or near carrying capacity (Mech *et al.* 1998), and therefore our results may represent the minimum impacts that breeder loss can have on pack and population dynamics.

We found that packs that lost both breeders were more likely to dissolve, as did Brainerd *et al.* (2008). However, loss of both breeders confounded the influence of sex of breeder loss with the numeric impacts of the loss of two individuals. The influence of female versus male loss was more explicit, and as expected, mortality of a female breeder destabilized packs more often than the loss of a male breeder. Female parturition and the care of neonates and young pups are essential to pack reproduction and recruitment. Thus mortality of female breeders, especially when timed during the breeding season, has disproportional impacts on pack fate and may represent a loss of the reproductive capacity for the entire pack for that year.

Overall, most packs maintained cohesion and reproduced despite breeder loss, indicating a high degree of resilience and rapid replacement of breeders. These high reproductive rates imply that either successful replacement of the lost breeder occurred prior to the breeding season, or that multiple breeders were present in the pack which mitigated the loss of one breeder. Interestingly, intact wolf packs in the eastern region of DNPP exhibited high den site fidelity, regardless of whether a pack experienced lost breeders or not. Den site fidelity may thus be related to pack persistence or other factors rather than breeder continuity. However, reproductive success was substantially reduced for packs that experienced breeder loss and remained intact. This result supports findings from other species that found reductions in reproductive capacity following disruption of the social group. For example, female African elephants (*Loxodonta africana*) from disrupted groups had a significantly lower reproductive output than females from intact social groups (Gobush, Mutayoba & Wasser 2008).

Although not explicitly considered in our analysis, additional sources of heterogeneity in individual breeders such as body mass, age or even coat colour may also affect reproductive success (Mech 1995; Stahler *et al.* 2013). Breeder age and experience may be particularly important, because younger individuals and those breeding for the first time have lower reproductive success (Anderson 1986; Stacey & Koening 1990; Mech *et al.* 1998; Heinze & Schrempf 2012). Thus, even if lost breeders are replaced by subordinates, recruitment success could be reduced. If replacement breeders tend to be younger than breeders that died, age effects may reduce the ability of populations to compensate for breeder losses.

Pack dissolution rates appeared to have weak negative effects on population growth of wolves in DNPP. However, population growth rates following years of high breeder loss and pack dissolution did not remain low, indicating that strong compensatory mechanisms buffered against longer term population level impacts. Because our regression analyses did not account for sampling and measurement variance in the population estimates, results should be interpreted with caution.

Annual rates of human-caused mortality in DNPP wolves ranged from 3 to 7% during 1986-2002 (Adams *et al.* 2008), well below the level expected to reduce rates of population growth (reviewed in Fuller, Mech & Cochrane 2003; Adams *et al.* 2008). Despite these low harvest rates, we found that anthropogenic mortality of breeders increased the probability of pack dissolution. Harvest may be a largely additive source of mortality for wolves rather than a compensatory one (Adams *et al.* 2008; Murray *et al.* 2010; Sparkman, Waits & Murray 2011), especially in small, isolated or recolonizing populations. The influence of breeder loss in small, isolated or recolonizing populations may be greater than reported in our study of a saturated wolf population, because the time for breeder replacement and subsequent reproduction is increased in those populations (Brainerd *et al.* 2008). Therefore, the loss of breeders in regions with higher harvest rates or in low density or unsaturated populations may have lasting negative effects on population growth.

Our study is the first to explicitly link the effects of breeder loss to population growth rates in wolves, and further research on these relationships is needed to quantify the importance of breeders within low density or unsaturated populations. With grey wolf recovery and delisting from the Endangered Species Act, wolf management plans in several states (Idaho, Michigan, Minnesota, Montana, Wisconsin and Wyoming) include public harvest seasons that overlap with the wolf breeding season. For regions with recovering wolf populations, and those with small average pack sizes, harvest that occurs during the breeding season could have disproportionate impacts on pack fate and population growth, indicating that wolf recolonization into new areas could be slower than expected. The implications of these findings extend to other socially structured species with reproductive suppression of subordinates and to species where harvest coincides with breeding season. In such cases, we may expect impacts on social structure and population growth beyond those anticipated by population models that ignore the role of reproductive individuals.

Acknowledgements

This study is dedicated to the memory of Thomas J. Meier, who successfully led the wolf monitoring programme in DNPP from 2004 until 2013 and provided invaluable mentorship and guidance to this study. Funding was provided by the National Park Service and the US Geological Survey. The Alaska Department of Fish and Game provided valuable assistance and cooperation. L. D. Mech, L. Adams, J. Burch, B. Dale and T. Meier pioneered the long term study and collected data from 1986 to 2012. J. Blake, C. Rosa and K. Beckmen conducted necropsies. L. Adams, S. Arthur, J. Falke, G. Hilderbrand, M. Lindberg, and K. Sivy, and K. Titus provided valuable comments on earlier versions of this manuscript. Work was conducted under annual National Park Service permits and Institutional Animal Care and Use protocol approval (NPS IACUC 2010-1), annual State of Alaska Department of Fish and Game scientific permits, and the University of Alaska permit (253217-3).

Data accessibility

All data are collected, maintained and archived by the National Park Service. Data can be accessed at the Integrated Natural Resource Applications Portal https://irma.nps.gov/ Reference code: 2210948

References

Adams, L.G. & Roffler, G. (2009) *Dynamics of the Denali Caribou Herd, Denali National Park, Alaska: Progress Report*. Anchorage, Alaska, USA.

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

Adams, L.G., Farley, S.D., Stricker, C.A., Demma, D.J., Roffler, G.H., Miller, D.C. *et al.* (2010) Are inland wolf - ungulate systems influenced by marine subsidies of Pacific salmon? *Ecological Applications*, **20**, 251–262.

Anderson, C.M. (1986) Female age: male preference and reproductive success in primates. *International Journal of Primatology*, **7**, 305–326.

Arnold, K.E. & Owens, I.P.F. (1998) Cooperative breeding in birds: a comparative test of the life history hypothesis. *Proceedings of the Royal Society B: Biological Sciences*, **265**, 739–745.

Asa, C. & Valdespino, C. (1998) Canid reproductive biology: an integration of proximate mechanisms and ultimate causes. *American Zoologist*, **259**, 251–259.

Ballard, W.B. & Stephenson, R.O. (1982) Wolf control - take some and leave some. *Alces*, **18**, 276–300.

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

Boyce, M.S. (1990) Wolf recovery for Yellowstone National Park: A simulation model. *Wolves for Yellowstone? A Report to the United States,* Volume 2, *Research and Analysis*. U.S. National Park Service, Yellowstone National Park, WY.

Brainerd, S.M., Andrén, H., Bangs, E.E., Bradley, E.H., Fontaine, J.A., Hall, W. *et al.* (2008) The effects of breeder loss on wolves. *Journal of Wildlife Management*, **72**, 89–98.

Burnham, K.P. & Anderson, D.R. (2002) *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*, 2nd edn. Springer Verlag, New York, NY.

Cassidy, K. (2013) *Group Composition Effects on Inter-Pack Aggressive Interactions Ofgray Wolves in Yellowstone National Park*. Master's Thesis, University of Minnesota.

Cochrane, J.F. & Fitts, J. (2000) *Gray Wolves in a Small Park: Analyzing Cumulative Effects through Simulation*. PhD Dissertation, University of Minnesota, Minneapolis, Minnesota.

Creel, S. & Rotella, J.J. (2010) Meta-analysis of relationships between human offtake, total mortality and population dynamics of gray wolves (*Canis lupus*) (ed GC Trussell). *PLoS One*, **5**, e12918.

Francis, C.M., Richards, M.H., Cooke, F. & Rockwell, R.F. (1992) Changes in survival rates of lesser snow geese with age and breeding status. *The Auk*, **109**, 731–747.

Fuller, T.K. (1989) Population Dynamics of Wolves in North-Central Minnesota. *Wildlife Monographs*, **105**, 3–41.

Fuller, T.K., Mech, L.D. & Cochrane, J.F. (2003) Wolf population dynamics. *Wolves: Behavior, Ecology and Conservation* (eds L.D. Mech & L. Boitani), pp. 161–191. University of Chicago Press, Chicago.

Gobush, K.S., Mutayoba, B.M. & Wasser, S.K. (2008) Long-term impacts of poaching on relatedness, stress physiology, and reproductive output of adult female African elephants. *Conservation Biology*, **22**, 1590–1599.

Gude, J.A., Mitchell, M.S., Russell, R.E., Sime, C.A., Bangs, E.E., Mech, L.D. *et al.* (2012) Wolf population dynamics in the U.S. Northern Rocky Mountains are affected by recruitment and human-caused mortality. *The Journal of Wildlife Management*, **76**, 108–118.

Haight, R.G. & Mech, L.D. (1997) Computer simulation of vasectomy for wolf control. *Journal of Wildlife Management*, **61**, 1023–1031.

Haight, R.G., Mlandenoff, D.J. & Wydeven, A.P. (1998) Modeling disjunct gray wolf populations in semi-wild landscapes. *Conservation Biology*, **12**, 879–888.

Haight, R.G., Travis, L.E., Nimerfro, K. & Mech, L.D. (2002) Computer simulation of wolf removal strategies for animal damage control. *Wildlife Society Bulletin*, **30**, 844–852.

Hauser, C.E., Cooch, E.G. & Lebreton, J.-D. (2006) Control of structured populations by harvest. *Ecological Modelling*, **96**, 462–470.

Hayssen, V. & van Tienhoven, A. (1993) *Asdell's Patterns of Mammalian Reproduction*. Comstock Publishing Associates, Ithaca, NY.

Heinze, J. & Schrempf, A. (2012) Terminal investment: individual reproduction of ant queens increases with age. *PLoS One*, **7**, e35201.

Keith, L.B. (1983) Population dynamics of wolves. *Wolves in Canada and Alaska: Their status, biology and management*, Report Ser (ed L.N. Carbyn), pp. 66–77. Canadian Wildlife Service, Edmonton, Alberta, Canada.

Kendall, B.E., Fox, G.A., Fujiwara, M. & Nogeire, T.M. (2011) Demographic heterogeneity, cohort selection, and population growth. *Ecology*, **92**, 1985–1993.

Kleiman, D.G. (1977) Monogamy in mammals. *Quarterly Review of Biology*, **52**, 39–69.

Kokko, H. (2001) Optimal and suboptimal use of compensatory responses to harvesting: timing of hunting as an example. *Wildlife Biology*, **7**, 141–150.

Lebreton, J.-D., Burnham, K.P., Clobert, J. & Anderson, D.R. (1992) Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecological Monographs*, **62**, 67–118.

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

Lindberg, M.S., Sedinger, J.S. & Lebreton, J.-D. (2013) Individual heterogeneity in black brant survival and recruitment with implications for harvest dynamics. *Ecology and Evolution*, **3**, 4045–4056.

MacDonald, D.W. (1983) The ecology of carnivore social behavior. *Nature*, **301**, 379–384.

MacNulty, D.R., Smith, D.W., Mech, L.D., Vucetich, J.A. & Packer, C. (2011) Nonlinear effects of group size on the success of wolves hunting elk. *Behavioral Ecology*, **23**, 75–82.

Mazerolle, M.J. (2013) AICcmodavg: model selection and multimodel inference based on (Q)AIC(c). R package version 1.32. http: CRAN.R-project.org/package = AICcmodavg.

Mech, L.D. (1995) A ten-year history of the demography and productivity of an arctic wolf pack. *Arctic*, **48**, 329–332.

Mech, L.D. (1999) Alpha status, dominance, and division of labor in wolf packs. *Canadian Journal of Zoology*, **77**, 1196–1203.

Mech, L.D. (2000) Leadership in wolf (*Canis lupus*) packs. *Canadian Field-Naturalist*, **114**, 259–263.

Mech, L.D. & Boitani, L. (2003) *Wolf Social Ecology*. *Wolves: Behavior, Ecology and Conservation*, (eds L.D. Mech & L. Boitani) pp. 1–34. University of Chicago Press, Chicago.

Mech, L.D. & Knick, S.T. (1978) Sleeping distances in wolf pairs in relation to breeding season. *Behavioral Biology*, **23**, 521–525.

Mech, L.D., Adams, L.G., Meier, T.J., Burch, J.W. & Dale, B.W. (1998) *The Wolves of Denali*. University of Minnesota Press, Minneapolis, MN, USA.

Meier, T. (2011) *Vital Signs Monitoring of Wolf (Canis Lupus) Distribution and Abundance in Denali National Park and Preserve, Central Alaska Network: 2011 Report*. *Natural Resource Data Series*. *NPS/CAKN/NRDS–2011/204*. Fort Collins, CO.

Meier, T.J., Burch, J.W., Mech, L.D. & Adams, L.G. (1995) Pack structure and genetic relatedness among wolf packs in a naturally-regulated population. *Second North American Symposium on Wolves* (eds L.N. Carbyn, S.H. Fritts & D.R. Seip), pp. 293–302. Canadian Circumpolar Institute Occasional Publication, Edmonton, Alberta, Canada.

Meier, T.J., Burch, J.W., Wilder, D. & Cook, M. (2009) *Wolf Monitoring Protocols for Denali National Park and Preserve, Yukon-Charley Rivers National Preserve and Wrangell-St. Elias National Park and Preserve, Alaska*. *Protocol-2167760*. Fort Collins, CO.

Murray, D.L., Smith, D.W., Bangs, E.E., Mack, C., Oakleaf, J.K., Fontaine, J. *et al.* (2010) Death from anthropogenic causes is partially compensatory in recovering wolf populations. *Biological Conservation*, **143**, 2514–2524.

National Park Service (2007) *Wolf-human conflict management plan*, *Denali National Park and Preserve*. Denali National Park and Preserve, AK.

Owen, P.A. & Meier, T.J. (2009) *2008 Aerial Moose Survey*. Denali National Park and Preserve, Denali Park, AK.

Peterson, R.O., Jacobs, A.K., Drummer, T.D., Mech, L.D. & Smith, D.W. (2002) Leadership behavior in relation to dominance and reproductive status in gray wolves, *Canis lupus*. *Canadian Journal of Zoology*, **1412**, 1405–1412.

R Core Team. (2013) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org/.

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

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

Sand, H., Wikenros, C., Wabakken, P. & Liberg, O. (2006) Effects of hunting group size, snow depth and age on the success of wolves hunting moose. *Animal Behaviour*, **72**, 781–789.

Smith, D.W., Bangs, E.E., Oakleaf, J.K., Mack, C., Fontaine, J., Boyd, D. *et al.* (2010) Survival of colonizing wolves in the northern Rocky Mountains of the United States, 1982–2004. *Journal of Wildlife Management*, **74**, 620–634.

Soule, M.E. (1980) Thresholds for survival: maintaining fitness and evolutionary potential. *Conservation Biology: An Evolutionary-Ecological Perspective* (eds M.E. Soule & B.A. Wilcox), pp. 151–169. Sinauer Associates, Sunderland, MA.

Soule, M.E. (1987) *Viable Populations for Conservation*. Cambridge University Press, New York, NY.

Sparkman, A.M., Waits, L.P. & Murray, D.L. (2011) Social and demographic effects of anthropogenic mortality: a test of the compensatory mortality hypothesis in the red wolf. *PLoS One*, **6**, e20868.

Stacey, P.B. & Koening, W.D. (eds.) (1990) *Cooperative Breeding in Birds: Long Term Studies of Ecology and Behaviour*. Cambridge University Press, Cambridge.

Stahler, D.R., MacNulty, D.R., Wayne, R.K., VonHoldt, B. & Smith, D.W. (2013) The adaptive value of morphological, behavioural and life-history traits in reproductive female wolves. *The Journal of Animal Ecology*, **82**, 222–234.

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

USFWS (2007) Rocky Mountain Wolf Recovery 2005 and 2006 Interagency Annual Report. Helena, MT.

Veall, M.R. & Zimmerman, K.F. (1992) Evaluating pseudo-R2′S for binary probit models. *Quality & Quantity*, **28**, 151–164.

Vucetich, J.A., Peterson, R.O. & Waite, T.A. (1997) Effects of social structure and prey dynamics on extinction risk in gray wolves. *Conservation Biology*, **11**, 957–965.

Wabakken, P., Sand, H., Liberg, O. & Bjarvall, A. (2001) The recovery, distribution, and population dynamics of wolves on the Scandinavian Peninsula. *Canadian Journal of Zoology*, **79**, 710–725.

Wilson, E.O. (1971) *The Insect Societies*. Belknap Press of Harvard University Press, Cambridge, MA.
Wydeven, A.P., Jurewicz, R.L., Van Deelen, T.R., Erb, J., Hamill, J.H., Beyer, D.E.J. *et al*. (2009) Gray wolf conservation in the Great Lakes Region of the United States. *A New Era for Wolves and People: Wolf Recovery, Human Attitudes, and Policy* (eds M. Musiani, L. Boitani & P.C. Paquet), pp. 69–94. University of Calgary Press, Calgary, Alberta.

Received 11 March 2014; accepted 22 May 2014
Handling Editor: Stan Boutin

Supporting Information

Additional Supporting Information may be found in the online version of this article.

Table S1. Pack life spans for gray wolf packs monitored in Denali National Park, Alaska, USA, 1986–2012.


SHUTTLE BUS
014

Delineating a Protective Buffer Zone for Eastern Denali Wolves

Gordon C. Haber

October 2002

Introduction

Full protection from hunting and trapping has long been advocated for the two major "road corridor" groups of wolves in Denali National Park and Preserve. The 63-year-old or older Toklat (East Fork) family lineage and at least four successive groups occupying the adjacent eastern area – Savage, Headquarters, Sanctuary, and Margaret - have provided more viewing opportunities and scientific insight than wolves anywhere else in the world. Yet they are not accorded full protection from hunting and trapping, and losses continue with serious harm to their world-class scientific and viewing values and despite legitimate ethical concerns (Haber 1996, 2002a). Three successive eastern groups - Savage, Headquarters, and Sanctuary – have been terminated over the past 20 years (in 1983, 1995, and 2001) due largely to hunting and trapping, and Toklat has been hit hard at least several times.

In November 1992, the Alaska Board of Game created a no-wolf-hunting/trapping buffer zone of approximately 600 square miles along the northeast and east park boundaries of Denali National Park, to better protect the eastern Denali wolves. However, the Board rescinded this buffer two months later after Gov. Walter Hickel suspended several proposed wolf control programs the Board had wanted for other areas. In November 2000, the Board again agreed that a buffer was justified but designated only 29 square miles along the northeast park boundary for this purpose. In May 2001 it expanded this to about 90 square miles.

In this report, I consider why the present Board of Game should restore a buffer virtually identical to the one the Board created in 1992 (widened somewhat on its northern end, narrowed on its southern end). The proposed buffer, shown in Figure 1, should eventually also include about 300 square miles of the 1980 national park addition, but this will require separate federal action.

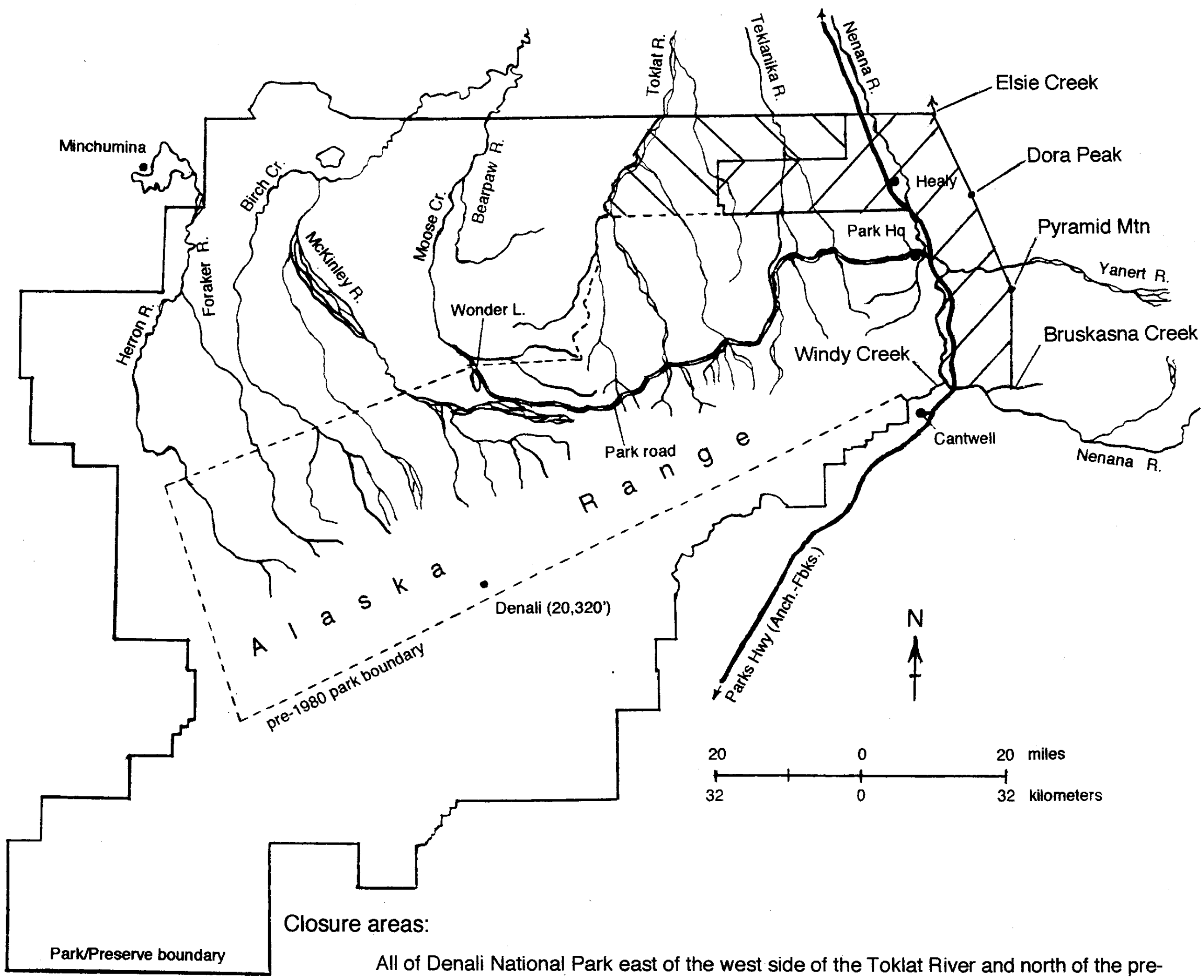
As of this writing (early October 2002), the new eastern group – Margaret – consists of four adult wolves and the six pups they produced in May 2002. I will not know Toklat's status for certain until completing intensive radio tracking surveys in late October. My current observations indicate Toklat's five 2002 pups probably died, due to unknown natural causes, and that there are 4-5 adults at present.

Wolf movements

To understand why a buffer is needed and how it should be delineated, it is necessary to distinguish among three types of movements: (a) the more-or-less routine, recurring movements that define the "territory" of each group, (b) the unpredictable *extraterritorial forays* by each group well outside these areas, and (c) dispersals, during which certain individuals – most commonly 2-3-year-olds – leave a group (depending on its size and other variables) and do not return, usually because they form/join a new group or die in a distant area.

