

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. Prugh¹

¹University of Alaska Fairbanks, Institute of Arctic Biology, 323 Murie Building, Fairbanks, AK 99775, USA; ²National Park Service, Denali National Park and Preserve, P.O. Box 9, Denali Park, AK 99755, USA; and ³Alaska 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, Mladenoff & 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.

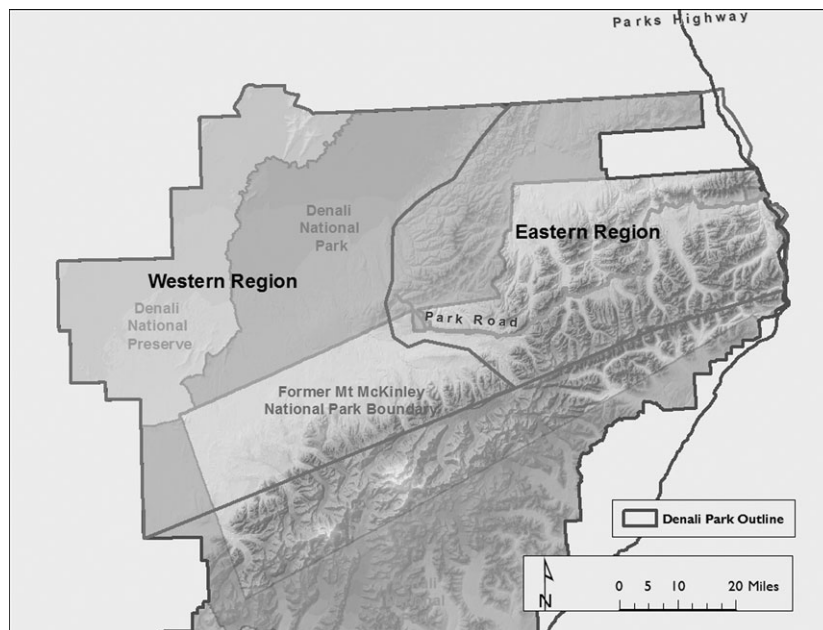
We evaluated the impacts of anthropogenic and natural mortality of breeders on wolf pack maintenance, reproduction and population growth using data on 387 radiocollared wolves in 70 packs. We hypothesized that the sex of breeder lost, pack size prior to loss and the timing of loss would influence pack 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 km² 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

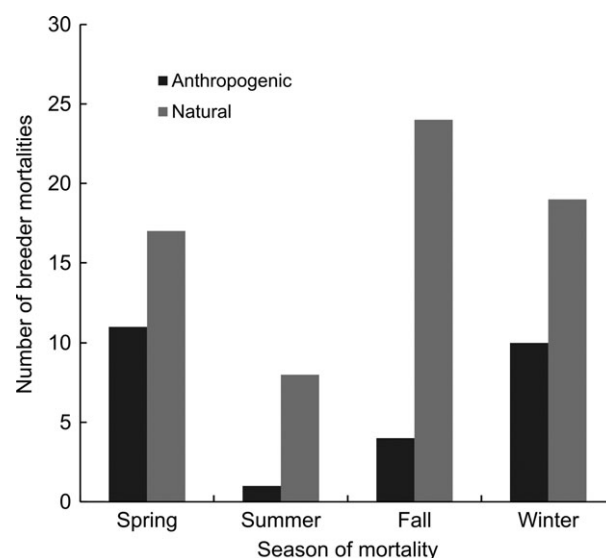


Fig. 2. Total number of mortalities of breeding grey wolves by season and type of mortality in Denali National Park, Alaska, USA, 1986–2012 ($n = 94$). Spring = February–April, Summer = May–July, Fall = August–October, Winter = November–January. Anthropogenic mortality includes hunting, trapping and 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	Δ AICc	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

^aPack size prior to breeder loss.^bSex of breeder loss.^cCause of mortality: natural or anthropogenic.^dSeason of breeder loss: spring, summer, fall or winter.^eGlobal 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 (Δ AICc < 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

