

The Effects of Breeder Loss on Wolves

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ABSTRACT Managers of recovering wolf (*Canis lupus*) populations require knowledge regarding the potential impacts caused by the loss of territorial, breeding wolves when devising plans that aim to balance population goals with human concerns. Although ecologists have studied wolves extensively, we lack an understanding of this phenomenon as published records are sparse. Therefore, we pooled data ($n = 134$ cases) on 148 territorial breeding wolves (75 M and 73 F) from our research and published accounts to assess the impacts of breeder loss on wolf pup survival, reproduction, and territorial social groups. In 58 of 71 cases (84%), ≥ 1 pup survived, and the number or sex of remaining breeders (including multiple breeders) did not influence pup survival. Pups survived more frequently in groups of ≥ 6 wolves (90%) compared with smaller groups (68%). Auxiliary nonbreeders benefited pup survival, with pups surviving in 92% of cases where auxiliaries were present and 64% where they were absent. Logistic regression analysis indicated that the number of adult-sized wolves remaining after breeder loss, along with pup age, had the greatest influence on pup survival. Territorial wolves reproduced the following season in 47% of cases, and a greater proportion reproduced where one breeder had to be replaced (56%) versus cases where both breeders had to be replaced (9%). Group size was greater for wolves that reproduced the following season compared with those that did not reproduce. Large recolonizing (>75 wolves) and saturated wolf populations had similar times to breeder replacement and next reproduction, which was about half that for small recolonizing (≤ 75 wolves) populations. We found inverse relationships between recolonizing population size and time to breeder replacement ($r = -0.37$) and time to next reproduction ($r = -0.36$). Time to breeder replacement correlated strongly with time to next reproduction ($r = 0.97$). Wolf social groups dissolved and abandoned their territories subsequent to breeder loss in 38% of cases. Where groups dissolved, wolves reestablished territories in 53% of cases, and neighboring wolves usurped territories in an additional 21% of cases. Fewer groups dissolved where breeders remained (26%) versus cases where breeders were absent (85%). Group size after breeder loss was smaller where groups dissolved versus cases where groups did not dissolve. To minimize negative impacts, we recommend that managers of recolonizing wolf populations limit lethal control to solitary individuals or territorial pairs where possible, because selective removal of pack members can be difficult. When reproductive packs are to be managed, we recommend that managers only remove wolves from reproductive packs when pups are ≥ 6 months old and packs contain ≥ 6 members (including ≥ 3 ad-sized wolves). Ideally, such packs should be close to neighboring packs and occur within larger (≥ 75 wolves) recolonizing populations. (JOURNAL OF WILDLIFE MANAGEMENT 72(1):89–98; 2008)

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Changes in human attitudes and government policies have enabled wolf (*Canis lupus*) to be restored to portions of its former range in North America and Europe (Mech 1995a, Boitani 2003, Musiani and Paquet 2004). A dilemma for

biologists responsible for managing populations of recolonizing wolves is the need to balance long-term population viability with the immediate necessity of limiting conflicts between people and wolves (Mech 1995a, Chapron et al. 2003). Recent studies indicate that local involvement in wolf management, including public hunts, can help reduce conflicts and perhaps increase local acceptance of wolves (Andersen et al. 2003, Ericsson et al. 2004). Removal of territorial wolves that cause conflicts with local human

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populations through livestock depredation or other undesirable behavior may sometimes be a necessary measure for managing recolonizing wolf populations (Mech 1995a, 2001; Fritts et al. 2003; Bangs et al. 2004, 2005). In this context, it is important for managers to understand effects breeder loss may have on wolf social groups relative to goals and strategies for population recovery and long-term viability, as well as ethical and animal welfare considerations.

We lack an understanding of the effects of loss of breeding wolves because published records are sparse and largely anecdotal (e.g., Mech and Boitani 2003). Thus, our objective was to assess the effects of breeder loss on territorial wolves by pooling available data. We hypothesized that breeder loss would negatively impact pup survival and reproduction within territories, as well as group integrity and territoriality. In this context, we examined how group composition and size, timing of loss, and population size and type (recolonizing vs. saturated) influenced outcomes.