The third type of movement, (c), is not relevant to the buffer objective; dispersers are "lost" from the original groups with or without a buffer. The two others, (a) and (b), are relevant. Figures 2-6 show the winter radio-tracking locations that I recorded for Toklat, Sanctuary, and Margaret involving these two types of movements from 1995-2002. Table 1 summarizes similar data that I recorded for Savage (a Sanctuary and Margaret predecessor) and Toklat during the same two kinds of movements from 1969-1974. In Figures 2-6, each location represents all radio-collared wolves that were present - e.g., two radio-collared wolves of the same group tracked to the same location at the same time are represented by one dot, not two. Two or more locations are plotted together only if I found the wolves there on separate dates, successive or otherwise. In some cases I tracked the wolves represented by these locations over extended routes for up to 7-10 days; this information is not shown in Figures 2-6. I emphasize that all of the outlying locations shown in Figures 2-6 represent forays from which the wolves returned, usually within a few days to a week; no dispersals are included.

The Table 1 data (Table 37 of Haber 1977) are derived from much longer, continuous sampling intervals, during which I followed and observed each group daily for up to three weeks at



Closure areas:

All of Denali National Park east of the west side of the Toklat River and north of the pre-1980 north park boundary (approx. 63° 48.00´N)

All other lands abutting the east and northeast boundaries of Denali National Park, within the following boundaries: Commencing at the far northeast corner of Denali National Park and Preserve (at approx. 64° 00.00´N, 149° 13.00´W), thence due east until intersecting Elsie Creek (at approx. 64° 00.00´N, 148° 53.00´W), thence southeastward along a straight line to the top of Dora Peak (at approx. 63° 49.20´N, 148° 41.00´W), thence southeastward along a straight line to the top of Pyramid Mountain (at approx. 63° 38.40´N, 148° 31.00´W), thence due south until intersecting Bruskasna Creek (at approx. 63° 27.00´N, 148° 31.00´W), thence westward (downstream) along the north side of Bruskasna Creek to its confluence with the Nenana River (at approx. 63° 26.10´N, 148° 37.80´W), thence westward (downstream) along the north side of the Nenana River to its confluence with Windy Creek at the east park boundary (at approx. 63° 27.90´N, 148° 49.00´W).

Figure 1. Proposed Denali no-wolf-hunting/trapping buffer zone. Cross-hatching indicates areas that would be closed to wolf hunting and trapping: right = areas outside park lands, left = inside.

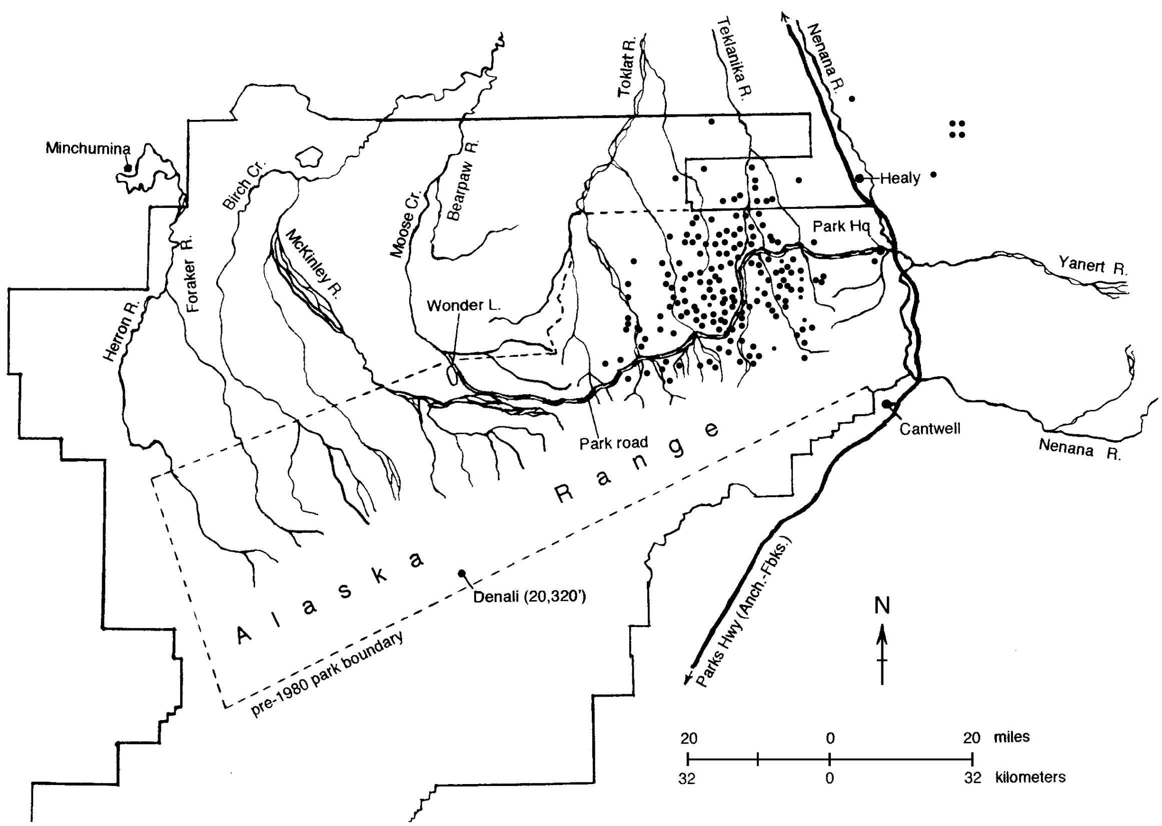


Figure 2. Toklat winter locations, October 1995-April 2001 (171).

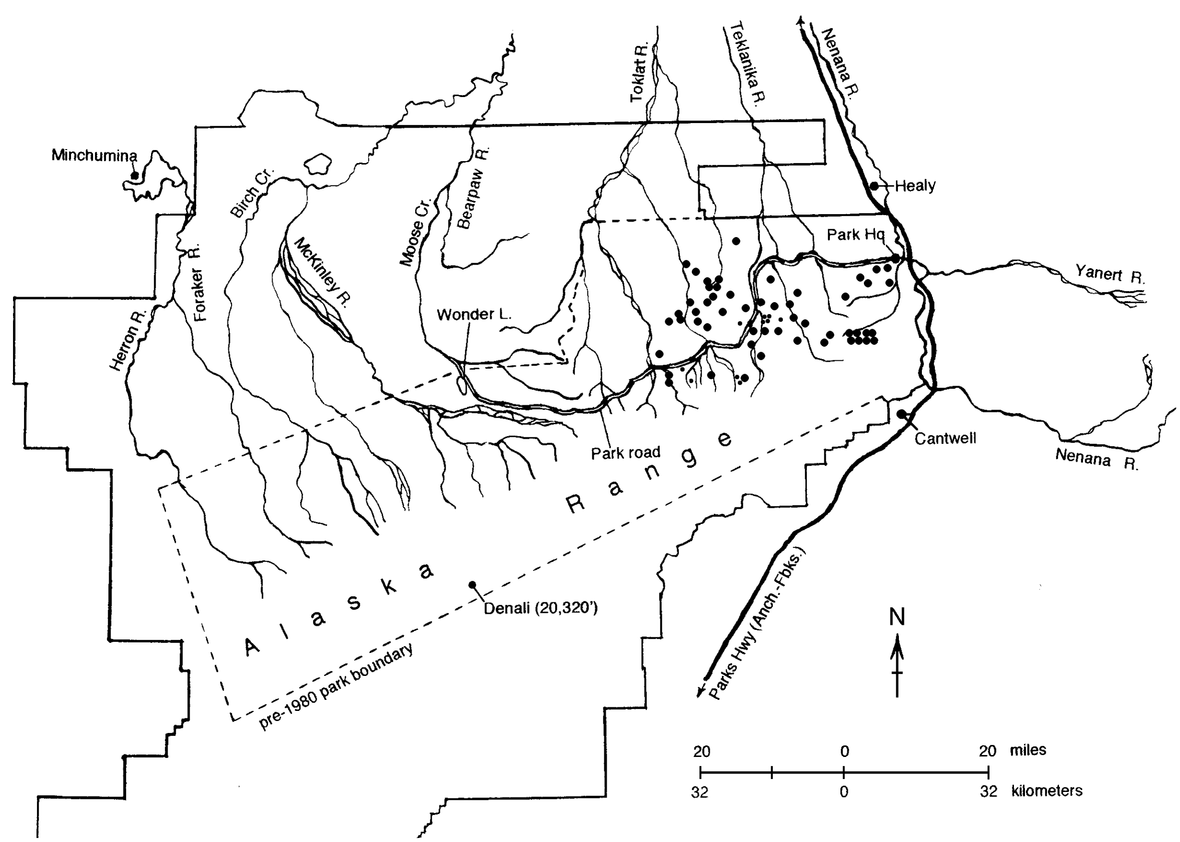


Figure 3. Toklat locations, May 2001-April 2002. Large dots=Oct-April (53), small=May-Sept (10).

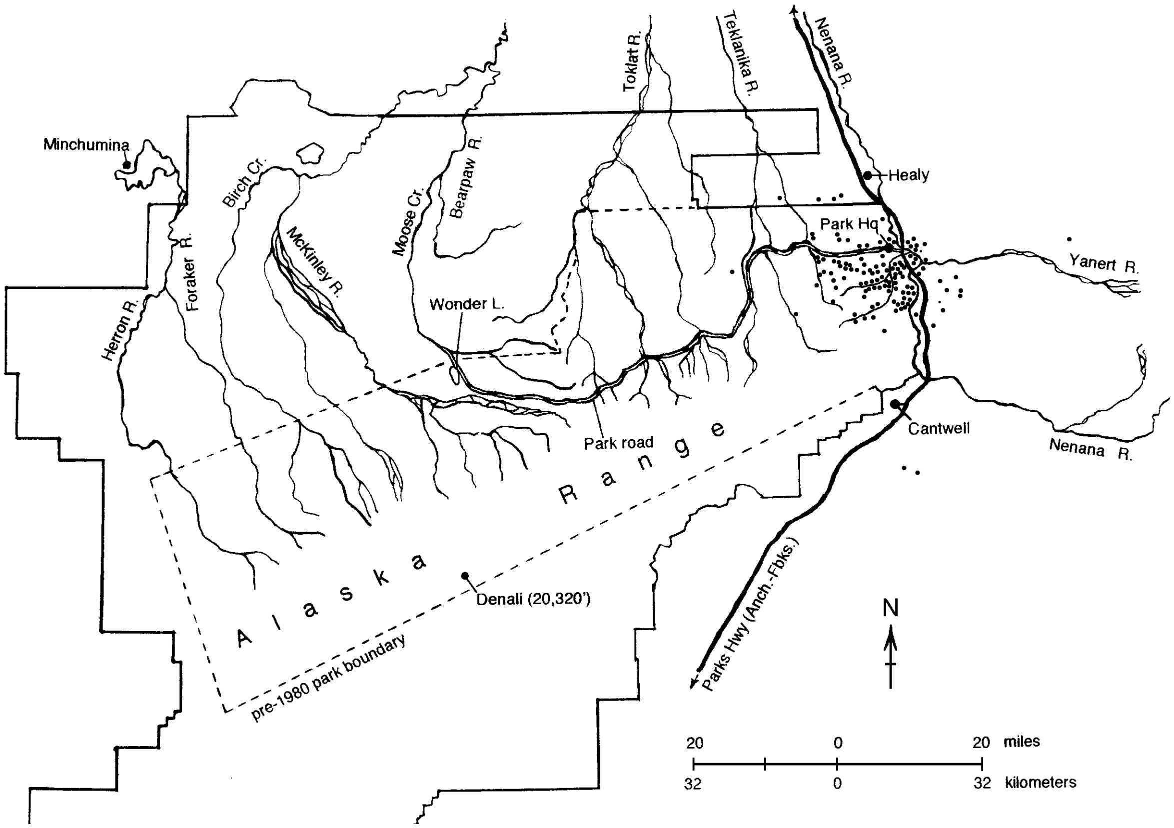


Figure 4. Sanctuary winter locations, October 1995-April 2001 (119).

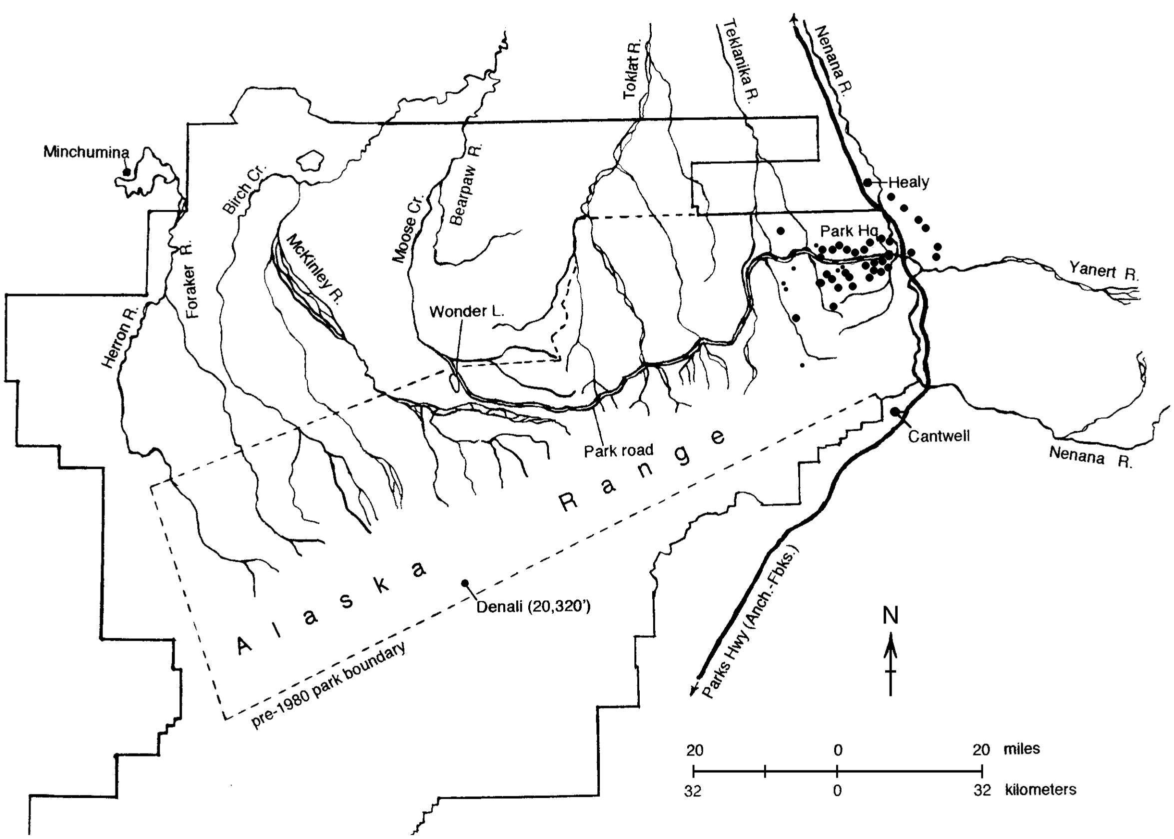


Figure 5. Margaret locations, May 2001-April 2002. Large dots=Oct-April (34), small=May-Sept (7).

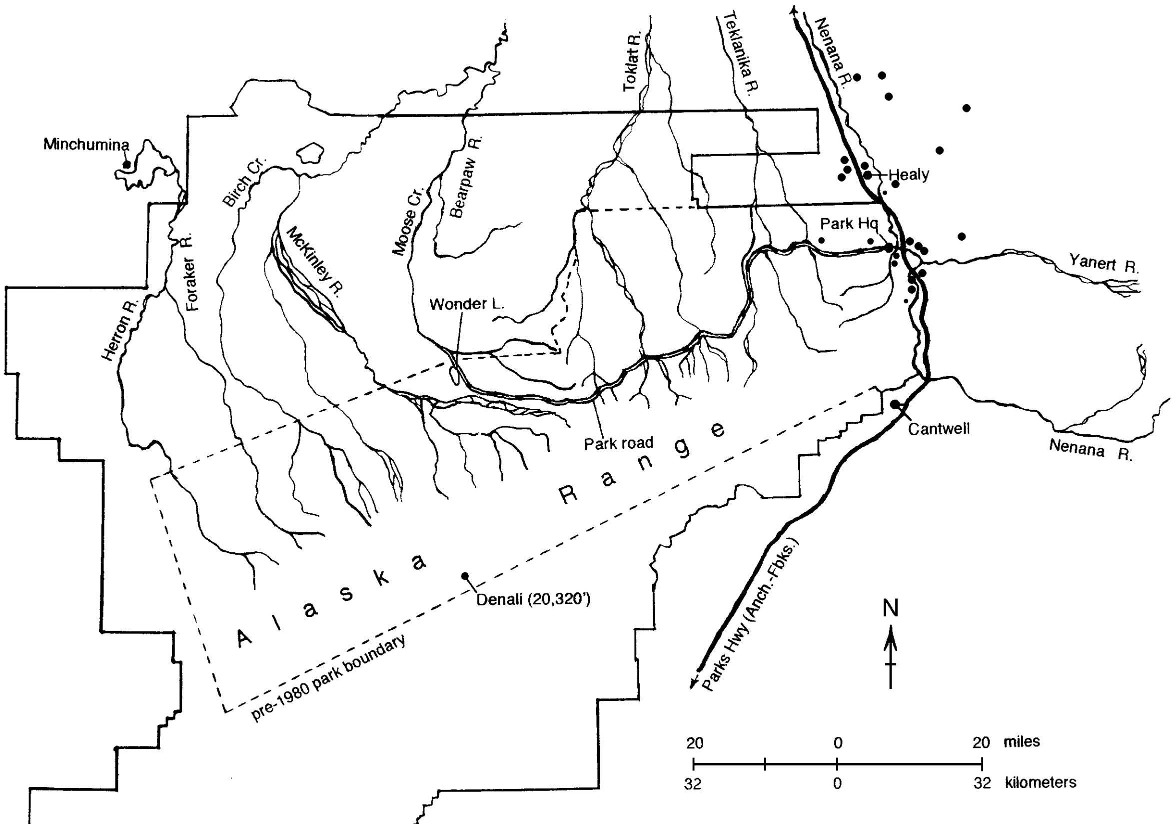


Figure 6. Sanctuary survivor locations, May 2001-March 2002. Large dots=October-March (17), small=May-September (6).

Table 1. Savage and Toklat winter travel mileages, 1969-1974 (Table 37 of Haber 1977).

	Savage – miles traveled				Toklat – miles traveled			
Winter	Inside territory	Outside	Total	Miles per day	Inside territory	Outside	Total	Miles per day
1969-70	269.3	0	269.3	17.3	210.7	48.3	259.0	25.4
1970-71	452.2	16.6	468.8	7.2	169.1	7.9	177.0	13.2
1971-72	288.3	128.7	417.0	10.8	68.1	9.5	77.6	7.9
1972-73	294.6	1.2	295.8	10.3	316.4	21.8	338.2	22.3
1973-74	254.2	6.3	260.5	12.5	102.6	0	102.6	20.2

a time via aerial snow tracking, the method used by researchers and aerial wolf hunters at that time (radio tracking was not yet available).

I have not included most of the summer data from either period of research, because of the wolves' much different routines at that time of the year. During summer, wolves base their activities at dens and rendezvous sites, whereas during winter they range more-or-less continuously as a single group or in varying subunits without any fixed bases. Combining summer and winter data disproportionately weights the overall sample within central areas (where most of the dens and rendezvous sites are located) and thus produces a misleading portrayal of the relationship between central and outlying movements during the winter, when most of the problems occur. There is some travel outside the park boundaries during summer, but this is generally negligible and much less than during winter.

Although the Figures 2-6 vs. Table 1 data are not strictly comparable, both samples illustrate an important aspect of behavior that is critical toward designating buffer zone boundaries: A relatively small but significant and widely-varying portion of the wolves' winter travel, excluding dispersals, is outside their established territories. During these extraterritorial forays, which range from a few miles to 40-50 miles or more and last from 1-2 days to a week or two, an entire family group or a temporary subunit hunts, explores, and/or aggressively pursues wolves from other groups (Haber 1977; Mech et al 1998). Table 1 indicates that from 1969-1974 - a five-winter sample covering a wide range of snow conditions - 9% of all travel (in miles) observed for *both* Toklat and Savage was outside their established territories but with wide variation in the winter-to-winter percentages: 0-19% for Toklat and 0-31% for Savage. Figures 2-4 indicate that from 1995-2002, 13-15% and 13% of my winter radiolocations for Toklat (n=224) and Sanctuary (n=119), respectively, were outside their established territories. The outside-location winter-to-winter variation was 0-32% for Toklat and 7-45% for Sanctuary. Sanctuary's successor, Margaret, recolonized approximately the northern half of the Sanctuary vacancy as of its first winter there (Figure 5). About 18% of its winter radiolocations (n=34) were outside the established (Sanctuary) territory. A female Sanctuary pup survived on her own for 12 months after the other Sanctuary wolves were gone, obviously without much knowledge of the established territory. 65% of my winter radiolocations for her during this period (Figure 6; n=17) were outside the established Sanctuary territory, although she ultimately returned to its eastern area and was trapped there in March 2002.

Figures 2-6 provide an indication of the importance of buffer areas to the two eastern groups relative to the total area that each uses. Buffer usage consists of routine, fairly regular movements within each of the two ("core") territories where these extend somewhat outside the protected park areas *and* sporadic extraterritorial forays (above) further into and through the buffer.

Combining the Figures 2-6 winter radiolocations from both kinds of movements produces overall "buffer-use indices" of 8-9% for Toklat (n=224), 20% for Sanctuary-Margaret (n=153) excluding the Sanctuary pup's locations, and 27% for Sanctuary-Margaret (n=170) including the pup locations.

These indices could change substantially over the next year or two, given that so far Margaret has recolonized only the northern half of the Sanctuary vacancy and much of the rest still seems open to dispute. Toklat's increased eastward probes in winter 2001-02 (Figs. 3 vs. 2) suggest that it may be in the running for a portion of the Sanctuary vacancy. On several of these forays Toklat wolves were within an easy 1-2 hour jaunt of crossing central and southern segments of the east park boundary, into areas of high hunting and trapping danger where at least two successive eastern groups (Headquarters and Sanctuary) were eliminated. This serves as a reminder as to how easily Toklat can get to these dangerous east boundary areas and how closely its safety from hunting and trapping is tied to what happens to the eastern group. Note from Figure 2 the Toklat radiolocations well to the north and east of Healy - in the Ferry, Jumbo Dome, and Usibelli coal mine areas, illustrating that its extraterritorial forays not only can but *do* take it into and through seemingly distant areas of the proposed buffer. Data from earlier years and decades on Toklat, Savage, Headquarters, and other Denali groups show much the same (Haber 1977 and unpubl.; Mech et al 1998), including forays into and beyond southern sections of the proposed buffer.