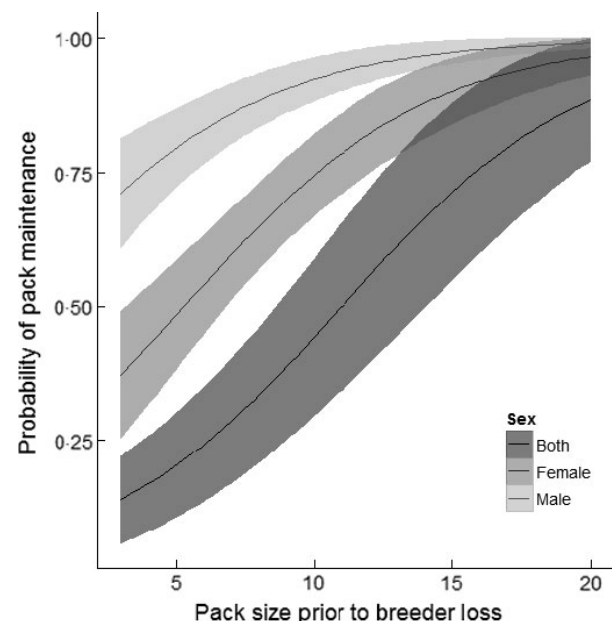
pack maintenance, whereas mortalities that occurred during the summer increased the probability of pack persistence relative to mortalities that occurred in the fall (Table 3).

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 : $\beta = -0.64$,

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

Parameter	β (Model averaged)	SE	95% CL		Odds ratio (Model averaged)
			Lower	Upper	
(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.**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} : $\beta = 0.23$, $F_{1,20} = 0.23$, $P = 0.63$, $R^2 = 0.01$, $n = 22$, Fig. 4b). Pack dissolution had a marginal negative effect on population growth in the current year but no effect the following year (λ_n : $\beta = -0.81$, $F_{1,21} = 3.10$, $P = 0.09$, $R^2 = 0.13$, $n = 23$, Fig. 4c; λ_{n+1} : $\beta = 0.71$, $F_{1,20} = 2.11$, $P = 0.16$, $R^2 = 0.10$, $n = 22$, 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%, $\chi^2 = 3.896$, d.f. = 1, $P = 0.049$, $n = 79$, recruitment: 70%, $\chi^2 = 5.697$, d.f. = 1, $P = 0.017$, $n = 72$).

Breeder loss did not significantly affect den site fidelity ($\chi^2 = 1.90$, 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

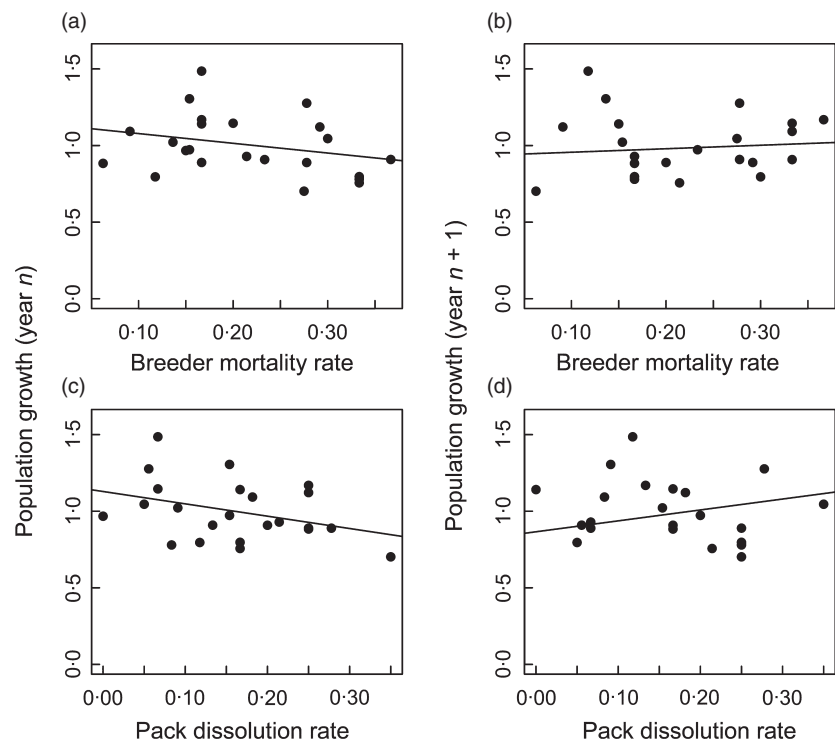


Fig. 4. Effect of breeder mortality and pack dissolution on annual population growth of grey wolves in Denali National Park, Alaska, USA, 1986–2012 with and without a time lag. Effect of breeder mortality rate in year n on population growth rate in (a) year n and (b) year $n+1$. Effect of pack dissolution 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

^aDen fidelity data are a subset of denning data for which we have information on denning in the prior year.

^bIncludes 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 & Koenig 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 of Gray 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 off-take, 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., Mladenoff, 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. & Schempf, 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. & Nogueira, 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) AICmodavg: model selection and multimodel inference based on (Q)AIC(c). R package version 1.32. <http://CRAN.R-project.org/package=AICmodavg>.
- 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. & Koenig, 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. & Bjørvall, 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.