STUDY AREA

We compiled data from our field studies and cases collected from the literature (Mech 1977a, b; Fritts and Mech 1981; Peterson et al. 1984; Ream et al. 1991; Boyd and Jimenez 1994; Meier et al. 1995; Jozwiak 1997; Mech et al. 1998; Table 1). For our field data, we refer to descriptions from previously published descriptions of our study areas in Alaska (Kenai: Petersen et al. 1984; Denali: Meier et al. 1995, Mech et al. 1998), the northern Rocky Mountain region of the United States (U.S. Fish and Wildlife Service 1994, Bangs et al. 1998, Oakleaf et al. 2006), Wisconsin, USA (Wydeven et al. 1995, Kohn et al. 2000), Greece (Migkli et al. 2005, Iliopoulos et al. 2006), and Scandinavia (Wabakken et al. 2001, Liberg et al. 2008).

METHODS

Data Collection

S. Brainerd, of the Scandinavian Wolf Project (SKANDULV), queried wolf biologists worldwide to request cooperation and original data for our study. We combined unpublished data respondents (coauthors) and SKANDULV with published records (Table 1). Data for some parameters, such as group sizes or specific dates of loss, were missing in some cases. Therefore, sample sizes vary among analyses.

Terminology

A breeder was a member of a mated, territorial pair that either was or had the potential to be a parent. Breeding wolves are the natural leaders of packs (Mech 1999, 2000; Peterson et al. 2002). Pup survival is defined as the frequency in which >1 pup survived the loss of breeders. The term implied that pups survived at least through the first winter after birth and up until the first birthday. We determined pup survival through observations, snow-tracking, genetic evidence (i.e., DNA markers: Liberg et al. 2005) and survival of radioinstrumented pups. We used direct

observations of pups or indirect evidence (e.g., telemetry locations, genetic evidence, and snow-tracking data) to determine successful reproduction.

We defined groups as breeding pairs or packs (i.e., pups and older wolves, including breeders). We quantified group size in 3 ways: 1) preloss, which included all wolves (breeders and others) that were subsequently lost; 2) at time of breeder loss, which subtracted breeders and other wolves lost at the time of the event; and 3) postloss, which included all known mortality (including pups) after the event and before the next reproductive season.

We classified wolves as either sexually mature adults (≥ 22 months old), subadult yearlings (≥ 12 to < 22 months old), and pups (< 12 months old; Mech 1970). For some analyses, we combined yearlings and adults (breeders and nonbreeders) as adult-sized wolves. We defined auxiliaries as adult-sized nonbreeders (e.g., Harrington et al. 1983; Mech 1995b, 1999; Packard 2003). According to our data, parturition in our northern study areas (Scandinavia and AK, USA) occurs in early to mid-May, whereas pups are born in mid-April in the northern contiguous United States and southern Europe. For analyses regarding pup age, we set pup birth month to April in the southern study areas and May for areas in the north. We also based time intervals to next reproduction on these parturition dates.

Groups dissolved when members died or dispersed from the original territory, leaving territories either vacant or occupied by solitary wolves. We classified territories as reestablished when occupied by new wolves or when remaining solitary wolves found new mates. However, we did not consider territories reestablished when neighboring wolves expanded their territories into vacant areas. Budding occurred when a wolf mated with an outsider and established a territory adjacent to its natal territory (Fritts and Mech 1981, Fuller 1989, Meier et al. 1995, Mech and Boitani 2003). Splitting differed from budding in that a subgroup of wolves permanently split off from the original pack and formed a new territory adjacent to the original (Meier et al. 1995, Mech et al. 1998, Hayes et al. 2000, Mech and Boitani 2003).

Saturated wolf populations were at or near carrying capacity, had relatively low prey biomass-to-wolf ratios, and displayed variable rates of population growth (Mech and Boitani 2003). We defined the Denali population (Meier et al. 1995, Mech et al. 1998), the Kenai population (Peterson et al. 1984, Jozwiak 1997), the northeastern Minnesota population (Mech 1977a, b), and the Greek population (Migkli et al. 2005, Iliopoulos et al. 2006) as saturated populations. In contrast, recolonizing wolf populations in Scandinavia (Wabakken et al. 2001, Liberg et al. 2008), Wisconsin (Wydeven et al. 1995, Kohn et al. 2000), northwestern Minnesota, USA (Fritts and Mech 1981), and the northern Rocky Mountains (Bangs et al. 1995, 1998, 2004, 2005) had high growth rates and high prey abundance. Recolonizing populations were initially small and isolated to some degree from larger, saturated populations and they were intensively monitored. As such,

Table 1. Cases ($n = 134$) of lost breeding wolves ($n = 148$) by study area and sex in Europe and North America, 1970–2003.