<u>Hunting-trapping risk and buffer protection</u>

It does not follow that drawing a protective buffer around *most* of the Toklat and Sanctuary-Margaret radiolocations shown in Figures 2-6 will eliminate *most* of the hunting-trapping risk for these wolves. The level of risk is not determined only by where the wolves go. It is determined by where they go *with respect to* hunting-trapping access. There are fewer outlying locations, but most of these represent known extraterritorial forays into northeast and eastern areas where the risk increases dramatically because of much higher human activity and easier hunting-trapping access.

The buffer area shown in Figure 1 includes Healy and extends southward almost to Cantwell. Between these two communities and west of Healy there are major residential subdivisions, commercial developments, and numerous individual residences. All of this is tied together along the east park boundary by the Parks Highway and Alaska Railroad, and west of Healy by the Stampede Trail/Road. Snowmachine and ATV access is enhanced by the Anchorage-Fairbanks Electrical Intertie right-of-way, major trails up the Yanert valley, secondary roads and trails in the Dry Creek-Healy-Usibelli-Ferry areas, other roads and trails, the gravel bars of numerous rivers and creeks, and large expanses of open tundra in the northeast boundary area, i.e., the so-called Wolf Townships. The Stampede Trail/Wolf Townships, Yanert valley, and Cantwell areas have become major snowmachining and dog-mushing destinations, complete with accommodations and weekly snow-condition reports in the Fairbanks Daily News-Miner.

Extraterritorial forays can take Toklat and Margaret unpredictably in almost any direction from their core territories. However, when they cross the northeast and east park boundaries - which becomes more likely because of the lure of traditional caribou wintering activity, the high human activity and easy hunting-trapping access gives special urgency to protecting them. It is relatively easy to identify from Figures 2-5 where the two core territories extend across the park boundaries but impossible to know where, beyond these cores, Toklat and Margaret will go on their next extraterritorial forays. Toklat's next trip outside its established territory might be five miles to the north for two days, or it might be 30 miles to the northeast for a week or two (as in 1999, when all six of the Toklat wolves went northeast to Jumbo Dome [northeast of Healy], then southward through the Usibelli area and to Montana Creek before re-entering the park near the main Parks Highway entrance). Margaret's next foray outside its territory might be 5-10 miles northward to the Healy area (as in March 2002) or 25 miles eastward up the Yanert valley.

The only way to reasonably ensure protection in the face of this unpredictability is to incorporate all of the developed and easily accessible northeast and eastern areas within the buffer, in a way that permits relatively easy field identification of the boundaries. Hence the buffer proposed in Figure 1, which the Board of Game first designated for these reasons (in nearly the same form) in 1992.

There will be continued risk for Toklat and Margaret when they venture north and east of the proposed buffer. However, the buffer is delineated so that it includes the bands of heavy development and easy access along and extending from the Parks Highway and Stampede corridors. The wolves will be legally protected while passing through these areas, and when they exit the north or east sides of the buffer the human activity and hunting-trapping access will have decreased just as dramatically as it increased when they entered on the opposite sides.

<u>Mobile protection</u>

The objective is to protect the Toklat and Margaret wolves from hunting and trapping. This can be done primarily with the Figure 1 no-wolf-hunting/trapping buffer. Nevertheless there should be additional flexibility when the buffer is not enough and there is an opportunity to do more. The Board should give the Commissioner of Fish and Game authority to take immediate emergency action to protect Toklat and Margaret (or any successor group) when they are on *any* unprotected state or private lands.

Toklat and Margaret are monitored regularly via aerial radio tracking. It will often be known when they are beyond protected areas. It should often be possible to watch them closely when this happens (as I am already doing). If they are radio tracked to an unprotected area where there is current snowmachine or aerial-assisted trapping activity, the Commissioner should have the authority to issue an immediate emergency order protecting them from shooting and new ground or aerial trapping. If any are caught in previously set traps or snares, the Commissioner should have the authority to immediately release them and provide whatever on-scene veterinary assistance is needed to help ensure recovery from trap or snare injuries. There could be a provision to pay the trapper above market value for wolves thus released, but the key would be fast action and hence authority for the Commissioner to act before the usually difficult process of identifying and contacting the trapper.

These will be rare occurrences. It will be possible to confirm the identity of the wolves and determine that they are not simply dispersing. Hence this kind of mobile protection is unlikely to be “abused“ or result in a serious burden for anyone.

Pitfalls and misconceptions

It is often assumed that separate buffers can be considered for Toklat vs. Margaret – one buffer along the northeast park boundary for Toklat and another along the east park boundary for Margaret. This is a serious mistake. Per above, the unpredictable extraterritorial forays of each group can extend in both directions. In addition, although Margaret's recent territorial (vs *extra*territorial) movements haven't extended into the northeast area yet, they likely will as recolonization of the Sanctuary vacancy continues. Both the Sanctuary (Fig. 4) and Savage (Haber 1977) territories extended into this area as well as outside the east park boundary. Indeed, Margaret's original territory – for about a year and a half prior to the Sanctuary vacancy – was “wedged” between the Toklat and Sanctuary territories and extended further to the north. Thus, whether the concern is for Toklat, Margaret, or both groups, a buffer including both areas (northeast and east) is needed for effective protection against hunting and trapping.

As also emphasized earlier, it is not possible to delineate an effective buffer based on the *core* radiolocations, because of the disproportionately much higher hunting-trapping risk associated with the outlying locations, however fewer in number they are. This was the flawed reasoning behind the delineation of a 90-square-mile northeast boundary “Toklat buffer” in 2001. The 2001 buffer has also enabled vindictive trappers to focus their revenge along a north-south line (lower Savage River – the east side of the 2001 buffer) right through the middle of a traditional caribou wintering area, where Toklat (and other groups) have hunted in past winters. I monitored a trapline along lower Savage River in winter 2001-02 but there was unusually low caribou activity. This and Toklat's eastward probes into the Sanctuary vacancy were among the lucky circumstances that forestalled Toklat trapping losses in the lower Savage area for at least one winter.

The Board declined to add any east boundary areas to the buffer in 2001 largely because it felt this would result in heavy habituation of the eastern Denali wolves and problems for east boundary residents. However, most of the contact that these wolves have with people takes place well *inside* the park, such that any additional "habituation" outside is likely to be of secondary importance. More to the point, the bold behavior of Denali wolves around people is typical of what is "natural" and "wild" for this species, probably results much less from habituation than is generally assumed, and has characterized these wolves for at least four decades without evolving into dangerous aggression (Haber 2002b).

An argument often heard in opposition to a Denali buffer is that wolf family groups disappear regularly due to natural causes, and that these mortalities essentially "swamp out" and render insignificant the effects of human-caused mortality. I challenged this argument in detail in Haber (1996, 1998, 1999, 2002a). But perhaps the most obvious counter to it is Toklat's long history, Savage's 17+ years, and the well-documented role of hunting and trapping in the succession of eastern turnovers. In other words, absent hunting and trapping, persistence would more likely be the rule than the exception in eastern Denali. Wolf family lineages ("packs") are the fundamental biological units of a wolf population. There are good scientific, esthetic, ethical, and viewing reasons why, at least in eastern Denali, these should be allowed to survive for however long – years, decades, or longer - natural circumstances alone may dictate in each case.

Another frequent argument is that the buffer is a back-door attempt to expand the park. Park entrance areas inherently attract people, development, and easy access. This usually creates sharp lines of demarcation, with natural conditions prevailing on the inside and development and access just outside. Resident wolves and other wildlife will continue using natural habitats close to the park boundary. Thus it is inevitable that their forays, migrations, etc will take them into areas of human activity and easy hunting-trapping access. The purpose of the proposed buffer is nothing more than to neutralize the negative impacts of this entrance-area activity and access on two especially vulnerable and valued park wildlife groups. The buffer is a response to a problem generated largely by human activity and access, not a back-door attempt to expand the park. It is a logical way to counter resulting hunting-trapping impacts and help to preserve what attracted most of the entrance-area human activity in the first place.

Opponents often imply that there is local subsistence dependency on wolf hunting and trapping in the proposed buffer area. To the contrary, most if not all of the wolf killing within this area is opportunistic and/or recreational. It is done primarily by a handful of local residents from households with one or more wage earners – not uncommonly earning more than $50,000 – and by weekend hunters/snowmachiners from Fairbanks and Anchorage. I am a resident of the proposed buffer and know most of the locals who trap or shoot wolves well enough to debunk the notion that any of them will suffer a significant lifestyle or income change if they cannot kill wolves in this area.

Literature cited

Haber, G.C. 1977. Socio-ecological dynamics of wolves and prey in a subarctic ecosystem. Ph.D. dissertation, Univ. of British Columbia, Vancouver. 817 pp. 1978, Special Report, Joint Federal-State Land Use Planning Commission For Alaska. Available from Arctic Environmental Information and Data Center, Univ. of Alaska, Anchorage.

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

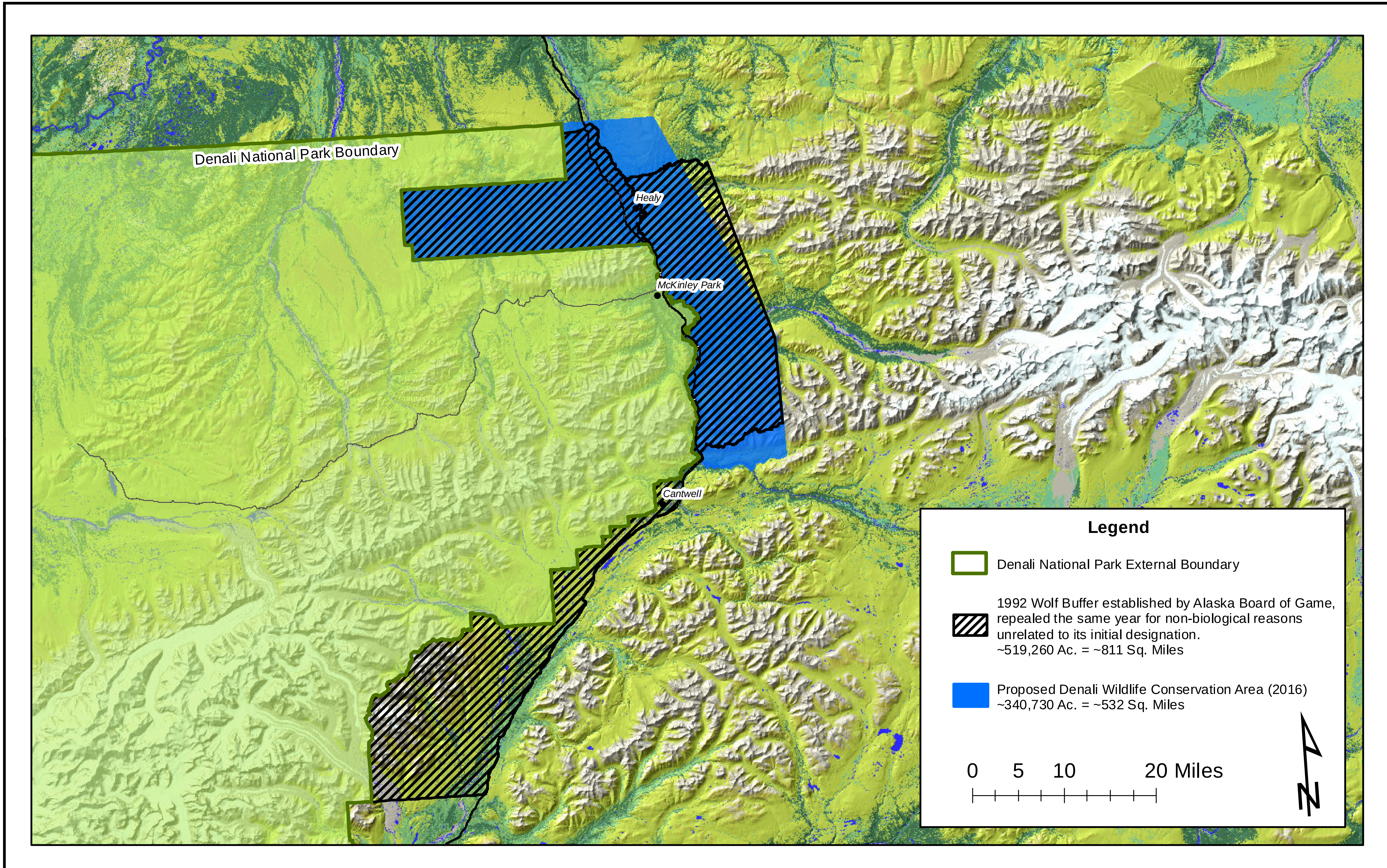
Haber, G.C. 1998. Review of, The wolves of Denali. Denali National Park resource management files or available from ghaber@mtaonline.net. 13 pp.

Haber, G.C. 1999. A selective view of wolf ecology. Conservation Biology 13: 460-461.

Haber, G.C. 2002a. Toklat, Margaret, and Sanctuary: The wolves of eastern Denali. Biological year 2001-02 responses to disruption. Annual research report, Denali National Park resource management files or available from ghaber@mtaonline.net. 32 pp.

Haber, G.C. 2002b. Wolves and people in Denali National Park. Memorandum to the Denali superintendent and Alaska regional director, National Park Service. Denali National Park resource management files or available from ghaber@mtaonline.net. 12 pp.

Mech, L.D., L.G. Adams, T.J. Meier, J.W. Burch, and B.W. Dale. 1998. The wolves of Denali. Univ. of Minnesota Press, Minneapolis. 227 pp.


Denali National Park Boundary
Healy
McKinley Park
Cantwell
Legend
Denali National Park External Boundary
1992 Wolf Buffer established by Alaska Board of Game, repealed the same year for non-biological reasons unrelated to its initial designation.
~519,260 Ac. = ~811 Sq. Miles
Proposed Denali Wildlife Conservation Area (2016)
~340,730 Ac. = ~532 Sq. Miles
0 5 10 20 Miles
N

By: Van Lawrence
Introduced: 08/25/2016
Adopted: 08/25/2016

FAIRBANKS NORTH STAR BOROUGH

RESOLUTION NO. 2016–39

A RESOLUTION URGING GOVERNOR WALKER TO CLOSE AREAS ADJACENT TO DENALI NATIONAL PARK AND PRESERVE TO THE TRAPPING AND HUNTING OF BEARS, WOLVES AND WOLVERINES

WHEREAS, Over a half a million annual visitors from around the world come to Denali National Park and Preserve, in large part, to see the iconic wolves and bears of the Park; and

WHEREAS, Both the Park and commercial tour companies advertise Denali National Park and Preserve as the best place in the world to see wolves within their natural habitat; and

WHEREAS, A large percentage of these visitors come to Fairbanks because of our proximity to the Park; and

WHEREAS, Hunters and trappers are allowed to use bait in the 22 mile long corridor, commonly referred to as the Wolf Townships or Stampede Trail corridor, to lure bears and wolves out of Denali National Park and Preserve and kill them; and

WHEREAS, The East Fork Pack was the most famous, the most studied and most viewed wolf-pack in the world and has now been decimated by hunters and trappers using bait to draw them just outside the Park boundary; and

WHEREAS, When this area was closed to hunting and trapping the East Fork Pack numbered 22; but has now been reduced to a single female wolf trying to raise pups alone; and

WHEREAS, When the Wolf Townships/Stampede Trail was closed to hunting there were 140 wolves in Denali National Park and Preserve and 49% of visitors saw wolves. Now the East Fork Pack has been almost wiped out and the total number of wolves within Denali stands at 48 - an all-time low - and the number of visitors who see wolves, for the last three years, is only 4%, also an all-time low; and

WHEREAS, This incredible and unique resource is being squandered for the satisfaction of just a handful of individuals; and

WHEREAS, The Alaska economy cannot survive unless we have a diversified economy that promotes tourism and other industries besides oil.

NOW THEREFORE BE IT RESOLVED the Fairbanks North Star Borough urges the Governor, through the Commissioner of Fish and Game to close the areas adjacent to Denali National Park and Preserve to the trapping and hunting of bears, wolves and wolverines.

BE IT FURTHER RESOLVED copies of this resolution shall be distributed to Governor Walker and Alaska Department of Fish and Game Commissioner Sam Cotten.

PASSED AND APPROVED THIS 25TH DAY OF AUGUST, 2016.

John Davies
Presiding Officer

ATTEST:

Nanci Ashford-Bingham

Nanci Ashford-Bingham, MMC
Borough Clerk

Yeses: Sattley,Westlind, Lawrence, Quist, Dodge, Davies
Noes: Cooper, Roberts, Hutchison
Other: None

Economic Values of Wolves in Denali National Park and Preserve (DNPP): Concepts, Literature Synthesis, Data Gaps and Study Plan

March 3, 2016

Dr. John Loomis*
Dept of Agricultural and Resource Economics
Colorado State University
John.Loomis@colostate.edu

NPS Photo/Woodward

*Views expressed in this report are those of the author and do not necessarily represent the views of Colorado State University.

Acknowledgements: I wish to thank Bridget Borg, Dave Schirokauer, Patricia Owen, Lynne Koontz, Bret Meldrum and Leslie Richardson, National Park Service for the many references provided as well as valuable comments and suggestions on the draft report. Any errors or omissions are the sole responsibility of the author.

Economic Values of Wolves in Denali National Park and Preserve (DNPP): Concepts, Literature Synthesis, Data Gaps and Study Plan

Dr. John Loomis
Dept of Agricultural and Resource Economics
Colorado State University
John.Loomis@colostate.edu

EXECUTIVE SUMMARY

This report identifies what is currently known about economic values of wolves in Denali National Park and Preserve (DNPP) to visitors, Alaska residents and residents of the rest of the United States (U.S.). Our literature review and synthesis found that little is known specifically about the economic value of wolf viewing in DNPP and about visitors that come to DNPP primarily to view wolves (Iverson and Borg, 2012).

However, wildlife viewing is clearly a source of socio-economic value in the state of Alaska. Wildlife viewing is a driver of tourism for DNPP (Stynes and Ackerman 2010) and the state of Alaska. For example, wildlife viewing activities in Alaska supported over $2.7 billion in economic activity in 2011 (ECONorthwest 2014a). In 1997, non-resident visitors who came to Alaska primarily to view wildlife had average expenditures of $6,000 per trip (Miller and McCollum, 1997). The benefits per trip in excess of their expenditures were on the order of $700 to $900 (Miller and McCollum, 1997). From economic valuation questions found in Alaska wildlife viewing literature, it can be inferred that a non-resident visitor may have an additional value in the range of $200-$300 per wildlife viewing trip to Alaska if a wolf is seen on their trip.

Based on our literature review, there is currently nothing known about the non-use/passive-use values (sometimes called existence and bequest values) of wolves in Alaska to Alaskan and other U.S. residents. What little literature exists on the passive-use values of wolves pertains to reintroduction of wolves in Yellowstone National Park (YNP) and wolf habitat protection in Minnesota (Chambers and Whitehead, 2003). Surveys of U.S. households indicated passive-use values were about $14 per U.S. household for wolf reintroduction into YNP (Duffield, et al. 1993). Similar values were published in the United States Fish and Wildlife Service Environmental Impact Statement on wolf reintroduction into YNP and Central Idaho (U.S. Fish and Wildlife Service, 1994). Minnesota household's passive-use values for wolf habitat protection range from $7 to $31 per household, with the value depending on the region of Minnesota. With millions of households in the U.S., these small passive-use values per household add up to a sizeable amount of total economic value.

The state of Alaska is mandated to provide for consumptive uses of wildlife, and harvest of wolves can provide significant economic benefits as well (National Research Council 1997). However, there is minimal information on the economic value of consumptive uses of wolves, including the value procured from hunting and trapping (harvest) in the region surrounding DNPP (Borg, personal communication). However, in 2011, hunting throughout Alaska supported over $1.3 billion dollars in economic activity (ECONorthwest 2014a).

Managers tasked with making decisions regarding wildlife management need accurate information on the economic values of wolves to viewers, hunters, trappers and the general public to make well informed decisions regarding management of wolves and their prey(NRC, 1997). Wolf management is particularly contentious in the areas surround DNPP (Borg 2015) and data are needed on the specific magnitude of revenues and other economic values derived from wolf harvest around DNPP. Specifically, data is needed that will support an analysis of existence value (or non-use value) of wolves in DNPP area that can be brought in as a direct comparison for the market values brought to local subsistence and sport hunters. In Alaskan culture, hunting and trapping have a high intrinsic value as cultural signifiers. Trapping practices of wolves also acts to maintain traditional and modern trapping knowledge specifically ("Alaska Trappers Association" 2015). Additionally, there are associated costs of limiting wolf harvest, given not only the revenue generated from hunting (Treves 2009; ECONorthwest 2014a) but also the potential of wolf harvest to increase land owner's acceptance of large carnivores (Treves 2009). Likewise, the non-consumptive economic value of wolf viewing in DNPP and the existence values of wolves in DNNP of the U.S. and wider public are predicted to bring significant "alternative" wolf value to bear on the market, given the findings of other wolf viewing valuation studies (CITE) and ongoing social science research in DNPP regarding wolf viewing tourism.

Luckily, there are well established methods for filling all these data gaps regarding hunter and viewer use values, as well as the general public's passive-use values of wolves in and around DNPP. In 1997, the NRC (1997) suggested a coordinated social science research program to address similar data gaps regarding consumptive and non-consumptive uses of wolves in Alaska. Our report provides many of the details of such a research program. In particular, our report provides details and examples of the economic methods for quantifying wolf related visitor spending and benefits, hunter spending and benefits, and passive-use values. This report also outlines several study plans to provide these values that are needed for informing local and regional wolf management strategies.

TABLE OF CONTENTS

Economic Values of Wolves in Denali National Park and Preserve (DNPP): Concepts, Literature Synthesis, Data Gaps and Study Plan

I. Study Purpose

Wolf management has proven controversial, whether in Alaska or in the lower 48 states of the U.S. (Huey, 2016). The controversy in Alaska resulted in the Natural Research Council (part of the National Academy of Sciences), evaluating wildlife management in Alaska in the 1990s with particular attention to wolves and their prey (NRC, 1997). The overall conclusion of the committee with regard to economics was that there are several information gaps that need to be filled before a complete economic analysis of wolf management can be performed. In the intervening years, wolf management has continued to be a source of often heated debate with many different stakeholders. Specifically, management of wolves at the boundaries of protected areas, such as National Parks and Preserves, has been subject to on-going debate and attention with ample rhetoric, but there has been a lack of quantitative evidence regarding economic valuation to inform management decisions (Borg 2015). The purpose of this study is to define specific data gaps related to wolf economic values in and around Denali National Park and Preserve and present a plan for addressing the current data gaps. Therefore, this study does the following: (1) describes the types of economic values associated with wolves in the Denali National Park and Preserve area (DNPP) area; (2) describes the methods available to measure these values; (3) defines the current state of empirical knowledge on these values; (4) identifies data gaps that need to be filled in order to quantify economic trade offs in wolf management in and adjacent to DNNP, and (5) proposes study plans to estimate the most relevant economic values of wolves in DNPP and the surrounding area.