Location	No. breeders lost		No. cases
	F	M	
AK, USA			
Denali National Park	19	14	27
Kenai Peninsula	7	2	9
Rocky Mountains, USA			
Yellowstone National Park	13	11	23
Northwestern MT	7	12	16
ID	4	6	6
Great Lakes, USA			
WI	15	11	26
Northeastern MN	1	1	2
Northwestern MN		3	3
Europe			
Scandinavia (Norway and Sweden)	7	14	21
Greece		1	1

recolonizing populations were ideal for studying the effects of population size on time to reestablishment of breeders and subsequent reproduction in wolf territories.

Statistical Analysis

We analyzed our data with SPSS version 15.0 (SPSS, Chicago, IL) statistical software and assessed normality with the Lilliefors test (Lilliefors 1967). Data were generally nonnormal in nature, and thus we used nonparametric methodology. For cross-tabulations, we used Pearson chi-squares to test for independence between data sets; however, for cases with cell counts ≤ 5 , we used likelihood ratios (G) and Fisher's exact test for 2×2 contingent tables. We used Mann–Whitney tests to compare between pairs of independent samples. We used multiple logistic stepwise regressions to determine the most important factors influencing binary parameters for pup survival and included factors for group size at the time of loss (total no. of adult-sized wolves and litter size), pup age, sex of remaining breeders, and presence or absence of breeders or auxiliaries. For correlative analyses, we used the Pearson correlation method. Statistical tests were 2-tailed unless otherwise indicated, and we assessed significance at $\alpha = 0.05$.

RESULTS

We recorded 134 cases involving the loss of 148 breeding wolves (75 M and 73 F; Table 1). Most breeding wolves (56.8%) were killed by humans (Table 2), although natural causes accounted for many losses (31.1%).

Effects on Pup Survival

Pups were present after breeder loss in 84 cases, and >1 pups survived in 58 of 71 cases (81.7%) with known outcomes (Table 3). Pup survival did not differ between cases where breeders of one sex remained and where breeders were absent (Fisher's exact test: $P = 0.60$, $n = 71$). For the combined data, we found no difference in pup survival between sexes of surviving solitary breeders (Fisher's exact test: $P = 0.19$, $n = 61$; Table 3).

Pup age averaged 5.49 months ($SD = 2.97$, $n = 67$) at the time of breeder loss. In the combined sample, we found similarities in pup survival between 4 3-month age categories ($G = 1.75$, $df = 3$, $P = 0.62$, $n = 67$). Between 3-month age categories, pup survival did not differ for solitary females ($G = 6.53$, $df = 3$, $P = 0.09$, $n = 31$), solitary males ($G = 2.72$, $df = 3$, $P = 0.44$, $n = 26$), or cases where breeding pairs were absent ($G = 2.83$, $df = 2$, $P = 0.24$, $n = 7$). Within 3-month pup age categories, we found no differences in pup survival between sexes of remaining solitary breeders for pups aged 0–2 months (Fisher's exact test: $P = 1.00$, $n = 11$), 3–5 months (Fisher's exact test: $P = 0.62$, $n = 20$), 6–8 months (Fisher's exact test: $P = 0.38$, $n = 16$), or 9–11 months (Fisher's exact test: $P = 0.13$, $n = 10$; Table 3).