II. Types of Economic Values and Methods for Quantifying Them

A. Types of Economic Values

Willingness to pay and Consumer Surplus

Benefits are defined in benefit-cost analysis as what a consumer or producer would pay to have or retain access to a private or public good. Economists call this *net willingness to pay* (WTP), or willingness to pay over and above costs. This concept is also known as *consumer surplus* and *producer surplus* (USWRC, 1983; OMB, 1992; 2000; EPA, 2000; Freeman, 2003). *Price* is the willingness to pay for one more unit of the good. The absence of price does not mean absence of value; if a good provides a person (not necessarily everybody) with enjoyment/satisfaction and is scarce, it has an economic value (Schuhmann and Schwabe, 2000:4). As Office of Management and Budget (1992:7) notes, "[P]rices sometimes do not adequately reflect the true value of a good to society." This is certainly the case of many natural resources, which are purposely non-marketed. For example, the fact that wildlife is not privately owned but held in public trust by government agencies does not diminish the fact that these species have an economic value to people. In the case of wildlife, the general concept of net WTP or consumer surplus applies, since the market price is zero for many species, or prices exist for just one attribute of the species (e.g., meat or fur or license).

While WTP is the measure of benefits to the user (hunter, viewer), there may also be spin-off economic effects in terms of jobs in a local community related to wildlife viewing, hunting, or trapping. Economists refer to these as local or regional *economic impacts*. The term local can be a community, county or borough when the data are available at that level of detail.

In some cases, the term regional indicates a substantial part of a state. In some cases, economic impact analysis can be conducted for an entire state.

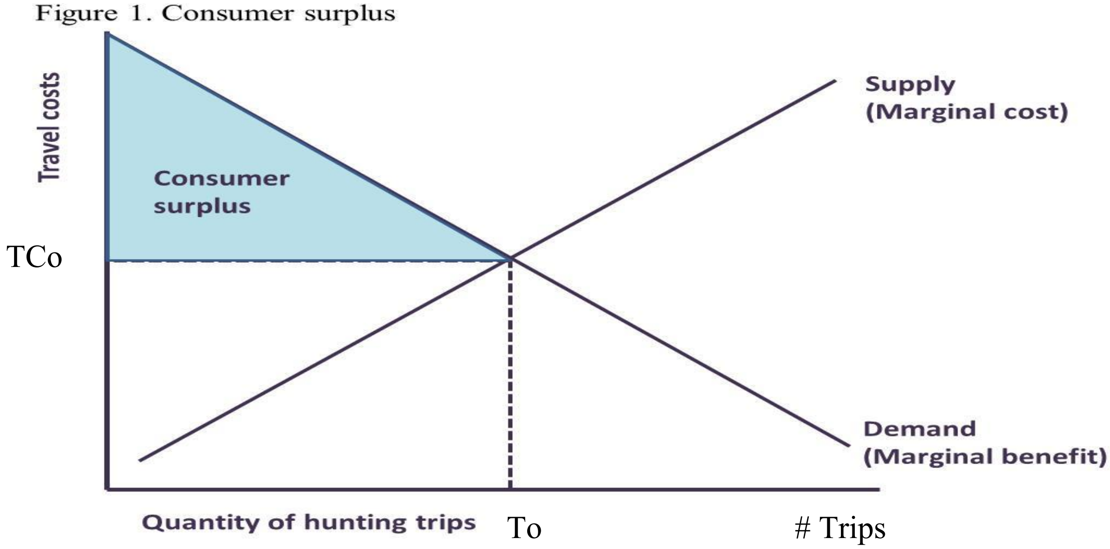
While much past economic analysis performed by federal agencies such as the United States Department of Agriculture Forest Service (USFS) or National Park Service (NPS) has emphasized economic impacts, these agencies are broadening their analysis to include net WTP for non-market resources as well. One of the reasons for this has been an increasing emphasis on valuing ecosystem services. The economic value of ecosystem services is the consumer surplus or cost savings arising from the benefits that an ecosystem provides people. Wildlife viewing and harvest of wildlife (hunting and trapping) are considered ecosystem services of wildlife. A complete economic analysis will consider an economic impact analysis to a regional or state economy **and** a benefit cost analysis of the benefits to the users themselves. In a sense there are two beneficiaries of wildlife management: (a) tourism related businesses—guides, hotels, etc. and (b) the hunters/trappers and viewers themselves. A complete economic analysis will include both.

Use Values: The economic value of market goods and recreational resources

For decades, people have recognized that many wildlife species provide direct use values to hunters and non-consumptive wildlife viewers (Loomis, et al. 1984). These benefits are measured by their net WTP or consumer surplus. As can be seen in Figure 1, which uses hunting as an example, the demand curve represents the incremental or marginal benefits to a hunter from additional hunting trips. As described in the methods section below, the major "price" of a trip is the travel costs to the site (especially for residents where the license cost is low and the license allows for numerous trips).

The amount the hunter would pay over and above the actual travel costs incurred is a measure of their consumer surplus. Essentially, they would have been willing to pay a higher cost on the first trip rather than not go hunting (much like most coffee drinkers would pay a great deal more than the price for the first cup of coffee in the morning than for the second or third cup). Each additional trip has less and less consumer surplus, until the travel cost of the trip equals the incremental (marginal) benefit of another trip. At that point they stop taking trips as the cost of another trip exceeds their benefit.

Figure 1. Consumer surplus



The amount the hunter actually spends (travel cost (TCo) times the number of trips (To)), is the expenditure used in a regional economic model to estimate jobs and wages resulting from the hunter expenditures. [1]

[1] The regional economic model used to convert hunter/viewer spending into regional income and employment is known as an input-output model. A commonly used input-output model is named IMPLAN for Impact Planning since estimating regional income and employment is known as economic impact analysis as distinct from economic efficiency analysis which is used in benefit-cost analysis.

Existence/Passive-Use/Non-Use Values

As first noted in 1967 (Krutilla, 1967) and empirically demonstrated beginning in the early 1980s (Brookshire, et al. 1983), wildlife also has an *existence value* to people who may never see the species in the wild. These people are often willing to pay for protection of these species. Other people would pay for protection of habitats for wildlife species to keep the wildlife species protected for future generations. This is known as *bequest value*. Evidence of existence and bequest values may be expressed in donations to conservation groups such as the World Wildlife Fund as well as donations to numerous state "Non-Game Wildlife check-offs" on State Income Tax forms. These *passive-use values* are recognized in federal natural resource damage assessment, when the U.S. District Court of Appeals in 1997 termed existence and bequest values "*passive-use values*" (*Ohio v. U.S. Department of Interior*, 880 F. 2d. 432, 444 (D.C. Cir. 1989)). Also called *non-use values*, these values are considered compensable damages arising from environmental damages (e.g., old hardrock mines) under the Superfund legislation as well as oil spills under the Oil Pollution Act of 1990.

In the case of wolves, research summarized below, indicates that people living hundreds of miles away from wolf habitat (e.g., southeastern U.S.) would still pay something to know there is a viable population of wolves today and that protection of this population and its habitat would provide wolf populations for future generations.

B. Methods for Quantifying Economic Values

Travel Cost and Valuation Methods

Economists have developed several methods for estimating the use and passive-use values of wildlife. In this section we review each of these methods in detail. The first method reviewed (*the travel cost method*) is based on actual visitor travel behavior and is used to estimate recreation use benefits. Specifically, the travel cost method (TCM) uses variations in visitor travel costs and their associated trips taken to trace out a demand curve like the one shown in Figure 1. Once the demand curve is estimated, the net WTP or consumer surplus is calculated. TCM is a preferred method for estimating **current** use values because it is based on visitors actual travel behavior (travel cost and travel time incurred) to obtain their **current** wildlife experience. However, future visitor benefits might change with potential wildlife management alternatives that have not yet been implemented. The benefits of the future scenarios are difficult to quantify with TCM. In this case the *contingent valuation method* (CVM) may be a better tool in these cases where management actions may change the populations of wildlife and hence the magnitude of use value of wildlife. This method (described in more detail below) constructs a simulated market to ask visitors what the maximum amount they would pay (WTP) for each scenario associated with a potential management alternative. For example, visitors might be presented a "payment card" that has ten alternative increases in trip costs to visit an area where they could view twice as many wolves as they might typically see now. The visitor would be asked to circle the dollar amount that represents the maximum <u>additional</u> amount they would pay to visit this area where they could see twice as many wolves. Although the TCM and CVM approaches are very different techniques for estimating WTP, both TCM and CVM provide comparable estimates of WTP. In a review of more than a hundred recreation studies where both TCM and CVM were used, Carson, et al. 1996 found that the WTP derived from TCM and CVM were not statistically different from one another.

Details of the Travel Cost Method (TCM) for Estimating Recreation Benefits

Travel Cost Method (TCM) is a method that uses variations in travel costs incurred by visitors living at different distances from the site and their corresponding number of trips taken to statistically estimate a *demand curve* like that shown in Figure 1. From the demand curve, the consumer surplus or net WTP beyond the current cost is calculated (see Loomis and Walsh, 1997 for details). The strength of this method is that it uses actual trips taken and actual travel costs to trace out the demand curve. Hence the measures of net WTP reflect actual behavior. Application of TCM can sometimes be accomplished using existing data (e.g. hunter zip codes found on hunting permits), but is typically performed using a short survey of hunters or viewers. This survey can be administered by the state fish and game agency during its post-season hunter survey. For example, in Idaho, this interagency approach was implemented by the Idaho Fish and Game in cooperation with the U.S. Forest Service (Donnelly, et al. 1985). TCM is a well established methodology as it has been used in nearly a hundred valuation studies of hunting and wildlife viewing conducted in the U.S., including many by state fish and game agencies, such as those in Alaska, California, and Idaho (Peterson, et al. 1992; Loomis, et al. 1989; Donnelly, et al. 1985).

Details of the Contingent Valuation Method (CVM)

CVM can provide information about the potential economic consequences of alternative possible management plans. CVM (and choice experiments) are the only methods that can estimate the non-visiting public's WTP for existence/non-use or passive-use values. Since those not visiting have no trips and incur no travel costs, their WTP has to be ascertained by asking them in a constructed market or simulated voter referendum.

CVM measures the use values of hunting, trapping and viewing of wildlife by employing simulated or constructed market. The simulated or constructed market provides a well defined description of the good to be valued (e.g., a specific increase in harvest success rate or a specific increase in number of animals a viewer would see) and a means by which the hunter or viewer would pay for this improvement. The simulated or constructed market then gives the hunter or viewer an opportunity to "use the market" and indicate their willingness to pay (if any) for the improvement. Using the example of the payment card described above, a hunter would circle the maximum amount they would pay for a specific increase in harvest success rate next year. Likewise a wildlife viewer would circle the maximum they would pay to see a specific increase in the number of animals. The dollar amount circled would reflect their maximum WTP or consumer surplus for the specific increase presented in the survey.

CVM is also more appropriate than TCM if visitors are on multiple destination trips in Alaska, where the travel cost to Alaska is not attributable to visiting just a single site or activity. In fact, most non-resident wildlife viewing tourists to Alaska may visit many different areas during their trip from home. This is especially true of visitors from the lower 48 states. Trying to attribute the travel cost to Alaska to any one site becomes problematic and hence the TCM is difficult to apply to wildlife viewing trips in Alaska.[2]

Thus, in the case of multiple destination trips a CVM scenario can be developed that allows the researcher to focus on just the wildlife viewing experience for a particular species in a specific area. For example, a visitor to DNPP could be asked if they would pay a given amount more for the trip they have taken to DNPP if they could see twice as many wolves as they saw on

---

[2] However, for big game hunting, many hunters do come to Alaska to hunt a specific species in a particular area. In this case the TCM would be applicable since the entire travel costs of the trip are attributable to hunting a particular species in a particular area. For hunters that come to Alaska to hunt multiple species in several different locations, then the CVM as described for wildlife viewing would be equally applicable to these multi-species hunters.

their current trip. This could be asked using the payment card that was described above, or a more preferred method the *dichotomous choice* approach. With this approach the dollar amount of the increase in trip cost is varied across the sample of visitors. For example, 10% of the sample could be asked if they would pay $10 more for a trip where they would see twice as many wolves, a different 10% of the sample could be asked $15 more per trip, and so on, until the last 10% of the sample might be asked $150 more per trip. The range of the dollar amounts presented would be pretested to make sure it covered the likely range of the visitor's maximum WTP. By analyzing the percentage of visitors that would pay the differing dollar amounts, a quasi-demand curve or marginal benefit function similar to Figure 1 can be estimated. From this curve, the net WTP or consumer surplus can be calculated. The reason the dichotomous choice method is the preferred method is that a dichotomous choice WTP question format mimics a market: the person is simply asked if they would "buy" the good at the price stated like people actually do in nearly all markets in the U.S. Asking a person to circle the most they would pay for a good, as is done in a payment card format, is unusual in most markets, although it is used by many charities such as United Way, or conservation organizations.

Methods for estimating Existence Values

Another strong feature of CVM is its ability to measure the monetary amount of existence values for maintaining a specific number of animals in a particular location. With CVM, a simulated or constructed referendum is often used to ask non-visiting households whether they would vote to pay for a well-defined change in the population of a given wildlife species. The general public is sampled usually via a mail survey using an USPS address based sample to ensure a random sample of whatever geographic area is being sampled.[3] The reason that a mail survey is needed is that individuals must be provided with sufficient information on the species they are being asked about so as to provide an informed valuation. This information would include a map showing where the species of interest is located, and what the management action would be to "produce" an increase in the number of animals or to reverse a decline in their population. How wide a geographic area of households to sample is often determined by whether the species is only of state significance (i.e., it is found in many other states) or of national significance (i.e., it is found in few other places in the U.S.). Species that are federally listed T&E species or found on federal public lands suggest that a survey of the entire U.S. be done because the resource "belongs" to everyone in the U.S. Further, management of the species will likely be paid from federal appropriations financed by national taxes such as an income tax. Loomis (2000) summarizes several empirical studies that estimate how WTP values change with increasing distance to where the wildlife resource is located. This research suggests that WTP can be significant even at a distance of 1,000 miles from the resource.

Even though the dollar amounts stated by people in response to a CVM survey are not actually paid, the method has shown to be reliable in test-retest reliability studies (Loomis, 1990; Reiling et al., 1990). Richardson and Loomis (2009) provide a listing of these passive-use value studies of wildlife and a meta-analysis of them as well.

Chambers and Whitehead (2003) provide an example of using a CVM scenario to estimate the existence value of preserving wolves. In their survey a Wolf Management Plan (WMP) is described to the household in the following way: the plan "…*would include*

[3] A combination mail and internet survey is also used, where the address based sample is given the option of filling out the survey on-line via a URL in their letter. Our experience in two different surveys (one of the U.S. population and one of New Jersey households with solar panels) indicates that only about 20% of the households offered the option of both survey modes choose the internet survey option.

monitoring the population and health of wolves and preserving their habitat and that of their primary prey." The respondents were informed that if the plan was passed, a stable wolf population goal of 1600 wolves would be sustained, and wolves would not be returned to the Threatened and Endangered species list in the near future. Respondents were asked if they would pay a one-time tax increase (of specified amount, $A) to fund this plan:

> *"These management activities are expensive. New state money would be needed to fund the management plan. Suppose that a one-time tax increase of $A would be required from each Minnesota household to support and fund the wolf management plan. Would you be willing to pay the one-time tax increase of $A to fund the Wolf Management Plan?"*

As the researchers described in the study:

"The values of this tax increase were varied across surveys. Some respondents were asked if they would be willing to pay $5, others $25, $50, $75 or $100. The question was followed by three answer categories: yes, no, and don't know."

Past research has shown recoding the "don't know responses" to 'no responses" increases the accuracy of the resulting WTP estimates (Loomis, 2014; Champ, et al. 1997; Champ et al. 2009). Chambers and Whitehead estimated the benefits to two different communities in Minnesota within the range of the wolves. Ely households would pay between $4.43 and $4.77 (about $7 in $2014). St. Cloud residents were willing to pay between $20.15 and $21.49 (about $31 in $2014).

Details of Choice Experiments

In the last 15 years a number of economists have embraced a method called *Choice Modeling* (CM) or *Choice Experiments* (CE) or *Attribute Based Modeling* (Holmes and

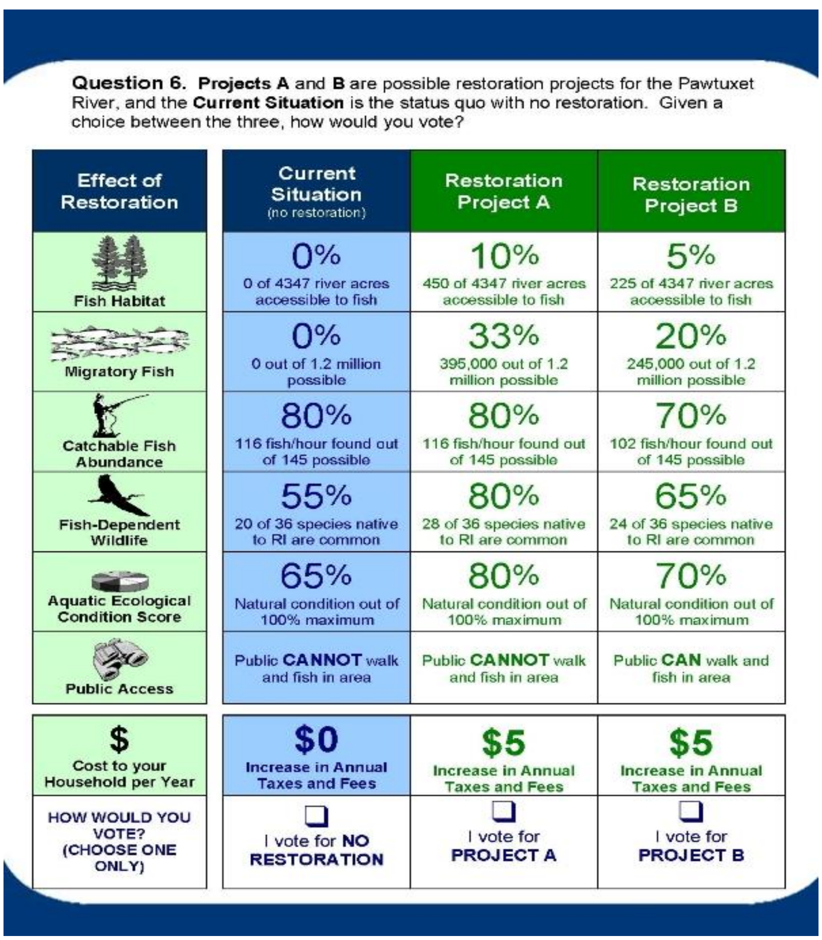
Adamowicz, 2003). The method originated in the marketing literature, where it was called *Conjoint Analysis*. Conjoint Analysis had been used for more than three decades by market researchers to determine which characteristics of proposed products were most desired by consumers. Jordan Louviere was one of the pioneers in the marketing field, and his expertise has been applied in the application of non-market valuation as well (see Louviere, et al. 2000).

The primary distinction between CE and CVM is how respondents are asked about their WTP. In contrast to a CVM survey where a WTP question is asked for a single "management action" program or policy, a CE survey presents the respondent with a set of alternative programs or management actions, each characterized by multiple attributes or characteristics (which can be thought of as different features) of a particular program. One characteristic of each alternative program is the cost of that program. Each respondent is typically asked to choose their most preferred alternative from a set of management alternatives. Each choice set has a "no change/current condition/status quo" alternative usually placed adjacent to one or more proposed management action alternatives. The alternative chosen by the respondent is assumed to yield the highest benefits to the respondent. Much like CVM, the range of program costs or "prices" varies across the sample. However, unlike CVM, in a CE survey, the non-price characteristics or attributes of each alternative management program also changes across the sample. Because one of the attributes included in each alternative management program is a price or cost for the management program, the monetary value for each of the program's attributes can be calculated. Thus with a CE survey, the analyst knows not only the total WTP for a possible management action but also how each feature (attribute or characteristic) is valued by the respondent.

It is easiest to visualize the CE approach with an example. Figure 2 presents an example of a CE for valuation of river restoration on the Pawtuxet River in the state of Rhode Island. It is a single choice task that would be presented to the respondent. A single survey might have two or three individual choice tasks. There are seven attributes for the choice task illustrated in Figure 2 (which is probably the upper limit on the number that most general public respondents can handle). Prior to this choice task, each of these attributes were explained to the respondent in more detail than is shown in the choice task table (Figure 2). Maps were provided to show what stretches of the river could be restored.

The first alternative is to maintain the current status of the river with no restoration and has zero cost to the household. The other two alternatives show different levels of restoration and annual taxes and fees that a household would pay for the action.

Figure 2. Example of a Choice Task for River Restoration



Question 6. **Projects A** and **B** are possible restoration projects for the Pawtuxet River, and the **Current Situation** is the status quo with no restoration. Given a choice between the three, how would you vote?

Effect of Restoration	Current Situation (no restoration)	Restoration Project A	Restoration Project B
Fish Habitat	0% 0 of 4347 river acres accessible to fish	10% 450 of 4347 river acres accessible to fish	5% 225 of 4347 river acres accessible to fish
Migratory Fish	0% 0 out of 1.2 million possible	33% 395,000 out of 1.2 million possible	20% 245,000 out of 1.2 million possible
Catchable Fish Abundance	80% 116 fish/hour found out of 145 possible	80% 116 fish/hour found out of 145 possible	70% 102 fish/hour found out of 145 possible
Fish-Dependent Wildlife	55% 20 of 36 species native to RI are common	80% 28 of 36 species native to RI are common	65% 24 of 36 species native to RI are common
Aquatic Ecological Condition Score	65% Natural condition out of 100% maximum	80% Natural condition out of 100% maximum	70% Natural condition out of 100% maximum
Public Access	Public **CANNOT** walk and fish in area	Public **CANNOT** walk and fish in area	Public **CAN** walk and fish in area
$ Cost to your Household per Year	**$0** Increase in Annual Taxes and Fees	**$5** Increase in Annual Taxes and Fees	**$5** Increase in Annual Taxes and Fees
HOW WOULD YOU VOTE? (CHOOSE ONE ONLY)	❑ I vote for **NO RESTORATION**	❑ I vote for **PROJECT A**	❑ I vote for **PROJECT B**

While this example has three alternatives (one "no action"—referred to as the Current Situation", and two "action" alternatives—Project A or Project B), there are some advantages of having just one "action" alternative paired with the "no action" alternative. The levels assigned to each attribute reflect a realistic range of that attribute for the location and management actions being proposed. This range is determined by discussion with scientists and managers to encompass what is feasible to attain, and what is credible to respondents (as determined in focus groups and pretests). The number of levels for each attribute are chosen to allow for estimation of a regression coefficient of the attribute. However, there is a trade-off between the number of levels desired and the associated number of survey versions required. For example, if there are three non-price attributes with five levels each, seven levels of the cost attribute then there are 24 survey versions that have to be printed and tracked. However, having a large number of cost levels is often critical to ensure enough variation in cost to estimate a statistically significant cost coefficient. If the cost coefficient is not significant, then the monetary values of the other attributes are non meaningful. Thus for survey implementation, 24 different versions of a survey would be printed.

Printing costs may influence how the choice experiment is designed, whether to use CVM and the type of CVM WTP question to be used. For example, printing 24 versions of a choice experiment survey can be expensive (especially if color is used) as compared to printing just seven versions of a CVM dichotomous choice survey or just one version of the survey if a CVM payment card is used. With the payment card everyone gets the same survey, so the economies of scale at the printer lower the cost of printing surveys as well as simplifying the mailing process. With a choice experiment not only must 24 versions of the survey be printed but there is complexity of tracking which person got which of the 24 choice experiment versions when doing follow up/repeat mailing to non-respondents.

Advantages and Disadvantages of CE versus CVM

The primary advantage of CE for non-market environmental valuation is its ability to provide more detail of respondents' valuation of the components of a particular policy or program than with CVM. CE can show the relative importance assigned to characteristics and derive estimated values associated with various levels of characteristics. The total value of a particular policy or program can also be calculated from a CE. This flexibility is particularly useful when policy makers or resource managers are uncertain about the final details of the program or policy at the time the survey is designed and implemented. As long as the likely range of the attribute levels are included in the survey versions, the value for any particular program can be calculated after the fact. There are two primary disadvantages of the CE approach: (a) survey implementation is more costly and complex due to the number of versions of the survey that need to be produced; (b) the available empirical evidence suggests that estimates of WTP from CE are greater than from CVM, a potentially worrisome problem (Stevens, et al. 2000; Richardson and Loomis, 2009).

III. Uses and Users of DNPP

A. Visitor Use of DNPP

In 2014, over a half million visitors (531,315) came to DNPP. This is a significant increase in the last few years over the slightly more than 400,000 visits recorded in 2011 (Stynes and Ackerman 2011). About 2% of the visitors were local Alaskans living in the area, 7% were Alaska residents living elsewhere and 91% were non-residents (U.S. and International). An increasing sub-demographic of international visitors is apparent in DNPP, and particularly, those focused on wolf viewing, as demonstrated by a preliminary study of visitor behavior and preferences in 2016 (Keller/NPS NRDS XX/2106). Visitors in this study are asked to allot preferences to wildlife viewing across an ungulate and meso-carnivore spectrum, as well as rank their importance to experiencing the "wilderness character" DNPP has to offer its backcountry visitors. Qualitative content analysis of structured interview material with these same surveyed visitors yields a primary theme of dissatisfaction of *not* seeing wolves. Deploying this theme as a factor in ANOVA yields especially significant loadings ($r = .77$; $p < 0.1$) with individual's relative rating of the importance of wolves for their overall DNPP wilderness experience. This preliminary study points to the need of including visitors to DNPP both on and off the shuttle and tour buses in a wolf viewing valuation study.

B. Visitor Interest in Wildlife Viewing in General and Wolves

Wildlife Viewing

Wildlife viewing is one of the two primary reasons people come to DNPP. The exact percentages vary from study to study and depend on the residence of the visitors. According to Fix, et al. (2013), only 20% of Alaskan residents cited wildlife viewing as the main reason for visiting DNPP (sightseeing and hiking were equally important at about 20% each). In comparison, they found that over half of the rest of U.S. visitors and international tourists cited wildlife viewing as the main purpose of their trip. When analyzing NPS Visitor Services Project (VSP) data Mani, et al. (2012) found that the most common activities in DNPP were viewing scenery (88%) and viewing wildlife (80%). These two percentages are similar for first time and repeat visitors, indicating that wildlife is a factor drawing people back to DNPP. Manning and Hallo (2010) found that the single most important experience for visitors on the Denali National Park road was seeing wildlife (70%). Related to this, visitors thought not seeing "enough wildlife" and "too few animals along the road" were a problem (50%, and 53%, respectively). This suggests that the quality of the visitor experience ***is*** influenced by the number of animals seen regardless of whether the animals seen were one of the "Big 5" species (grizzly bears, wolves, caribou, Dall sheep and moose).

Wolves

Just how important is wolf viewing to visitor satisfaction? A 2012 survey in DNPP found that, while wolves were seen by about 26% of the visitors, seeing a wolf was a statistically significant contribution to wildlife viewing satisfaction (Skibins, et al. 2012). However, the contribution of wolves toward wildlife viewing satisfaction was not statistically different than was the contribution of moose, despite the fact that moose were seen two-thirds of the time.

IV. Economic Impacts Associated with DNPP and Wildlife Viewing

Economic impact analyses evaluate the direct and indirect effects of spending by visitors living outside the economic impact area. Specifically, positive economic impacts arise when visitors living outside the geographic impact area, visit the economic impact area and spend money inside the economic impact area. In essence, these visitors living outside the impact area inject "new" money into the impact area by their spending in the impact area.

There have been two economic impact studies of DNPP in recent years. The first was the economic impact study by Stynes and Ackerman (2010) which was based on 2008 visitation data (432,309 visitors). This study evaluated two impact areas: (a) the State of Alaska as a whole; (b) the DNPP region. To evaluate the positive economic impact that visitors to DNPP have on the State of Alaska economy as a whole, the study focused on the spending of non-Alaskan resident visitors (rest of the U.S. and international) while visiting DNPP. In 2008 these non-resident visitors' spending supported 2,319 jobs with $77.4 million in wages and an additional $48.52 million in other income (profits, rents and indirect business taxes) in the State of Alaska.

Stynes and Ackerman also estimated the economic impact of DNPP visitor spending to just the Denali Region (defined as the Denali Borough). For this analysis, Alaska resident spending inside the Denali Region represents new money injected into the Denali Region because nearly all Alaska residents live outside the Denali Region. In 2008, spending by Alaskan residents, rest of U.S. residents and international tourists supported an estimated 1,491 jobs in the Denali Region. This was associated with $45.4 million in wages and $26 million in other income (profits, rents and indirect business taxes).

A more recent study using the much higher 2014 visitation rate to DNPP numbers (531,315 visits)[4] and improved economic impact modeling calculated significantly higher positive economic impacts. Specifically, the results indicated that visitor spending supported 6,800 jobs with $249.4

[4] 2014 visitation data from http://www.nps.gov/dena/learn/management/statistics.htm

million in labor income and an additional $231 million in other income (profits, rents and indirect business taxes (Cullinane, et al. 2015).

Total Economic Impacts Attributable to Wolves

As noted by Iverson and Borg, “Currently, there is no accurate assessment of how many people visit the park primarily for the purpose of viewing wolves”. This is an important data gap to fill because even if a few percentage points of the Denali Borough jobs or the State of Alaska jobs were directly related to visitors coming primarily to see wolves, it could amount to several hundred jobs.

V. Economic Benefits (WTP) Associated with DNPP Wildlife Viewing

In terms of economic values, McCollum, et al. (1998) found that visitor benefits (as measured by WTP) increased with wildlife viewing success. In particular, WTP rose from $47.58 per person per day trip ($70 in $2014) to $63.49 ($94 in $2014) when a trip involved the visitor seeing all of the Big 5 species (Grizzly bear, caribou, Dall Sheep, moose and wolf), and when the number of individual Big 5 animals seen increased from an average of 6 individual Big 5 animals to 21 individual Big 5 animals. This suggests that the probability of seeing a species such as a wolf and the number of wolves seen likely has a significant effect on wildlife viewing benefits.

VI. The Importance of Wildlife and Wolves in Alaska

Given the very limited information on the economic impacts and values of wolves in DNPP we synthesized the economic information on wolf values in the entire state of Alaska.

A. Uses of Wildlife in Alaska

ECONorthwest (2014b) surveyed Alaskan residents and found that well over 50% of respondents felt that wildlife was either “extremely important or very important” to their reason for living in Alaska and their quality of life. Alaskans interact with wildlife through hunting (about 100,000 participants) and wildlife viewing (about 200,000 participants). Of the residents that hunt, slightly less than 10% hunt wolves (moose are the most commonly hunted species). Of the visitors coming to hunt in Alaska, about 20% come to hunt wolves (ECONorthwest, 2014b). However, the vast majority of visitors (90%) that come to Alaska do so to view rather than hunt wildlife. Among Alaska residents and visitors to Alaska, 25% of residents and 40% of non-residents wanted to see wolves on their wildlife viewing trips.

The ECONorthwest (2014b) report briefly summarized what is known from secondary sources about trapping in Alaska, as too few residents participated in trapping to make a survey feasible. In particular, less than 1% of hunters in Alaska are trappers (ECONorthwest, 2014b:29). The ECONorthwest (2014b:30) report also indicates that Alaska contains plentiful areas for traplines. Data obtained by ECONorthwest (2014b:30) indicated that the total estimated value of fur trapping in Alaska in 2010-2011 was $1.54 million with lynx representing about half the value, and wolves representing about $175,000.

Dorendorf (2015) conducted a mail survey of trappers in the interior of Alaska (the geographic area spanning Delta Junction, McGrath, Fairbanks and Fort Yukon). Across the entire sample of 344 active trappers who returned surveys Dorendorf (2015:30) noted that "Outdoor recreation formed the most important motivation to trap in interior Alaska." He also noted that "…economic and subsistence uses of wildlife scored the least important motivations to trap in this study." (Dorendorf, 2015:31). In contrast to EcoNW (2014b), perceptions of interior Alaska trappers in Dorendorf's survey reported that finding access to land for trapping was difficult.

To further investigate the motivations of trappers, Dorendorf performed a cluster analysis of his data. This analysis statistically grouped trappers based on their primary motivations for trapping. Dorendorf found there were four types of trappers: (1) a recreation group (by far the largest group at 40% of the sample); (2) a solitary group (the second largest group); (3) a subsistence group; (4) a wildlife management group. The recreation group is distinguished by their desire to participate in trapping as a way to get exercise and appreciate nature. In contrast, trapping was part of a lifestyle to the subsistence trappers. Dorendorf (2015: 34) noted that in small remote villages, fur was used for "…cultural crafts and ceremonies as well as a source of income in the winter". The "solitary" trappers were distinguished by trapping as an individual activity (as opposed to group or social activity) with solitude as the primary motivating factor. Finally, the wildlife management group of trappers was motivated in part by the desire to reduce predators for the species the trappers hunted (e.g., moose and caribou). In sum, trappers are not a homogenous group. For many, trapping is a means to other ends, is not heavily dependent on the abundance of the target species.

B. Economic Impacts of Wildlife Viewing and Hunting in Alaska

Miller and McCollum (1997) studied non-resident visitor expenditures and net WTP of visitors beyond their expenses. These authors used a diary survey of non-resident visitors including those that were taking trips for multiple purposes (i.e., for some visitors wildlife viewing was only a secondary trip purpose). Given the topic of our study, we focused on the subset of non-resident visitors that came to Alaska primarily to view wildlife. The total trip expenditures of non-resident visitors who came to Alaska primarily to view wildlife were \$3,982 in 1994 (\$6,361 in \$2014).

ECONorthwest (2014a,b) performed a survey of both Alaska residents and non-resident visitors to Alaska about their use and spending related to hunting and wildlife viewing. The economic activity associated with wildlife viewing and hunting was measured in these studies by resident and non-resident visitor spending. Economic impacts were measured by jobs supported by the activity. Hunting expenditures by residents and non-resident visitors supports \$457 million in wages associated with 8,400 jobs statewide (Table 1). This hunting activity also provides \$112 million in various types of revenue to local and state governments in Alaska. Wildlife viewing provides \$976 million in wages to 18,820 workers statewide (Table 1). In addition \$231 million in revenues are provided to various levels of government in the State of Alaska.

Table 1. Economic Activity Associated with Wildlife Viewing and Hunting in Alaska and Denali National Park and Preserve (Denali NP&P), Alaska. There are several blank cells as not all the studies reported economic activity or economic impacts consistently.

Area/Activity	Per Visitor Spending per Trip	Total Jobs	Reference
Alaska			
Wildlife Viewing		18,820	(ECONorthwest, 2014a)
Wildlife Viewing	$6,361		Miller & McCollum (1997)
Hunting		8,400	(ECONorthwest, 2014a)
Denali NP & P			
Wildlife Viewing		2,319	Stynes & Ackerman (2010)

C. Economic Values of Non-Resident's Wildlife Viewing and Hunting in Alaska

Miller and McCollum (1997) surveyed non-resident visitors after their trips to Alaska were completed and asked if the trip was worth more than what they spent. The average additional WTP of a primary purpose wildlife viewing trip in Alaska was estimated (Miller and McCollum (1997: page C-21) at $422 in 1997 ($674 in 2014 dollars). The net WTP dropped to $310 ($495 in $2014) for those that saw no big game (but did see other species such as birds). For those that saw at least one wolf, the net WTP was $539 ($861 in $2014). A simplified comparison of the value of seeing a wolf might be the difference in trip value from seeing a wolf and not seeing any big game. Using this simplified comparison, the additional value from seeing a wolf on a non-resident trip taken primarily for wildlife viewing would be $238 ($366 in $2014).

The survey also asked non-residents about the economic value of a future trip *"…where you could expect to see a pack of wolves either from the ground or from an airplane."* (Miller and McCollum, 1997: page E-11). A dichotomous choice CVM WTP question was designed to elicit an *ex-ante* future

WTP, similar to what economists would call an option price for future viewing use. The net WTP per trip to see a pack of wolves on a future trip was $212 ($339 in $2014). The authors termed this value a gross WTP and used it to measure the potential demand for future wildlife viewing activity. This value per trip is similar to what was calculated above as the additional value of seeing a wolf on a wildlife viewing trip. Using a CVM survey, ECONorthwest, (2014b) estimated that non-residents' net WTP was $765 for a hunting trip and $858 for a wildlife viewing trip to Alaska.

D. Economic Values of Alaska Residents for Wildlife Viewing and Hunting in Alaska

ECONorthwest (2014b) used CVM to estimate residents' net WTP of $438 per trip for hunting trips and $268 per trip for viewing trips. While the value per trip to Alaska residents is smaller than for non-residents cited in the prior section, the larger number of trips taken by Alaska residents results in annual resident hunting benefits of $4,828 and $8,050 for viewing, quite a bit larger than non-resident's annual values. The National Research Council (NRC, 1997: 150), using unpublished data, reports that Alaskan residents' net WTP specifically for wolf hunting was $1500 ($2,212 in $2014). This is notably greater than the value of moose hunting of $181 ($273 in $2014) and $168 ($253 in $2014) for caribou hunting.

An additional CVM question was asked by ECONorthwest (2014b) to estimate how much respondents' economic value of a wildlife viewing trip would increase if they could visit an area specifically managed for wildlife, such that they would be assured of seeing one or more species particularly important to them. While the authors of the report indicate the question was not as precise and concrete as would have been desirable, they felt it was indicative of the extra value of a "successful" wildlife viewing trip for species of importance to the respondent. The additional WTP beyond the current trip was $400 per household for non-resident visitors and $150 more for Alaskan residents. It would seem that this type of question is particularly relevant for valuing improved wildlife viewing in Denali NP & Preserve. While the specific question scenario and wording could be improved, the refined question could be included in future Visitor Service Project (VSP) surveys in Alaska national parks.

As part of the survey, ECONorthwest (2014b) asked about general willingness to pay into a wildlife conservation fund to maintain current wildlife populations and their habitat in Alaska. Their report acknowledged that the question did not specify the decline in wildlife populations that would occur in absence of this payment. But the authors felt the results nevertheless provided some sense of the values of wildlife conservation in general. The survey responses indicated that Alaskan residents would pay $59 per year to maintain wildlife in general, while non-resident visitors would pay $32 per year. Alaska residents were also asked if they would pay for wildlife conservation to maintain the current population and habitat for four types of wildlife (Brown Bears, Seabirds, Caribou and Moose). Alaska residents indicated they would pay $40 a year for Brown bears, $90 a year for seabirds, $53 per year for caribou, and $46 per year for moose. The results provide some information on relative values of these four different types of wildlife. To increase the usefulness for economic analysis the WTP questions could be improved upon, and wolves included as a species in future surveys.

E. Summary of Resident and Non-resident Values for Viewing and Hunting in Alaska

Table 2 summarizes studies to date on economic values of viewing wildlife and wolves, as well as big game hunting, and wolf hunting. While non-resident hunting and viewing values are similar, resident hunting values per trip are substantially larger (Table 2). However, as noted in the text, there are twice as many wildlife viewers than hunters (ECONorthwest, 2014b:15). Wolf hunting by residents has a very high value per trip, but the total number of hunters is quite limited.

Table 2. Economic Values of Wildlife or Wolf Viewing and Hunting in the State of Alaska and Denali National Park and Preserve, Alaska, USA. ($2014)

Area/Activity	Per Visitor WTP/Trip	Reference
Alaska		
Non-resident Viewing	$674	Miller & McCollum
Non-resident Viewing	$858	(ECONorthwest, 2014b)
Resident Viewing	$268	(ECONorthwest, 2014b)
Residents Wolf Viewing	$288	NRC Report
Non-resident Wolf Viewing	$339	Miller & McCollum
Resident Hunting	$438	(ECONorthwest, 2014b)
Resident Hunting	$247	NRC Report
Non-resident Hunting	$765	(ECONorthwest, 2014b)
Non-resident Hunting	$650	NRC Report
Residents Wolf Hunting	$2,212	NRC Report
Non-resident Wolf Hunting	$518	NRC Report
Denali NP & P		
Wildlife Viewing	$94	McCollum, et al

VII. Visitation and Economic Impacts of Wolf Viewing in Yellowstone National Park (YNP)

The only studies that have estimated the economic impacts associated with wolf viewing itself (as distinct from wildlife viewing in general) have taken place in Yellowstone National Park (YNP). Duffield, et al (2008) estimated that 1.5% of spring visitors to YNP and 5% of fall visitors specifically came to view wolves in YNP. Applying this percentage of visitor use to YNP total visitation and multiplying by average visitor spending in YNP yields $35 million annually. However, even among visitors who come to YNP for reasons other than to view wolves, Duffield et al's (2008) visitor data from the summer of 2005 indicates that 44% of the general visitors stated that wolves were one of the animals they most wanted to see on a trip to YNP. Wolves ranked as the second most important species to view (slightly below grizzly bears).

In a 1993 U.S. Fish and Wildlife Service (USFWS) study for the Final EIS on wolf reintroduction, a contingent behavior or intended behavior question was used to estimate the increase in visitation (if any) from a recovered wolf population in YNP. The study found that reintroduction would result in an estimated 10% average increase in visitation to YNP by residents of MT, ID and WY and 4.8% increase in visitation among those visitors living outside of the three states.

VIII. Visitors' Use and Existence Value of Wolves in YNP

Duffield et al (1991) and Duffield (1992) conducted surveys of visitors to estimate their Total Economic Value (composed of use and existence values) for wolves in YNP. This section reviews the Total Economic Value (TEV) of visitors and the next section reviews the TEV of non-visiting households. Duffield's two studies utilized the contingent valuation method (CVM) to estimate the existence value portion of a visitor's value. He used visitors' willingness to pay (WTP) for a lifetime membership in a trust fund (what he also refers to as a donation) to support wolf reintroduction in YNP. The visitors are told that wolf recovery may reduce populations of deer, elk, bison and moose in YNP so they are informed of this trade off when answering the CVM WTP question for wolves.

The particular type of CVM used was a dichotomous choice method, where a visitor answers either "Yes, I would pay that amount for a membership" or "No, I would not". The dollar amount of the membership was varied across the sample, so essentially a quasi-demand curve for wolf recovery was estimated. The use of the dichotomous choice method was a strong feature of this study. However as was common at the time, the survey told respondents that the scenario was a hypothetical situation. In the last 10 years CVM researchers no longer use the term hypothetical, but rather emphasize that the respondent's answer could have real consequences to policy decisions made and the likelihood of actual payment in the future. Telling respondents that the survey is hypothetical has the potential to result in increased hypothetical bias in the form of inflated WTP estimates (Carson and Groves, 2007). Thus the reader should keep in mind this concern when interpreting the absolute magnitude of the WTP estimates.

The results of the Duffield et al. (1991) study estimated that median WTP (the amount that 50% of the visitors would pay) was \$15.38 (\$27.86 in \$2014) for visitors living in MT, ID and WY and \$20.27 (\$36.71 in \$2014) for visitors living in the rest of U.S. However, some of these visitors have relatively higher values for wolf reintroduction, and this is reflected in a higher mean WTP. Even truncating the upper end of the WTP distribution at the highest dollar amount asked in the survey ($300), the mean WTP was $62 ($112 in $2014) for visitors from MT, ID and WY and $97 ($176 in $2014) for visitors from the rest of the U.S.

Using two different innovative methods to separate TEV into use and existence value, Duffield et al. (1991) found that MT, ID, and WY visitors' existence value for wolves ranged between 46% and 61% of their TEV. Using the same procedures, the existence value of out-of-region visitors ranged from 74% to 75% of their TEV for wolves. The fact that much of the TEV is existence value, even for visitors, suggests the importance of including existence value for wolves and not just focusing on visitor use values when calculating the societal or national benefits of maintaining and protecting wolf populations.

Duffield (1992) did a follow up CVM study of visitors to YNP the following year using basically the same procedure as the year before except for one important difference. An innovative feature of the Duffield (1992) study of the divisive issue of wolf reintroduction was to the tailor the CVM WTP question to whether the respondent initially indicated they were in favor of or opposed wolf reintroduction. If they favored it, they were asked what they would pay into a trust fund to **support** wolf recovery. If they opposed it, the respondent was asked what they would pay into a trust fund where the money would be used to **oppose** wolf reintroduction.

In this CVM study Duffield (1992) estimated that YNP visitors **favoring** wolf recovery/reintroduction have a median WTP into the trust fund of $23 ($40 in $2014) to aid wolf recovery. Those visitors **opposed** to wolf recovery/reintroduction had a median donation of $1.68 ($2.82 in $2014) to a trust fund for a policy effort to stop wolf reintroduction. Given that there were nearly three times as many visitors that would purchase a wolf recovery membership (i.e., donate to the pro-wolf trust fund) as there were visitors who opposed, the overall median WTP is quite similar to the $40 in 2014 dollars. Once again, the mean WTP was substantially higher than the median WTP. In particular, those favoring wolf reintroduction would pay on average $65 ($113 in $2014) while those opposing would pay $21.24 ($37 in $2014). Consistent with the previous summer survey, about three-quarters of the overall visitor TEV was existence value, once again illustrating the importance of including existence values. The conclusion of these economic studies that ask respondents either WTP to support wolf recovery or WTP to oppose wolf recovery is that while there is certainly a segment of visitors that do not favor wolves, in the aggregate, the benefits to those that want wolves are substantially large than those that do not. Specifically, the mean WTP of visitors favoring wolves is three times larger compared to those opposed to wolves ($65 versus $21), and there are three times as many visitors favoring wolves than opposing wolves. Taken together, the aggregate WTP of visitors favoring wolves is nine times that of those opposed to wolves. Thus the benefits to those visitors favoring wolves outweigh the reduction in benefits to those visitors opposed to wolves.