Younger (<6 months) and older (≥ 6 months) pups survived equally when we considered all cases (Fisher's exact test: $P = 0.54$, $n = 67$). Likewise, pup survival did not differ between younger and older pups where solitary breeders remained (Fisher's exact test: $P = 0.20$, $n = 57$) or where breeding pairs were absent (Fisher's exact test: $P = 1.00$, $n = 7$). Younger and older pups survived equally where solitary males remained (Fisher's exact test: $P = 1.00$, $n = 26$), whereas survival of older pups (100.0%, $n = 16$) differed from survival of younger pups (73.3%, $n = 15$) where solitary female breeders remained (Fisher's exact test: $P = 0.43$, $n = 31$). Sex of solitary breeders did not influence the survival of younger pups (Fisher's exact test: $P = 1.00$, $n = 31$). However, survival of older pups differed between solitary female (100.0%, $n = 16$) versus male breeders (70.0%, $n = 10$; Fisher's exact test: $P = 0.046$; Table 3).

For cases where older (>6 months) pups survived, group sizes did not differ between cases where solitary female ($\bar{x} = 6.50$, $SD = 2.56$, $n = 16$) and male ($\bar{x} = 6.14$, $SD = 4.06$, $n = 7$) breeders remained (Mann–Whitney: $U = 42.50$, $Z = -0.92$, $P = 0.36$). However, group sizes for surviving older pups ($\bar{x} = 6.39$, $SD = 2.99$, $n = 23$) were larger than group sizes where older pups did not survive ($\bar{x} = 3.00$, $SD = 1.00$, $n = 3$; Mann–Whitney: $U = 5.50$, $Z = -2.36$, 1-tailed $P = 0.01$; Table 3).

Pup survival generally varied with group size at the time breeders were lost ($G = 4.89$, $df = 2$, $P = 0.006$, $n = 69$). Pup survival was greater in groups of >6 wolves (90.0%, $n = 40$) versus groups with fewer wolves (68.9%, $n = 29$; $G = 18.02$, $df = 6$, 1-tailed $P = 0.02$). Pup survival also varied with litter size ($G = 20.11$, $df = 6$, $P = 0.003$, $n = 68$), and it was greater in litters with >1 pup (85.2%, $n = 61$) versus litters with solitary pups (42.9%, $n = 7$; Fisher's exact test: 1-tailed $P = 0.01$, $n = 68$). In addition, pup survival was also lesser in litters with 1 or 2 pups (66.7%, $n = 21$) versus larger litters (87.2%, $n = 47$; Fisher's exact test; 1-tailed $P = 0.04$, $n = 68$; Table 4). Mean litter sizes before breeder loss were larger for litters with surviving pups versus litters where pups did not survive (1-tailed $P = 0.03$). Litter sizes generally declined after breeders were lost ($P < 0.001$; Table 5).

The number of surviving pups correlated with the number of surviving adult-sized wolves in groups (Pearson correla-

Table 2. Causes of lost of breeding wolves ($n = 148$) in Europe and North America, 1970–2003.

Cause of loss	<i>n</i>
Anthropogenic mortality	
Capture-related	5
Euthenasia	2
Illegal kill (including probable)	34
Legal kill	9
Lethal control	20
Translocation	5
Vehicle collision	9
Natural mortality	
Accident	8
Disease or malady	10
Intraspecific strife	24
Other	4
Unknown mortality	17
Dispersal	1

tion: $r = 0.41$, $P = 0.001$, $n = 67$). Auxiliary nonbreeders benefited pup survival ($\chi^2 = 7.59$, $df = 1$, 1-tailed $P = 0.003$), with pups surviving in 91.9% of cases where auxiliaries were present ($n = 37$) and 64.3% of cases where auxiliaries were absent ($n = 28$). The number of adult-sized wolves was greater in groups where pups survived both before (1-tailed $P = 0.002$) and after (1-tailed $P = 0.001$) breeders were lost. In general, group sizes naturally diminished as a consequence of mortality and dispersal after breeder loss (1-tailed $P < 0.001$; Table 5).

The most important factor influencing whether pups survived was the number of adult-sized wolves remaining in the pack at the time breeders were lost (logistic regression: log likelihood ratio test: $G = 20.11$, $df = 1$, $P < 0.001$, $n = 66$). Addition of the term for pup age (logistic regression:

partial log likelihood ratio test, $G = 5.30$, $df = 1$, $P = 0.02$, $n = 66$) improved the explanatory power of the model.

Effects on Future Reproduction

Wolves reproduced within territories the season after breeder loss in 46.8% of cases ($n = 111$). Breeders were more likely to be replaced within 12 months where breeders of one sex remained (60.7%) than where breeding pairs were absent (27.3%; $\chi^2 = 7.92$, $df = 1$, 1-tailed $P = 0.002$, $n = 111$). Consequently, the ability of wolves to reproduce the season after breeder loss was greater in cases where one breeder had to be replaced (56.2%) versus cases where both breeders had to be replaced (9.1%; $\chi^2 = 15.71$, $df = 1$, 1-tailed $P < 0.001$, $n = 111$). Breeders mostly persisted to the birth of pups (96.2%), although 2 males that fathered pups (3.8%) died before litters were born ($n = 52$). The sex of remaining solitary breeders did not influence the ability of wolves to reproduce the season after breeder loss ($\chi^2 = 0.00$, $df = 1$, $P = 0.98$, $n = 86$; Table 6). Group size after breeder loss was greater for wolves that reproduced the following season ($\bar{x} = 6.46$, $SD = 5.24$) than for wolves that did not reproduce ($\bar{x} = 3.16$, $SD = 2.95$; Mann–Whitney: $U = 797.50$, $Z = -3.97$, $n_1 = 52$, $n_2 = 55$, 1-tailed $P < 0.001$).

For the combined data, we found that time interval did not influence the frequency of reproduction the next season ($\chi^2 = 3.34$, $df = 3$, $P = 0.34$, $n = 111$), which held for cases where solitary males ($G = 0.58$, $df = 3$, $P = 0.90$, $n = 42$) or female breeders remained ($G = 1.80$, $df = 3$, $P = 0.61$, $n = 44$). Frequency of reproduction the next season did not differ between sexes of remaining solitary breeders when the time remaining to the reproductive season was 1–3 months (Fisher's exact test: $P = 0.62$, $n = 18$), 4–6 months ($\chi^2 = 0.04$, $df = 1$, $P = 0.85$, $n = 25$), 7–9 months (Fisher's exact test: $P = 0.65$, $n = 20$), or 10–12 months (Fisher's exact test: $P = 1.00$, $n = 23$). Likewise, frequency of reproduction did

Table 3. Wolf pup fate classified by number and sex of breeders remaining and pup age at time of event in Europe and North America, 1970–2003 ($n = 84$).

Pup age (months)	Breeder(s) remaining	>1 pup survived	No pups survived	Unknown
0–2	F	2	1	1
	M	5	3	2
	Multiple ^a	1	0	0
	None	0	0	0
3–5	F	9	3	0
	M	7	1	0
	Multiple ^b	1	0	0
	None	1	0	1
6–8	F	10	0	0
	M	5	1	0
	Multiple ^c	1	0	0
	None	2	2	2
9–11	F	6	0	1
	M	2	2	3
	Multiple	0	0	0
	None	2	0	2
Unknown	F	3	0	0
	M	1	0	1
	Multiple	0	0	0
	None	0	0	0

^a F lost; 1 M and 1 F breeder remained.

^b F lost; 1 M and 2 F breeders remained.

^c M lost; 2 F breeders remained.

Table 4. Wolf pup fate in relation to group size ($n = 84$) and litter size ($n = 81$) at the time of breeder loss^a in Europe and North America, 1970–2003.

Variable	>1 pup survived	No pups survived	Unknown
Group size			
2	2	3	3
3	3	3	2
4	11	2	0
5	4	1	3
≥6	36	4	5
Unknown	2	0	0
Litter size			
1	3	4	2
2	11	3	3
≥3	41	6	8

^a Adjusted for known mortalities at time of breeder loss. Later pup mortality not included.

not differ between cases where one breeder had to be replaced versus situations where both had to be replaced for time intervals of 4–6 months (Fisher’s exact test: $P = 0.60$, $n = 30$), 7–9 months (Fisher’s exact test: $P = 0.08$, $n = 24$), or 10–12 months (Fisher’s exact test: $P = 0.17$, $n = 29$). However, when the next reproductive season was ≤ 3 months away, frequency of reproduction differed between cases where one breeder had to be replaced (58.3%, $n = 24$) versus cases where both breeders had to be replaced (20.0%, $n = 5$; Fisher’s exact test: $P = 0.01$, $n = 28$; Table 6).