IX. Use and Existence Value of U.S. Households for Wolves

A. Yellowstone NP Wolf Reintroduction Program

Duffield, et al. (1993) conducted a phone CVM survey of households in the Greater Yellowstone Area (GYA)—made up of the counties in ID, MT and WY contiguous to YNP (the primary area of the wolf reintroduction). As part of the same study, the same CVM survey was conducted on a sample of U.S. households living outsides of the GYA. The same structure of CVM WTP questions were asked of households as was done for visitors: those who stated they were in favor of wolf reintroduction were asked their WTP for it, and those opposed were asked what they would pay to prevent wolf reintroduction. As in the visitor survey, households were told the CVM WTP questions were hypothetical, something no longer done in CVM surveys. Thus, the reader should keep in mind that there is a potential for the absolute magnitude of the WTP estimates to be somewhat higher than would otherwise be the case had respondents not been told the survey was hypothetical.

Given this CVM study design with two geographic areas (GYA and rest of the U.S.) and two WTP questions (one for those respondents favoring wolf reintroduction and one for those opposing wolf reintroduction), there are four WTP estimates. The estimates are:

a. GYA local residents WTP **for** wolf reintroduction of \$22.69 (\$38 in \$2014), with an n=189.

b. GYA local resident WTP to **oppose** wolf reintroduction of \$2.63 (\$4.45 in \$2014), with an n=212.

c. Rest of U.S. households WTP **for** wolf reintroduction of \$8 (\$13.50 in \$2014), with an n=753.

d. Rest of U.S. households WTP to **oppose** wolf reintroduction of 16 cents with an n=368.

As can be seen in these four estimates of WTP, those in favor of wolf reintroduction have a WTP that is nearly ten times higher than those opposed. While the number of households in the GYA are nearly evenly split for and against, in the rest of the U.S. there is nearly a two to one split in favor of wolf reintroduction. Combining the respective WTP's and sample proportions, the aggregate benefits are overwhelmingly positive. The aggregate benefits range from at least \$12 million (\$20 million in \$2014) to \$38 million (\$64 million in \$2014), with the range dependent on different aggregation assumptions made by Duffield, et al.

A slight re-analysis of the Duffield et al. (1993) CVM study results were used by the USFWS in its Final EIS on the reintroduction of gray wolves into Yellowstone National Park and Central Idaho. The inclusion of households use and passive-use/non-use values in the EIS provides evidence that federal agencies feel the CVM methodology in general, and its specific implementation in the wolf study, contributes valuable information to the wolf management policy decisions.

B. Wolf Habitat Protection in Minnesota

Chambers and Whitehead (2003) estimated the benefits of protecting wolf habitat for two different communities in Minnesota within the range of the wolves by using a CVM survey of households (this study was described in detail in the prior section entitled Methods for Quantifying Economic Values). The results indicated that Ely, Minnesota households would pay between $4.43 and $4.77 (about $7 in $2014) "*… for protecting wolf habitat and that of wolves primary prey*." St. Cloud, Minnesota residents were willing to pay between $20.15 and $21.49 (about $31 in $2014) for the same public good.

Table 3 summarizes the Total Economic Values in the literature reviewed above. As might be expected, visitor values are substantially about household values. Values of households that live nearer wolves are higher than households that live away from wolves.

Table 3. Total Economic Values (use and non-use/existence and bequest values) that the visitors and households would pay to either reintroduce wolves into the GYE or protect wolf habitat and their prey to maintain stable wolf populations in Minnesota **($2014)**

Location	One time WTP	Authors
Yellowstone NP		
Visitors living near GYE*	$112	Duffield, et al. 1991
Visitors living in rest of US	$176	Duffield, et al. 1991
Visitors living in rest of US	$113	Duffield 1993
Households living near GYE	$38	Duffield, et al. 1993
Households in living in rest of US	$13.50	Duffield, et al. 1993
Minnesota		
Ely MN Households	$7	Chambers & Whitehead
St. Cloud Households	$31	Chambers & Whitehead

* GYE is Greater Yellowstone Ecosystem, generally counties in Idaho, Montana and Wyoming contiguous to Yellowstone National Park.

C. Summary of Data Gaps

While the report to this point indicates that some information exists on the economic value of wolves in 2 areas in the lower 48, and for Alaska in general, little is known about the economic value of wolves in and around DNPP. Wolves in and around DNPP are likely to provide economic benefits to: (a) an unknown number of visitors coming to the DNPP primarily to view wolves; (b) the general public of the U.S. through existence values of a self sustaining wolf population in DNPP; (c) wolf hunters around DNPP and (d) trappers around DNPP. In the following sections we identify the types of studies needed to quantify the economic benefits that wolves provide to these four different stakeholder groups.

A. Data Gaps About Visitors to Denali NP and Preserve (DNPP)

i. What percent and how many visitors to DNPP come for the primary purpose of viewing wolves?

ii. What expectations did people bring to DNPP about viewing wolves?

iii. What basic knowledge do visitors have regarding the wolf population in DNPP? In Alaska? In the U.S.?iv. What are the expenditures of these visitors in the DNPP region and State of Alaska?

v. Did these visitors see a wolf, and if yes, how many?

vi. If they saw a wolf, what are these visitors' net WTP for their experience?

vii. If they did not see a wolf, what are these visitors' net WTP to be certain they would see at least one wolf?

viii. How would their trips to DNPP change if they could see a specific increase in the number of wolves?

ix. How would their net WTP increase if they could see a specific increase in the number of wolves?

x. How do visitors divvy preferences for wolf and other wildlife viewing?

xi. How do visitors perceive the notion of *paying* for wolves?

xii. What is the intrinsic value of wolves for visitors to DNPP? And broadly, in the U.S.?

D. Data Gaps about Big Game Hunting and Trapping around DNPP

Hunters

As noted by NRC (1997) little is known about big game (caribou and moose) hunters around DNPP. In particular it would be important to know what percentages of hunters' motivations are primarily: (1) harvesting for meat; (2) trophy hunts; (3) to be with family and friends; or (4) to be in the out of doors. This information would provide insights into how important the abundance of big game is for the decision to (1) purchase a big game hunting license; and (2) make multiple hunting trips.

Trappers

While ECONorthwest (2014b) indicated that not a great deal is known about Alaska trappers, that data gap has narrowed with the thesis of Dorendorf (2015) in August of 2015. This thesis provides significant amounts of information on motivations for trapping and determinants of trappers' behavior. However, this effort covers Interior Alaska broadly, so segmenting Dorendorf's data down to the geographic areas of interest (around the boundaries, particularly eastern boundary of DNPP would be needed to determine if the thesis contains sufficient data or a more localized survey is required).

C. Data Gaps about Household Use and Existence Values

In its review of the Alaska predator control program the National Research Council (NRC is part of the National Academy of Sciences), stated that values of wolves include not only use values such as viewing, hunting, and fur but also non-use or passive-use or existence values to households that may never see a wolf in the wild (NRC, 1997:9). The NRC (1997: 9) states that the current magnitude of the existence values for wolves is not known because the necessary studies have not been conducted in Alaska or for the Alaskan wildlife species. The NRC indicates that the Contingent Valuation Method (CVM) is one of the only methods capable of estimating these existence values. The absence of information on existence values of wolves is an important gap to fill to improve wildlife management in Alaska. Along these lines the NRC (1997:12) recommends more social science research in Alaska is needed to support management decisions related to wolves.

XI. Study Plan to Fill Data Gaps

A. Visitor Surveys at Denali NP and Preserve

The most straightforward approach to address existing data gaps would be to conduct a survey of visitors to DNPP. This survey will target three major visitor groups: those on a tour, those using a shuttle bus to camp or day hike, and those trekking overnight in the backcountry. The shuttle buses should be canvassed, to capture the diversity of day hikers, wildlife viewers, bikers, and international groups that populate the shuttles. The overnight backcountry users should be sampled due to the different expectations, especially regarding wilderness experience, they bring to DNPP. Finally, the tour buses should be canvassed for the dominant tour user type of higher income, age, American (non-Alaskan) and white. Following the design of prior DNPP wildlife surveys (McCollum, et al. 1998), we recommend distributing surveys during the last leg of the bus tour back to the entrance Visitor

Center. This time of survey distribution would: (a) minimize inconvenience to visitors' experience; (b) provide the most reliable responses since they will have just experienced their trip so that recall bias would be at a minimum; (c) obtain a very high response rate (which is necessary if this survey must go through OMB); (d) be a relatively cost effective survey approach (as more than a dozen surveys, one to each group/family of visitors, could be obtained at one time on a single bus); (e) allow some degree of external validity of the surveys by comparison with wildlife viewing records kept by the bus driver. Ideally the surveys would be conducted throughout the summer, including weekdays and weekends (to increase the odds of intercepting an Alaskan resident).

1. The type of questions to be asked to fill data gaps

a. What were the primary and secondary purposes of their trip to DNPP? One of the response categories for primary purpose and secondary purposes would be "viewing wolves". Collectively responses to this question would provide data on what percent and how many visitors to DNPP come for the primary purpose and secondary purposes of viewing wolves.

b. Whether they saw a wolf, and if yes, how many.

c. What is the visitor's WTP for their current trip. To obtain WTP, a dichotomous choice CVM question for the visitor's current trip into DNPP would be asked. We would statistically test if the economic value of a trip to DNPP is significantly affected by whether they saw a wolf, and if yes, by the number of wolves they saw. An increase in trip cost would be the payment vehicle.

d. For visitors who reported they did not see a wolf, they would be asked a second CVM WTP question to estimate their value of a trip in which they would be certain to see a wolf. This question will test the relative importance of wolves in the visitor's economic benefits from a trip to DNPP. We would also ask if they would take more trips if they could be certain they would see a wolf on each trip. This question tests the responsiveness of trips taken (and hence visitor spending) to presence of wolves in DNPP.

e. For visitors who reported they did see at least one wolf, they would be asked their WTP to see some reasonable (to be determined) increase in the number of wolves. This would allow us to estimate how the benefits of the trip change with the abundance of wolves seen. We would also ask if they would take more trips if they would see some reasonable increase in the number of wolves. To obtain a better understanding of whether wolves play a critical role in determining whether to visit DNPP, we could ask if they would have made their trip to DNPP if they did not expect to see any wolves.

f. Trip expenditures in and around DNPP (disaggregated by spending category) would be asked so that we would know if the visitor spending is significantly different among those visitors who came to view wolves versus general DNPP visitors.

g. Attitude questions regarding wildlife, wolves, hunting, and trapping would be asked to obtain an understanding of what DNPP visitors think of consumptive uses of wildlife in general, and wolves in particular.

h. Demographics (zip code, age, education, membership in conservation organization, race/ethnicity, and income). This information will help provide a demographic profile of visitors who came to view wolves in contrast to the general DNPP visitors.

i. On other factor that may be worth recording are weather conditions, which may influence visitor satisfaction.

2. *Prepare Office of Management and Budget (OMB) Survey Clearance Package*

If the survey is funded by an agency of the Federal government (e.g., NPS) then Office of Management and Budget (OMB) clearance would be needed even before conducting pretests. The clearance process begins with filling out two packages of information for OMB for approval. The two packages include the agency's need for the information to be obtained by the study, and the entire study design. The study design and survey design would start with the prior survey of McCollum, et al. 1998. The study team would revise the survey with feedback from Dr. McCollum, and input from NPS staff at DNPP. Specifically, the study design would address procedures for implementing the survey, the survey design (with justification for each question being asked), sample design including sample size determination, and statistical analysis procedure. Several months of review and revision is typically required before OMB usually approves the survey.

3. Pre-test the survey

The approved survey would be pretested over the course of two weeks with a total of 30 people completing their bus tour. The pre-test would occur at a NPS facility such as the Visitor Center at the end of their trip. A monetary incentive (typically $80 per person) is usually required to get people to sit down and take about an hour to go over the survey. In order to have a good representation of visitors, one person from each returning bus would be invited to participate in the pre-test. The selection of buses would alternate between the Shuttle Bus going only to Eielson Visitor Center and those buses going to Wonder Lake, as well as a bus from the Tundra Wilderness Tour. Each section of the questionnaire would be read, questions answered and then discussed to ensure that the visitor interpreted the questions as they were intended by the survey designers. A complete "debriefing" would also be conducted to obtain feedback on the skip patterns, question response categories, and overall layout of the survey.

4. Revise the survey with feedback from the pre-test

A second small pretest of 10 people (also paid $80) would be required to make sure any issues raised in the original pre-test have been completely resolved and that no new issues have arisen.

5. Sample frame and selecting a representative sample

Before discussing the sample size, it is important to discuss how the sample would be selected in order to ensure the sample is representative of visitors at DNPP. First, we define the sample frame as "those visitors riding buses into the park" as these are visitors most likely engaged in sightseeing and wildlife viewing in DNPP. In particular, visitors on the Shuttle Bus, the Tundra Wilderness Tour and Kantishna Experience Tour will all be sampled. However, they will be sampled in proportion to their share of the total amount of visitor use. In addition, one adult person from each group/family will be sampled so as not to double-count trip expenditures. This person can of course consult with other family or group members to determine their answers. The group size will be reported as part of the survey. One weekend day (alternating between Saturday and Sunday) and four week days (selected at random) would be sampled.

6. Sample size

A relatively large sample is needed because a dichotomous choice WTP question will be used, and because visitors who do not see wolves will get a different WTP question from those who did see wolves. Guidance from Dillman (2000) for surveys in general, and Champ (2003) for CVM, suggests that a population of 100,000 requires a minimum of 383 completed surveys would be sufficient to obtain a ±5% sampling error (95% confidence interval in a conservative 50/50 population split). Given that there are three major types of buses (shuttle bus, and two types of tour buses) each of which have different prices and may attract different types of visitors, I recommend 380 surveys be collected from each of the three types of buses. This will ensure the composition of the final combined sample will represent a cross section of the three different types of busvisitors to DNPP. Special attention should be given to the tour bus, Tundra Wilderness Tour, because it is set aside from the other tour and shuttle bus offerings as a specifically "wildlife viewing safari" tour.

As previously mentioned, visitors to DNPP that are trekking overnight into the Park must be surveyed to capture the effective variance of visitor demographics, and their assumed divergent recreation goals and expectations.

7. Printing final survey booklets

Following Dillman (2000), the survey questions would be contained in an eight page survey booklet. The booklet would consist of an interesting cover, 6 pages of questions (with demographics being the last inside page), and a blank back cover for the visitor to write comments. The surveyors will conduct non-response checks, especially focused on residency, so as to develop an appropriate weighting mechanism regarding the oversampling that will occur of non-Alaskans. Additionally, an Alaska specific survey will be mailed to a random selection of households in the greater Denali area to compare responses of visitors to non-visitors to DNPP.

8. Implement survey over the summer season

Starting Memorial Day weekend and going through Labor Day, 2 people would be employed to hand out surveys on the return trip back to the visitor entrance. One employee would ride the Shuttle Bus and one would ride one of the Tour Buses each sampling day. Each employee would also maintain a count of the types of wildlife and number of wildlife seen to corroborate visitor counts of wildlife sightings. Each employee would work 4 week days and 1 weekend day. One person from each group or family on the bus would be selected to answer the survey for their family or group. A target of 10 visitors per bus per day to hand out surveys to would be ideal.

9. Data Entry and Error Checking

Data entry would occur via spreadsheet for compatibility with statistical packages. Two forms of data error checking would occur: (a) screening data for maximum and minimum values to ensure data is within ranges allowed for in surveys (e.g., 0, 1 for dichotomous variables like gender), and that there are no outliers; and (b) a small subsample of surveys would be re-keyed and compared to the original surveys to determine the accuracy of the original coding.

The non-response checks mentioned above will be coded and combined with the compiled visitor survey dataset, in order that a split-halves reliability check is feasible and accurate in testing the independence of recorded observations, and a heteroskedastic distribution of error terms.

10. Statistical analysis

Descriptive statistics for the three types of bus trips and for the overall sample for all variables would be presented either in tabular form in the main report or in an appendix. The dichotomous WTP questions would be analyzed using logistic regression model. A two part model may be employed to better estimate the actual dollar value visitors (and later Alaskan, and U.S. households) attribute to wolves, as the a 2-part model first models the likelihood of visitor type to have an expectation of wolves, and then, based on their expectation, how much in dollars they would be willing to pay to fulfill these wolf viewing expectations. The mean and median WTP would be calculated for the three types of bus trips and the overall sample. The sample WTP results would be scaled up to the population using the number of visitors riding each type of bus over the summer.

11. Draft report writing

A draft report presenting the methodology employed, sample design, sample implementation, descriptive statistics, WTP results, and providing interpretation of what these results imply about wolf viewing would be written.

12. NPS review of draft report

13. Report revision in response to NPS review comments and final report.

Costs Associated with the Visitor Study

There are two major types of costs associated with this study:

Fixed costs to design, prepare OMB package and pretest the survey

This would require Ph.D. level social scientist/economist with training and experience in conducting visitor non-market valuation surveys. Depending on whether the person is an NPS employee or external to NPS (e.g., academic's or consulting firm employees), the labor costs would be on the order of $45,000. The travel costs for scoping out the logistics of the survey and pretesting would be in the range of $10,000 given the high expense in traveling to and staying in the area around DNPP. The actual pre-testing participant costs would be $3,200. I assume a NPS facility would be available free of charge to conduct the pre-test interviews.

Variable costs of conducting the survey

Printing: about 1200 survey booklets, cover letter and envelopes: $3,600

Labor for sampling days: Assume a GS-9 level employee working 10 hours a day (due to the length of typical bus rides) and being paid $28 an hour for eight hours and $40 an hour for two hours overtime, the cost per day would be $304. With 60 sampling days this would be $18,240 without benefits.

Data entry: Assume the same GS-9 level employee for data entry, 20 minutes to input data for each survey and 1200 surveys is 400 hours for a total data entry cost of $10,400.

Statistical analysis: this would be conducted by a Ph.D. social scientist/economist. The cost is estimated to be $30,000 given there are three sub-samples to analyze plus a total sample.

Draft report writing: this would be conducted by a Ph.D. social scientist/economist. The cost is estimated to be $30,000.

Final report writing: this would be conducted by the same Ph.D. social scientist/economist who wrote the draft report. The cost is estimated to be $15,000 to make the revisions and finalize the report.

Thus an estimated direct cost of the entire effort would be $165,440 without employee benefits and any overhead. Table 4 summarizes the budgetary costs of the study.

Table 4. Summary of Estimated Costs for DNPP Visitor Survey

Cost Element	**Est. Cost**
Labor	
Study/Survey Design	$ 11,250
Prepare OMB Pkg	$ 11,250
Pretesting Survey in AK	$ 11,250
Revise & Finalize Survey	$ 11,250
Visitor Sampling	$ 18,240
Data Entry	$ 10,400
Statistical Analysis	$ 30,000
Draft Report Writing	$ 30,000
Revise & Finalize Survey	$ 15,000
Subtotal Labor	**$ 148,640**
Travel	
Pretesting travel to DNPP	$ 10,000
Other Expenses	
Participant Incentives	$ 3,200
Survey Printing	$ 3,600
Total Study Costs	$ 165,440

Study Timeframe

The time from needed for the initial overall study design, initial survey design, and preparation of OMB package would be three months. There would be about 4 months of waiting for and engaging with OMB to obtain their approval (only about 1 work month required during this time for engaging with OMB and revising study plan and OMB package). Depending on the timing of the OMB approval, this could determine whether the survey would be implemented during the summer of 2017 or 2018. The actual survey pre-testing, implementation, analysis and report writing would be about 8 months. Thus the total work time would be about 11 months with an additional 1 month of conference calls and OMB package revisions for a total of 12 months of work if all goes well at OMB. These 12 work months might stretch over two years however, depending on the timing of the OMB review relative to the summer visitor sampling season.

B. Hunter Surveys

To fill the data gaps identified for hunting we would ideally work with Alaska Dept of Fish and Game (ADFG) to obtain a list of big game hunters (caribou, moose) in Game Management Unit #20. The particular units to sample are 20A (on the eastern boundary of the Denali National Park), and 20C (which includes Denali National Park and areas to the north of the Park). In addition, a list of hunters engaged in wolf hunting would need to be obtained. Then a mail survey of hunters in the region around DNPP would be undertaken to fill the data gaps identified by NRC. In particular, the surveys would ask about their harvest success rate, expenditures and net WTP for their current hunt. Then questions would be asked regarding how their number of trips and net WTP would change with a specified (perhaps varying across the sample) lower harvest success rate. In addition, a question would be asked regarding whether the possible lower harvest success rates would reduce their likelihood of buying a hunting license for the next season (e.g., if the lower success rate were expected next hunting season for their target species, would that influence their decision to buy a license?).

If it is not possible to obtain licensing information for these two Game Management Units directly from ADFG in the near term, there are two other options that are possible (pers comm T. Brinkman):

1. Partner with Dr. Todd Brinkman to develop a proposal to ADFG to perform the survey described above as Dr. Brinkman has good working relationships with ADFG.

2. Develop a working relationship with the local Advisory Committee (AC) made up of local hunters (and anglers) who develop recommendations for the Alaska Board of Game. In particular, the Minto/Nenana Advisory Committee would be the relevant one for the Game Management Units around DNPP. The goal would be to develop a shared vision of the types of data gaps that need to be filled by the survey, types of questions to be asked to fill those data gaps, and the mechanics of performing the survey. If the Advisory Committee were to recommend hunters surveys for Game Management Units 20A and 20C, Dr. Brinkman suggested that the Alaska Board of Game and then ADFG might honor that request and provide hunter license lists for those two Game Management Units. Such a collaboration with the Minto/Nenana Advisory Committee is a long term option. This hunter survey would also need to be coordinated with ADFG's post harvest season surveys to clearly differentiate them in the minds of hunters and not have the surveys go out at the same time.

At this time it is premature to go into details on sample size and other study details. We do know that if a survey can be accomplished it would likely be a mail survey given that we want hunters to:
(a) indicate on a map of the Game Management Unit roughly the general area where they hunt;
(b) provide detailed information on hunter expenditures in and around the Denali Borough;
(c) respond to willingness to pay questions.

C. Household Total Economic Value Surveys (TEV)

A survey of a random sample of Alaskan and rest of the U.S. households regarding the amount they would pay to maintain a stable population of wolves in DNPP would be a more significant undertaking than the visitor and hunter surveys. While nearly all households in Alaska and the rest of the U.S. are certainly aware of wolves, it can be challenging to communicate with the lay public the ecological importance of wolves to the DNPP ecosystem, a possible management plan, and an equitable means of paying for the management plan. The study design would involve 11 steps.

1. Draft Initial Survey

A team of Ph.D. economists and social scientists would start with the prior TEV surveys for wolf reintroduction in YNP, and re-orient the survey to fit the situation in DNPP with input from Dr. Duffield who conducted the YNP surveys (and who is recommended to serve as a consultant on this study). The general survey outline would include: (a) background on DNPP, wildlife and wolves; (b) questions about attitudes toward National Parks, wildlife, hunting, wildlife viewing, and wolves; (c) current wildlife management issues; (d) proposed management program to address the problem (e.g., land acquisition, easements, compensation payments, etc); (e) how the Program would be funded (e.g., federal income tax); (f) willingness to pay question, protest response question for those stating they would not pay their "bid amount"; (g) demographics including gender, age, education, ethnicity, zip code, whether they hunt, membership in wildlife, conservation and environmental organizations and income.

2. *Circulate the survey to NPS DNPP staff and wolf biologists, conduct conference calls and revise the survey accordingly.*

3. Prepare Office of Management and Budget (OMB) Package

Since the survey is funded by an agency of the Federal government (e.g., NPS) then Office of Management Budget clearance would be needed even before conducting the focus groups with the general public. This involves filling out two packages of information for OMB for approval. The two packages include the agency need for the information contained in the survey, and the entire study design. Specifically, the OMB package would present procedures for conducting the focus groups, the survey design (with justification for each question being asked), sample design including sample size determination, and statistical analysis procedure. Several months of review and revision is typically required before OMB usually provides approval.

4. Conduct Focus Groups

Organize two focus groups of the general public in Alaska, and 4 general household focus groups in the lower 48. These focus groups are essential to establish face validity of the survey. Specifically, to determine whether respondents understand the survey materials and questions they are reading as intended by the researcher. This face validity check can be done in the focus group by introducing each section of the survey separately, having the participant read that section, and answer the questions, and then a group discussion of the material. This is repeated until all the pages of the survey have been reviewed. The team then takes the marked up survey sheets and points from the discussion (as recorded on flip charts) and revises the survey. This process repeats itself sequentially through the series of focus groups over the course of several months. Usually, it is most effective to start the focus group process with a relatively knowledgeable population, in this case, Alaska residents. If the survey is not clear to knowledgeable Alaska residents it will not be clear to those in the lower 48 who are less familiar with wolves and Denali NP and Preserve. Scheduling of the focus groups would be sequential with 1-2 weeks between each focus group to allow the team to revise the survey prior to the next focus group.

5. Survey Pretesting

After the focus groups, formal pre-tests can be conducted to refine the range of the dollar amounts households will be asked to pay in the survey. The pre-tests can be a phone recruitment followed by a mailed survey followed by a phone discussion of each part of the survey. About 30 of these are needed in different places in the U.S. After the first 10 pre-tests refinement of the survey could be made, then the other 20 pre-tests conducted.

6. Finalize Mail Survey Package

(a) draw an address-based sample (total n=6,000); I would propose that a minimum sample of 2,000 Alaska residents be made so that we have an adequate subsample of Alaska residents to compare to the lower 48 states where n=4,000; with an expected 25% response rate, this would provide 500 Alaska resident responses and 1,000 lower 48 responses. Both of these samples are over the n=380 recommended by Dillman (2000) and Champ (2003) to provide ±5% error; (b) write an advanced cover letter; (c) finalize survey booklet mailing with new cover letter, postage paid return envelope and a $2 bill; (d) write reminder postcard; (e) write second survey mailing cover letter to non respondents of survey, print replacement surveys and postage paid return envelope; (f) do phone reminders for the portion of the non respondents with phone #'s; (g) perform non-response follow up check questions of a sample of non-respondents using added survey incentive.

7. Data Entry and Error Checking

Data entry would occur via spreadsheet for compatibility with statistical packages. Two forms of data error checking would occur: (a) screening data for maximum and minimum values to ensure data is within ranges allowed for in survey questions (e.g., 0, 1 for dichotomous variables like gender), and there are no outliers; (b) a small subsample of surveys would be re-keyed and compared to the original surveys to determine accuracy of original coding.

8. Statistical analysis

Calculate descriptive statistics for the subset of Alaska residents and the lower 48 sample for all the variables. The results would either be presented in a tabular format in the main report or in an appendix. The dichotomous choice WTP questions would be analyzed with a logistic regression model. The mean and median WTP would be calculated for Alaska residents and the lower 48. The sample WTP results would be scaled up to the population using the total number of households in the respective populations.

9. Draft Report Writing

A draft report presenting the methodology employed, sample design, sample implementation, descriptive statistics, WTP results, and providing interpretation of what these results imply about wolf management options would be made.

10. NPS Review of draft report

11. Report Revision in response to NPS comments and final report.

Costs Associated with the TEV Study

1. Survey Development Costs

a. Personnel Costs: There are fixed costs to design the survey, develop the OMB package and respond to OMB, conduct six focus groups, revise surveys after each focus group, and conduct pretests of the survey. The personnel involved in these tasks should ideally be Ph.D. level social scientists and economists with training and experience in conducting household non-market valuation surveys. The labor costs can range from $60,000 to $80,000 depending on the number of people involved and their pay rate (GS level, academic rank, etc.).

b. Six Focus Group Costs: Focus groups can be held at hotels or professional focus group facilities. When the focus groups are held at a hotel conference room and each respondent is paid a $90 participation fee then the total "out of pocket" cost is about $2,500 per focus group. This covers focus group participant recruitment, conference room fees, coffee, and focus group supplies (flip charts). Focus groups at professional facilities cost about $5,000 each but they recruit and pay participants, provide light refreshments, flip charts, etc. These professional facilities offer the possibility of video links for off-site observers or recording the focus group on DVD's. Thus the decision of whether to use a "do it yourself" focus group in a hotel or a professional facility depends on how involved the other members of the team want to be in the focus groups and the available budget. Thus the costs of six focus groups range from $15,000 for hotel focus groups to $30,000 for professional facilities. Of course half the focus groups could be at hotels and half at professional facilities, which would make the costs $22,500. Travel for the two focus group moderators is a total of $2,000 to $3,000 per focus group depending on the location, so total travel cost for six focus groups is $12,000 to $18,000.

c. Pre-test Costs: The primary costs are participant incentives ($90 per person), minimal printing and mailing costs ($10 per survey express mail).

d. Peer review of survey and report: About $10,000 should be budgeted for a peer reviewer to help in developing and peer reviewing the survey and the results in the report.

2. Variable Costs of Conducting the Survey

a. Printing: printing the 5,000 surveys for the initial mailing of the color 8 page survey booklets, cover letters and outgoing and return envelopes would be $30,000 for the first mailing.

b. Survey response incentive: A $2 survey participant response incentive has been found to be very effective at increasing survey response rates and is recommended by Dillman (2000). The survey participant incentive would cost $12,000.

c. Postage: First class postage out 10x12 envelope and first class back ($3.60) so first mailing postage is $20,000.

d. Follow up mailings: Second mailing to 85% of the initial sample (assumes a 15% initial response rate) is $25,500. Postage is A third mailing for a survey non-response check to a subset of 500 non-respondents by special mail (USPS Express Mail @$6.50 plus first class return of $1.50, for a total of $8) is $4,000.

e. Data entry: Assuming 20 minutes to input data for each survey and 1,500 returned surveys is about 500 hours for a total data entry cost of $10,000 based on $20 per hour wages.

3. Statistical Analysis

This would be conducted by a Ph.D. social scientist/economist. Given the two subsamples (one for Alaska, one for lower 48), the cost is estimated to be $20,000 to $30,000 depending on GS level or academic rank of analyst.

4. Draft report writing

Writing would be conducted by a Ph.D. social scientist/economist. The cost is estimated to be $30,000 to $40,000 depending on GS level or academic rank of writer.

5. *Final report*

A final report would be written which incorporates responses to NPS comments. The cost is estimated to be $15,000 to $25,000 depending on the GS level or academic rank of writer.

Thus an estimated cost of the entire effort would range from $270,800 to $346,800 without employee benefits and any overhead. The lower range assumes two Ph.D. social scientists/economists leading the design and the OMB submission as well as all six focus groups at hotels without video streaming or DVD. The upper level assumes three Ph.D. social scientists/economists and all six focus groups at professional focus group facility with video streaming or DVD of focus group. Table 5, presents a summary of the TEV study costs.

Table 5. Estimated Costs of TEV Study

Cost Element	**Min Estimate**	**Max Estimate**
Labor		
Study/Initial Survey Design	$ 7,750	$ 11,000
Prepare OMB Pkg	$ 7,750	$ 11,000
Conduct 6 Focus Groups	$ 14,400	$ 21,600
Revise survey after Focus Groups	$ 5,400	$ 7,200
Pretesting Survey	$ 13,500	$ 18,000
Revise & Finalize Survey	$ 11,200	$ 11,200
Data Entry	$ 10,000	$ 15,000
Statistical Analysis	$ 20,000	$ 30,000
Draft Report Writing	$ 30,000	$ 40,000
Revise and Finalize Report	$ 15,000	$ 25,000
Labor Subtotal	$ 135,000	$ 190,000
Travel		
6 Focus Group	$ 12,000	$ 18,000
Presentation of Results	$ 3,000	$ 3,000
Travel Subtotal	$ 15,000	$ 21,000
Other Expenses		
Focus Group Cost (facility, fees)	$ 15,000	$ 30,000
30 Pre-tests Participant Fees	$ 2,700	$ 2,700

30 Survey Express Mail	$ 300	$ 300
Peer Review of survey, analysis	$ 10,000	$ 10,000
Printing surveys, envelopes	$ 59,500	$ 59,500
Postage 1st & 2nd mailings	$ 33,300	$ 33,300
Other Expenses Subtotal	$ 120,800	$ 135,800
Estimated Total Costs	$ 270,800	$ 346,800

Time Needed for the TEV Study

The time for initial study design would be about three months to do initial survey design and sample design, one month to develop OMB package for submission, four months waiting and responding to OMB (only about one month of work), six months of final survey development work (focus groups and pretesting), four months of data collection (with data entry occurring as surveys are returned), two months data analysis and two months of reporting, one month report review and one month report revision. Thus a total of a minimum of 21 months of work spread over as much as 24 months (two years) from start to finish.

XII. Conclusion

There is no doubt that wolves are a high profile species, and one whose management has been controversial (Huey, 2016). Yet, at present there is insufficient economic information to inform wolf management decisions at a regional level (National Research Council--NRC, 1997; Iverson and Borg, 2012). While there is data and literature about the economic values of general wildlife viewing in Alaska, there is little known about wolf viewers' economic benefits and their trip spending in the DNPP region specifically. Likewise, little is known about wolf, caribou and moose hunter and wolf trapper expenditures. To my knowledge there is nothing known about wolf trapper economic benefits. This may be due in part, to the possibility there are very few wolf trappers, especially in the region near DNPP.

Nothing is known about the non-use (existence and bequest) values of wolves in DNPP to Alaska residents and to lower 48 populations.

A coordinated social science research program is needed to fill the data gaps related to wolf management in Alaska (NRC 1997) and inform management of wolves in and around DNPP specifically (Iverson and Borg, 2012). Established methods exist to fill all of these data gaps and have been used in other regions of the U.S. for economic valuation of wolves and for other species in Alaska. Our report detailed the types of methods and studies that would need to be conducted to fill the identified data gaps.

Visitor surveys of wolf viewers and hunters can be conducted in a fairly straightforward manner. Nonetheless, survey development, the OMB approval process, pretesting, data collection, and statistical/economic analysis require careful thought, adequate time (8-14 months for viewer survey) and budget for implementation (about $165,000 for viewer survey—see text for detailed budget). The U.S. (Alaska and lower 48) household non-use value surveys are more challenging in terms of time and budget to design and implement, and would take up to two years from start to finish, and cost in the range of $270,800 to $346,800 . However the general household survey can be done at any point in the year. The visitor surveys would need to be implemented during the summer season. The hunter surveys would need to be implemented after the hunting season, and no doubt after, Alaska Department of Fish and Game does its post-harvest survey. In sum, filling the economic data gaps to inform wolf management in and around Denali National Park and Preserve is amenable to research and can help provide a quantifiable comparison of the economic values of wolf viewing, hunting, wolf trapping and passive-use/non-use benefits.

XIII. **References**

Borg B. L. 2015. Effects of harvest on wolf social structure, population dynamics and viewing opportunities in National Parks. Ph.D. Dissertation. University of Fairbanks, Alaska.

Carson, R. N. Flores, K. Martin and J. Wright. 1996. Contingent Valuation and Revealed Preference Methodologies: Comparing the Estimates for Quasi Public Goods. Land Economics 72(1): 80-99.

Carson, R. and T. Groves. 2007. Incentive and Informational Preference Questions. *Environmental and Resource Economics* 37: 181-210.

Chambers, C. and Whitehead, J., 2003. A Contingent Valuation Estimate of the Benefits of Wolves in Minnesota. *Environmental and Resource Economics* 26: 249-267.

Champ, P. 2003. Collecting Survey Data for Nonmarket Valuation. in Champ, P., K. Boyle and T. Brown. A Primer for Nonmarket Valuation. Kluwer Academic Publishers, Boston, MA.

Champ, P. A., Bishop, R. C., Brown, T. C., and McCollum, D. W. 1997. Using Donation Mechanisms to Value Nonuse Benefits from Public Goods," *Journal of Environmental Economics and Management* 33:151-162.

Champ, P., R. Moore and R. Bishop. 2009. A Comparison of Approaches to Mitigate Hypothetical Bias. *Agricultural and Resource Economics Review* 38: 166-180.

Cullinane Thomas, C., C. Huber, and L. Koontz. 2015. 2014 National Park visitor spending effects: Economic contributions to local communities, states, and the Nation. Natural Resource Report NPS/NRSS/EQD/NRR—2015/947. National Park Service, Fort Collins, Colorado.

Dillman, D. 2000. Mail and Internet Survey: The Tailored Design Method, 2nd edition. John Wiley and Sons. New York, NY.

Donnelly, D., J. Loomis, C. Sorg, and L. Nelson. 1985. Net Economic Value of Recreational Steelhead Fishing in Idaho. Resource Bulletin RM-9. Rocky Mountain Forest and Range Experiment Station, U.S. Forest Service, Fort Collins, CO.

Dorendorf, R. 2015. Motivations and Drivers of Trapper Catch Per Unit Effort in Alaska. M.S. Thesis, Department of Biology and Wildlife, University of Alaska, Fairbanks.

Duffield, J., 1991. Existence and non-consumptive values for wildlife: application of wolf recovery in Yellowstone National Park. W-133/Western Regional Science Association Joint Session. Measuring Non-Market and Non-Use Values. Monterey, CA.

Duffield, J. 1992. An Economic Analysis of Wolf Recovery in Yellowstone: Park Visitor Attitudes and Values. in J.D. Varley and W.G. Brewster, Editors, Wolves for Yellowstone? A Report to the United States Congress, Volume IV Research and Analysis. National Park Service, Yellowstone National Park.

Duffield, J., D. Patterson and C. Nehr. 1993. Wolves and People in Yellowstone: A Case Study in the New Resource Economics. Report to the Liz Claiborne and Art Ortenberg Foundation. Dept of Economics, University of Montana, Missoula, MT.

Duffield, John, Chris Neher, and David Patterson. 2006. Wolves and People in Yellowstone: Impacts on the Regional Economy. Prepared for Yellowstone Park Foundation.

Duffield, J. W., C. J. Neher, and D. A. Patterson. 2008. Wolf recovery in Yellowstone: park visitor attitudes, expenditures, and economic impacts. Yellowstone Science 16:20–25.

ECONorthwest. 2014a. The Economic Importance of Alaska's Wildlife in 2011. Summary Report to the Alaska Department of Fish and Game, Division of Wildlife Conservation, contract IHP-12-052. Portland, Oregon.

ECONorthwest. 2014b. The Economic Importance of Alaska's Wildlife in 2011. Final Report to the Alaska Department of Fish and Game, Division of Wildlife Conservation, contract IHP-12-052. Portland, Oregon.

Fix, P. J., A. Ackerman, & G. Fay. 2013. 2011 Denali National Park and Preserve visitor characteristics. Natural Resource Technical Report NPS/AKR/NRTR—2013/669. National Park Service, Fort Collins, Colorado.

Freeman, M. 2003. The Measurement of Environmental and Resource Values: Theory and Methods, 2^{nd} Edition. Resources for the Future, Washington DC.

Holmes, T.P., and W.L. Adamowicz. 2003. Attribute-Based Methods. In *A Primer on Nonmarket Valuation*, edited by Patricia A. Champ, K.J. Boyle, and T.C. Brown. Dordrecht: Kluwer Academic Publishers.

Huey, A. 2016. How Can 6 Million Acres at Denali Still Not Be Enough? National Geographic, February 2016. http://ngm.nationalgeographic.com/2016/02/denali-national-parks-text

Iverson, M. and B. Borg. 2012. Economic Impact of Wolf-Viewing Opportunities in Denali National Park and Preserve. Denali National Park, Denali, AK.

Koontz, L. 2016. DENA Visitor Spending Issues. Email from Lynne Koontz, NPS economist. January 13, 2016.

Krutilla, J. 1967. Conservation Reconsidered. American Economic Review 57(4): 777-786.

Loomis, J., G. Peterson and C. Sorg. 1984. A Field Guide to Wildlife Economic Analysis. Transactions of 49th North American Wildlife and Natural Resources Conference. Wildlife Management Institute, Washington DC

Loomis, J., D. Updike and W. Unkle. 1989. The Consumptive and Nonconsumptive Values of a Game Animal: The Case of California Deer. Transactions of 54th North American Wildlife and Natural Resources Conference. Wildlife Management Institute, Washington DC.

Loomis, J. 1990. Comparative Reliability of the Dichotomous Choice and Open Ended Contingent Valuation Techniques. *Journal of Environmental Economics and Management*, Volume 18(1)

Loomis, J. and P. Fix. 1998. Testing the Importance of Fish Stocking as a Determinant of the Demand for Fishing Licenses and Fishing Effort in Colorado. *Human Dimensions of Wildlife* 3(3): 46-61.

Loomis, J. and R. Walsh. 1997. *Recreation Economic Decisions: Comparing Benefits and Costs*. 2nd, Edition. Venture Publishing, State College, PA.

Loomis, J. 2000. Vertically Summing Public Good Demand Curves: An Empirical Comparison of Economic versus Political Jurisdictions. *Land Economics*, 76 (2): 312-321.

Loomis, J. 2014. Strategies for Overcoming Hypothetical Bias in Stated Preference Surveys. *Journal of Agricultural and Resource Economics* 39(1): 34-46. 2014

Louviere, J.J. 2001. Choice Experiments: an Overview of Concepts and Issues. In *The Choice Modeling Approach to Environmental Valuation,* edited by Jeff Bennett and Russell Blamey. Northampton, MA: Edward Elgar Publishing.

Louviere, Jordan J., D.A. Hensher, andJ. D. Swait. 2000. *Stated Choice Methods: Analysis and Applications*. New York, NY: Cambridge University Press.

Manni, M. F., Y. Le, G. A. Vander Stoep, & S. J. Hollenhorst. 2012. Denali National Park and Preserve visitor study: Summer 2011. Natural Resource Report NPS/NRSS/EQD/NRR—2012/524. National Park Service, Fort Collins, Colorado

Manning, R. E., and J. C. Hallo. 2010. The Denali park road experience: Indicators and standards of quality. Park Science 27:33–41.

McCollum, D., M. Haefele and S. Miller. March 1998. "Attributes and the Value of a Wildlife Viewing Experience: A Preliminary Analysis of Wildlife Viewing in Denali National Park," USDA Forest Service (internal document).

Miller, SuzAnne and D. McCollum. 1997. Alaska Non Resident Visitors. Alaska Dept of Fish and Game, Anchorage, Alaska.

National Research Council. 1997. Wolves, Bears, and Their Prey in Alaska. Washington, DC.

Schuman, P. and K. Schwabe. 2000. Fundamentals of Economic Principles and Wildlife Management. Human Conflicts with Wildlife: Economic Considerations. USDA National Wildlife Research Center Symposia. University of Nebraska, Digital Commons.

Peterson, G., C. Sorg-Swanson, D. McCollum and M. Thomas, eds. 1992. Valuing Wildlife Resources in Alaska.Westview Press, Boulder, CO.

Reiling, S., K. Boyle, M. Phillips and M. Anderson. 1990. Temporal Reliability of Contingent Values. Land Economics 66(2): 128-134.

Richardson, L. and J. Loomis. 2009. The Total Economic Value of Threatened, Endangered and Rare Species: An Updated Meta Analysis. Ecological Economics 68(5): 1535-1548

Schuman, P. and K. Schwabe. 2000. Fundamentals of Economic Principles and Wildlife Management. Human Conflicts with Wildlife: Economic Considerations. USDA National Wildlife Research Center Symposia. University of Nebraska, Digital Commons.

Skibins, J. C., J. C. Hallo, J. L. Sharp, and R. E. Manning. 2012. Quantifying the Role of Viewing the Denali "Big 5" in Visitor Satisfaction and Awareness: Conservation Implications for Flagship Recognition and Resource Management. Human Dimensions of Wildlife 17:112–128.

Stevens, T., R. Belkner, D. Dennis, D. Kittrredge, C. Willis. 2000. Comparison of Contingent Valuation and Conjoint Analysis in Ecosystem Management. *Ecological Economics* 32(1): 63-74.

Stynes, D. J. and A. Ackerman. 2010. Impacts of visitor spending on the local economy: Denali National Park and Preserve, 2008. Department of Community, Agriculture, Recreation and Resource Studies, Michigan State University, East Lansing, Michigan.

Treves, A. 2009. Hunting for Large Carnivore Conservation. *Journal of Applied Ecology* 46: 1350-1356.

U.S. Environmental Protection Agency.2000. Guidelines for Preparing Economic Analyses. September 2000. Washington DC.

U.S. Fish and Wildlife Service. 1994. The Reintroduction of Gray Wolves to Yellowstone National Park and Central Idaho. Final Environmental Impact Statement. http://www.fws.gov/mountain-prairie/species/mammals/wolf/eis_1994.pdf

U.S. Office of Management and Budget. 1992. Guidelines and Discount Rates for Benefit-Cost Analysis of Federal Programs. Washington DC. Available at http://www.whitehouse.gov/omb/circulars_a094

U.S. Office of Management and Budget. 2000. Guidelines to Standardize Measures of Costs and Benefits and the Format of Accounting Statements. M-00-08, from Jacob Lew, Director. Washington DC.

U.S. Water Resources Council. 1983. Economic and Environmental Principles and Guidelines for Water and Related Land Resources Implementation Studies. U.S. Government Printing Office, Washington DC. March 10, 1983. http://www.usace.army.mil/CECW/Documents/pgr/pg_1983.pdf

Rationale for boundary of proposed *Denali Wildlife Conservation Area* (DWCA)

Knowles, Steiner; Nov. 2016

1. The area within the DWCA needs to be sufficient to achieve the joint state/federal goal -- **To restore, sustain, and enhance the valuable wildlife viewing resource of Denali National Park & Preserve**. Based upon decades of radio collar data, the proposed Area would protect most animal (predator) transits in-and-out of the Park (note: this will not provide 100% protection, but perhaps 80% - 90% of predator transits in-and-out of the Park will be protected). This is the minimum conservation area needed to reasonably meet the joint state/federal goal.

2. The proposed DWCA area (340,000 acres) represents a reasonable compromise between the 1992 buffer established by the Alaska Board of Game (519,000 acres), and the 2000-2010 buffer, also established by the Board of Game (80,000 acres). In addition, the proposed DWCA is comparable in size to the bison conservation area established earlier this year along the boundary of Yellowstone National Park by the Governor of Montana.

3. Landmarks along the proposed boundary of the DWCA – Elsie Creek, Dora Peak, Pyramid Mountain, Nenana River, etc. - are easily recognizable from the ground or air. Thus even without a GPS unit, it will be easy to tell whether one is in the Conservation Area or not, thereby simplifying compliance and enforcement.

4. The proposed DWCA area is precisely the same area that was proposed as a buffer in 2010 by the Anchorage Fish & Game Advisory Committee to the Board of Game (Proposal #58), based on recommendations by wildlife biologists studying Denali wildlife migration along the northeast boundary of the Park. (The proposal, along with several others to expand the small existing buffer, was declined, and the existing buffer was eliminated in its entirety).

5. Establishing the DWCA is seen as a one-time opportunity – there should be no additional such requests in the future. Thus, it is important to establish boundaries appropriate to the joint state/federal goal at this time.

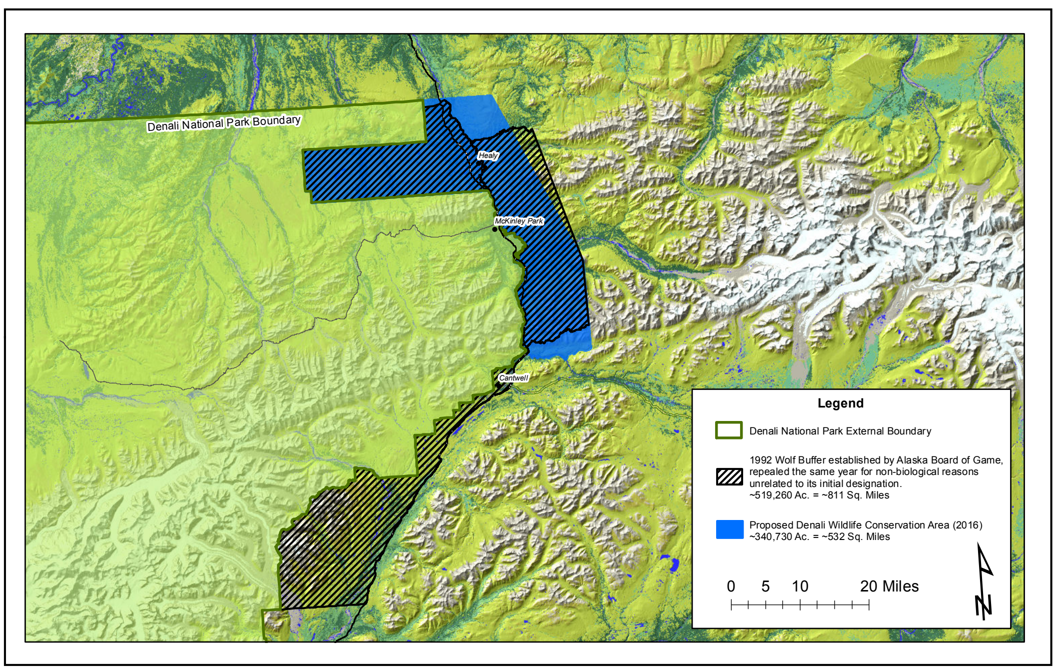
6. The boundaries of the Area will displace activities of only a few predator hunter/trappers, thus having minimal impact on overall wildlife use patterns in the region. ADFG reports annual predator take within the proposed Area averages approx. 7 grizzly bears, 5 lynx, 4 wolves, 4 wolverine, and 2 black bears. And, the Conservation Area will benefit over 70,000 Alaskans visiting Denali each summer hoping to view these same animals in the Park, along with another 600,000 paying out-of-state tourists also hoping to view these animals.

7. The proposed DWCA boundary excludes the area south of Cantwell/south of the Alaska Range, which had been protected in the 1992 Board of Game buffer, as it is felt that this area may be less critical to the protection and restoration of wildlife viewing along the Park road, north of the Alaska Range.

Description of *Denali Wildlife Conservation Area* Boundary:

All lands abutting the east and northeast boundaries of Denali National Park & Preserve (the Park), within the following boundaries: Commencing at the far northeast corner of the Park (approx. 64° N, 149° 13’ W), thence due east until intersecting with Elsie Creek (approx. 64° N, 148° 53’ W), thence southeastward along a straight line to the top of Dora Peak (approx. 63° 49.20’ N, 148° 41’ W), thence southeastward along a straight line to the top of Pyramid Mountain (approx. 63° 38.40’ N, 148° 31’ W), thence due south until intersecting Bruskasna Creek (approx. 63° 27’ N, 148° 31 W), thence westward (downstream) along the north side of the Nenana River to its confluence with Windy Creek at the east boundary of DNP (approx. 63° 27.90’ N, 148° 49’ W).

Map of Proposed *Denali Wildlife Conservation Area*
(Blue area)



Rationale for *Denali Wildlife Conservation Area (DWCA)*

Rick Steiner, Professor (Univ. of Alaska, ret.)
Oasis Earth, Anchorage
January 1, 2017

Discussions are currently ongoing between Alaska citizens, the State of Alaska, and the U.S. Department of Interior to establish a *Denali Wildlife Conservation Area* (DWCA) on state lands along the northeast boundary of Denali National Park & Preserve. The goal of the proposed DWCA is to restore, sustain, and enhance the valuable wildlife viewing resource of Denali National Park & Preserve. The following points are compiled in support of the establishment of the DWCA.

I. Economics of wildlife viewing at Denali

Denali National Park & Preserve (DNPP) is Alaska's most visited national park (650,000 visits in 2016, 70,000 of who were Alaska residents), and is the third largest revenue generating national park in the nation (exceeded only by Blue Ridge Parkway and Grand Canyon).

DNPP total visitor spending was $567 million in 2015 (exceeding Yellowstone and Yosemite), generated 7,300 jobs; labor income of $269 million; value added revenue of $499 million; and a total economic output $810 million that year alone (NPS, 2016; https://www.nps.gov/subjects/socialscience/vse.htm).

One of the primary reasons visitors come to Alaska is to view wildlife. In 2011, wildlife viewing in Alaska supported over $2.7 billion in economic activity, while hunting in Alaska supported approximately $1.3 billion in economic activity (ECONorthwest 2014a – see attached report summary). Wildlife viewing supports an estimated 18,820 jobs in Alaska (with visitor spending per trip of $6,361), while hunting supports approx. 8,400 (ECONorthwest, 2014a). Wildlife viewing contributes over twice the economic activity in Alaska as does hunting.

Similarly, most visitors to Denali from the U.S. and internationally cite wildlife viewing as the main purpose of their trip (Loomis, 2016).

Loomis 2016: "Manning and Hallo (2010) found that the single most important experience for visitors on the Denali National Park road was seeing wildlife (70%). Related to this, visitors thought not seeing "enough wildlife" and "too few animals along the road" were a problem (50%, and 53%, respectively). This suggests that the quality of the visitor experience ***is*** influenced by the number of animals seen regardless of whether the animals seen were one of the "Big 5" species (grizzly bears, wolves, caribou, Dall sheep and moose)." Note: most Alaska visitors do not venture from the road system, thus DNPP is their best chance to view wildlife.

Loomis, 2016: "ECONorthwest (2014a,b) performed a survey of both Alaska residents and non-resident visitors to Alaska about their use and spending related to hunting and wildlife viewing. The economic activity associated with wildlife viewing and hunting was measured in these studies by resident and non- resident visitor spending. Economic impacts were measured by jobs supported by the activity. Hunting expenditures by residents and non-resident visitors supports $457 million in wages associated with 8,400 jobs statewide (Table 1). This hunting activity also provides $112 million in various types of revenue to local and state governments in Alaska. Wildlife viewing provides $976 million in wages to 18,820 workers statewide (Table 1). In addition $231 million in revenues are provided to various levels of government in the State of Alaska."

Loomis, 2016: "In 1997, non-resident visitors who came to Alaska primarily to view wildlife had average expenditures of $6,000 per trip (Miller and McCollum, 1997). The benefits per trip in excess of their expenditures were on the order of $700 to $900 (Miller and McCollum, 1997). From economic valuation questions found in Alaska wildlife viewing literature, it can be inferred that a non-resident visitor may have an additional value in the range of $200-$300 per wildlife viewing trip to Alaska if a wolf is seen on their trip." (For more detailed discussion see Loomis, 2016 attached).

Visitor viewing of large carnivores, particularly wolves and grizzly bears, is a main indicator of a satisfying visitor experience in Denali (Manning & Hallo 2010).

As example, the value of wolf viewing in Yellowstone National Park, with an average visitor viewing success for wolves at 45% - 85% (Borg, et.al., 2016), was estimated at $35 million/year (Duffield, et.al., 2008).

Total annual lethal take of wildlife along the NE boundary of DNPP was estimated by ADFG in 2015 as follows: brown (grizzly) bear 7.3; lynx 5.3; wolf 4.3; wolverine 4.3; black bear 2. ADFG reports that the average number of active trappers in the area is between 1-3 individuals in any given year (ADFG, 2013).

Visitor viewing success for wolves (the only species for which viewing data exist) in DNPP dropped from 45% in 2010 (when the State of Alaska removed the small protective buffer), to only 5% in 2016 (the rate has remained at about 5% for the past 4 seasons). This reduction in wolf viewing success translates into 260,000 paying visitors/year being denied the opportunity to view wolves in DNPP.

Borg et.al., 2016: regarding wolf sightings by visitors to Yellowstone National Park (YNP) and Denali National Park & Preserve (DNPP): "…sightings in both parks were significantly reduced by harvest. Sightings in YNP increased by 45% following years with no harvest of a wolf from a pack, and sightings in DNPP were more than twice as likely during a period with a harvest buffer zone than in years without the buffer."

National Park Service, 2016: "…we found that the presence of the trapping and hunting buffer zone during 2000-2010 was associated with increased wolf sightings in Denali National Park compared to 2011-2013 and 1997-2000 (Borg et al 2016). Both the wolf population size and an index measuring the number of wolves denning near the park road, which were strongly associated with increased wolf sightings, were also greater during the period when the buffer zone was in place. Thus, the presence of the buffer may have increased local population size and the likelihood that wolves would den near the park road."

The loss of just one significant breeding individual in a social carnivore group (e.g. wolves) can lead to disproportionate consequences (Haber, 2008; Borg, et.al., 2015), including disintegration and loss of entire family groups (as occurred recently with the Grant Creek and East Fork wolf family groups in DNPP). After the loss of the Grant Creek female wolf in 2012, the group did not pup or den, dispersed, and visitor viewing success dropped from 21% to only 12% that summer. The loss of one park wolf to hunting or trapping along the boundary can lead to significant reduction in visitor viewing success and economic value in the Park.

At an estimated passive-use value of $14/wolf sighting (U.S. household value estimated for reintroduction of wolves to Yellowstone National Park by Duffield, 2013), the reduction in wolf sightings alone in DNPP in the past 6 years would equate to the loss of approximately $3.6 million/year. The actual loss to the potential revenue growth in wildlife tourism, while speculative, is considerably larger.

Good data do not yet exist re: the impact of take of other Park predators along the boundary (brown bear, black bear, lynx, wolverine, coyote, etc.) on visitor viewing experience in the Park, but it is likely such take also reduces the visitor viewing experience.

Anecdotal evidence suggests that visitor sightings of lynx and wolverine in DNPP are even more rare than of wolves. Thus the value of visitor sightings for these Park species is correspondingly high. In addition, the value of viewing other Park predators - brown bear, black bear, and coyote - is significant.

The total value of consumptive use of DNPP wildlife is minimal, on the order of $ thousands/year. In contrast, the total value of reallocating these animals to sustainable wildlife viewing in DNPP is in the $ millions/year.

With establishment of the *Denali Wildlife Conservation Area* (DWCA), the few hunter/trappers that had used the area would be displaced to other lands to the north, east, and south, where millions of acres of state and federal lands remain open to hunting and trapping as permitted by the State of Alaska.

Wildlife viewing (including wolf viewing) in DNPP, and its associated economic activity, would be significantly enhanced by the establishment of the DWCA, with minimal impact to local consumptive wildlife use patterns.

The relative value of reallocating these few Park animals to remain alive for viewing in DNPP is easily ***hundreds of times greater*** than allowing these animals to be lethally taken each year outside the boundary. It is conservatively estimated that, over time, a DWCA could increase Alaska tourism revenue by $ tens of millions. Establishing the DWCA will also enhance the visitor experience by assuring visitors that they are experiencing a subarctic terrestrial ecosystem relatively undisturbed by human activities (one of the mandates of the Park, which currently most visitors are unable to do at Denali).

Denali's watchable wildlife resource is one of the most important tourism assets in the State of Alaska. The net economic benefit of establishing the *Denali Wildlife Conservation Area* (DWCA) adjacent to the Park is overwhelming and clear.

II. Public Support for *Denali Wildlife Conservation Area*

Over the past 6 or 7 years, hundreds, if not thousands, of emails and other communications have been sent to the Governor and ADFG Commissioner in support of permanent protection for DNPP wildlife along the boundary of the Park.

In the past 2 years, several citizens groups have met with the Governor and other senior administration officials to support of a Denali Wildlife Conservation Area.

The state's main tourism business association – the *Alaska Travel Industry Association (*ATIA) - supports a wildlife protection area along the NE boundary of DNPP, and has voiced its support directly to Governor Walker.

Several Alaska citizen groups have repeatedly petitioned the Board of Game and ADFG Commissioner for protection of DNPP wildlife along the boundary of the Park (including the Alaska Wildlife Alliance, Denali Citizens Council, and Alaskans for Wildlife), yet all such petitions have been denied (see Wolf Township History below, post-2000).

An on-line citizens petition in support of the effort has over 325,000 signatures, from over 100 countries, all U.S. states, and many from Alaska: http://www.thepetitionsite.com/423/700/229/halt-the-killing-of-denali-national-park-wolves/

On Aug. 26, 2016, the Fairbanks North Star Borough adopted as follows:
"A Resolution Urging Governor Walker To Close Areas Adjacent to Denali National Park & Preserve To The Trapping and Hunting of Bears, Wolves, and Wolverines."

It is probable that a majority of Alaskans, many of whom will visit Denali in the future, and certainly most Americans, support establishment of the DWCA.

III. Denali - Wolf Townships History

(Compiled by E. Davis and R. Steiner, 2016)

1917 – McKinley Park established, Wolf Townships not included.

1922 – AK Railroad proposes to include Wolf Townships in McKinley Park to protect Park wildlife.

1965 – State selects Wolf Townships, but cites need to expand Park to protect caribou, and that existing Park boundary is “an arbitrary line.”

1969 – Johnson administration considers, but declines, to add Wolf Townships to Park.

1978 – Wolf Townships found worthy for inclusion in Denali National Monument, but lands had been selected by State.

1980 – The original version of ANILCA included the Wolf Townships within the new park boundaries because this area provides critical habitat for park wildlife. Although this area was removed from the final bill, the Senate report accompanying ANILCA made it clear the expectation was for the wolf townships to become part of Denali:

> *The prime resource for which the north addition is established is the critical range necessary to support populations of moose, wolf, and caribou as part of an integral ecosystem. Public enjoyment of these outstanding wildlife values would thus continue to be assured.*
>
> Senate report 96-413, 1980, page 166

> *In the northeast portion of the area, near the existing headquarters, there are some 3 townships of state lands which are critical for sheep, caribou, and wolf habitat and should eventually become a part of the park. … The Committee recognizes that these areas are important to the park and recommends that the Secretary seek land exchanges with the State of Alaska that would serve to bring these areas into the Park.*
>
> Senate report 96-413, 1980, page 167.

1985 – State proposes to bring Wolf Townships into Park in exchange for Kantishna/Dunkle Mine being excluded from Park.

1992 – Alaska Board of Game establishes 811 sq. mile wolf buffer on Wolf Townships and along eastern boundary of the park, but rescinds buffer two months later in political retaliation for Gov. Walter Hickel’s suspension of some wolf control programs elsewhere.

1995 – State proposes rail line through Wolf Townships, and NPS plan cites need to protect area affected by rail line as Park.

2000 – Board of Game reestablishes small no-kill wolf buffer, expands it in 2002 to 122 sq. mile (western part of Stampede Trail and Nenana Canyon).

2001 – State (Knowles administration) proposes to convey Wolf Townships to UA, to then sell to Park.

2008 – Scientists propose that ADFG Commissioner use Emergency Order authority to expand existing buffer to 530 sq. mile – denied.

2010 – Four Alaska citizen groups independently propose to Board of Game significant expansions of the existing wolf buffer – Denali Citizens Council, Denali National Park & Preserve, Defenders of Wildlife, and the Anchorage Fish & Game Advisory Committee - all denied. Board instead eliminates the existing buffer entirely, and adopts a moratorium on considering any further Denali buffer proposals for 6 years.

2010-2013 – Alaska citizens groups (including Alaska Wildlife Alliance, Denali Citizens Council, National Parks Conservation Association) file three Emergency Petitions asking Board of Game to reestablish the buffer (two in 2012, one in 2015) - all denied.

Alaska citizens repeatedly petition ADFG Commissioner to use emergency closure authority to close the area. Except for one 2-week closure ordered in May 2015 after the pregnant female of the East Fork wolf family group was killed in the area - all denied.

Alaska citizens propose in 2013 that the Board of Game lift its moratorium - denied.

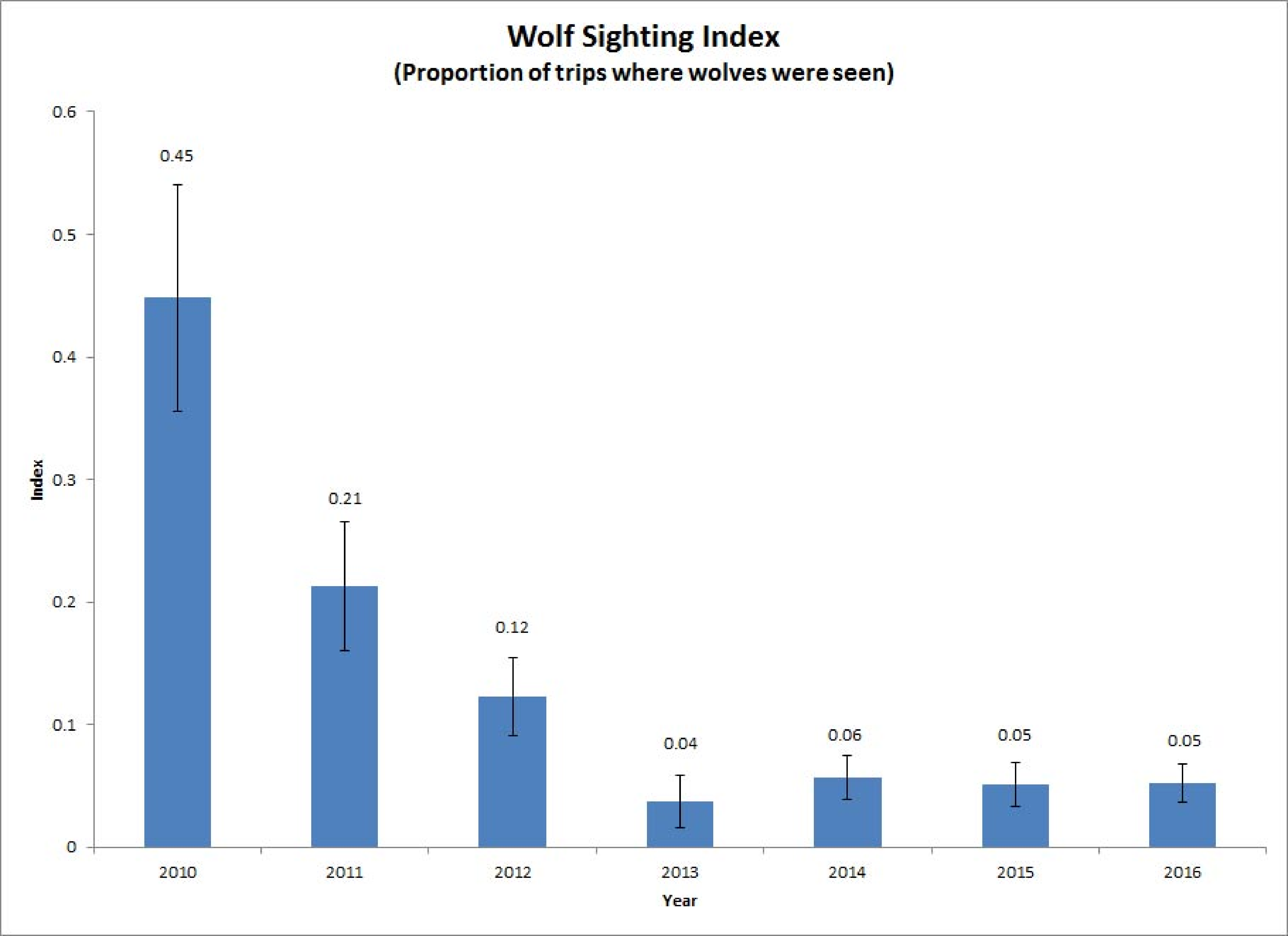
Despite moratorium, Alaska citizens propose to Board of Game a wolf buffer in GMU 13, along south Denali boundary - denied.

2013 – Present – It had become obvious that the Board of Game will not and cannot provide a lasting solution to the Denali watchable wildlife problem. Proposals to the Board are limited in species and area to be protected; the Board remains ideologically opposed to protecting watchable wildlife in parks; and most significantly, even if the Board were to enact a legitimate closed area, the closure would not be permanent and could easily be removed by subsequent Board action. As example, the initial wolf buffer established by the Board in 1992 was then removed by the same Board only 2 months later, due to unrelated political issues. To restore and enhance the valuable wildlife viewing resource of DNPP, a permanent solution is needed.

> Thus, seeking final resolution of this century-old issue, Alaska citizens proposed on Nov. 27, 2013 to the Governor and U.S. Interior Secretary the establishment of a permanent *Denali Wildlife Conservation Easement/Area* along the NE boundary, including the Wolf Townships/Stampede Trail, in order to permanently protect Denali wildlife along the NE boundary of the Park, while leaving land title in current ownership. Discussions ongoing.

The issue of conserving Park wildlife along the NE boundary of Denali has persisted for a century. It is clearly in the interest of Alaska, the U.S., the tourism industry, and the Park ecosystem to solve the issue once and for all by establishing the *Denali Wildlife Conservation Area*.

Rick Steiner is a conservation biologist in Anchorage, was a professor with the University of Alaska from 1980-2010, and consults on conservation issues globally through his Oasis Earth project (www.oasis-earth.com).


Wolf Sighting Index
(Proportion of trips where wolves were seen)
Index
Year
0.45
0.21
0.12
0.04
0.06
0.05
0.05
0
0.1
0.2
0.3
0.4
0.5
0.6
2010
2011
2012
2013
2014
2015
2016