We found that mean time to breeder replacement differed between small (≤ 75 wolves) recolonizing populations (19.1 months) and larger (> 75 wolves) populations (9.3 months);

Mann–Whitney: $U = 318.00$, $Z = -3.05$, $n_1 = 34$, $n_2 = 33$, $P = 0.002$); similarly, average times to next reproduction differed between small (22.6 months) and larger (12.1 months) recolonizing wolf populations (Mann–Whitney: $U = 258.50$, $Z = -3.26$, $n_1 = 33$, $n_2 = 30$, $P = 0.001$). For saturated versus small recolonizing wolf populations, we also found similar differences in times to breeder replacement (Mann–Whitney: $U = 313.50$, $Z = -2.81$, $n_1 = 34$, $n_2 = 31$, $P = 0.005$) and next reproduction (Mann–Whitney: $U = 333.50$, $Z = -2.05$, $n_1 = 33$, $n_2 = 29$, $P = 0.04$). However, we found no differences between large recolonizing and saturated wolf populations for times to breeder replacement (Mann–Whitney: $U = 504.50$, $Z = -0.10$, $n_1 = 33$, $n_2 = 31$, $P = 0.92$) or next reproduction (Mann–Whitney: $U = 377.00$, $Z = -0.88$, $n_1 = 30$, $n_2 = 29$, $P = 0.38$; Table 7). We found inverse relationships between the size of recolonizing populations and times to breeder replacement (Pearson correlation: $r = -0.37$, $P = 0.002$, $n = 67$) and next reproduction (Pearson correlation: $r = -0.36$, $P = 0.004$, $n = 63$; Fig. 1). Time to breeder replacement correlated strongly with time to next reproduction (Pearson correlation: $r = 0.97$, $P < 0.001$).

Impacts on Groups and Territories

In 47 of 123 cases (38.2%), groups dissolved and abandoned their territories after breeder loss (Table 8). Of dissolved groups, territorial wolves became reestablished in 25 cases (53.2%), and in an additional 10 cases (21.3%) neighboring wolves usurped vacant territories. The proportion of groups dissolving did not differ between sexes of remaining solitary

Table 5. Wolf group sizes and pup survival before^a and after^b breeders were lost in Europe and North America, 1970–2003.

Categories	>1 pup survive?	>1 pup survived						Before vs. after breeder loss	
		<i>n</i>	\bar{x}	SD	<i>U</i> ^c	<i>Z</i>	(1-tailed)	<i>Z</i> ^d	(1-tailed)
Pups									
Before loss	Yes	55	4.49	3.30	242.50	-1.82	0.034	-3.54	<0.001
	No	13	3.00	2.00				-3.20	<0.001
	Total	68	4.21	3.14				-4.74	<0.001
After loss	Yes	55	3.80	3.04	0.00	-5.65	<0.001		
	No	13	0.00	0.00					
	Total	68	3.07	3.12					
Ad-sized wolves									
Before loss	Yes	56	4.57	3.06	179.00	-2.95	0.002	-6.76	<0.001
	No	13	2.31	0.63				-3.28	<0.001
	Total	68	4.18	2.92				-7.75	<0.001
After loss	Yes	55	3.33	2.85	177.00	-2.90	0.002		
	No	13	1.23	1.01					
	Total	68	2.87	2.69					
All wolves									
Before loss	Yes	56	9.27	5.15	164.00	-3.09	0.001	-6.80	<0.001
	No	13	5.31	2.06				-3.12	<0.001
	Total	69	8.52	4.97				-7.39	<0.001
After loss	Yes	56	7.30	4.77	18.00	-5.34	<0.001		
	No	13	1.23	1.01					
	Total	69	6.16	4.93					

^a No mortalities included.

^b Includes all known mortalities after the event.

^c Mann–Whitney *U* test.

^d Wilcoxon signed rank test.

Table 6. Frequency of reproduction within wolf pack territories the season after breeder loss relative to time remaining to next season and number of breeders remaining in Europe and North America, 1970–2003 ($n = 120^a$).

Months to next season	Remaining breeder(s)	Reproduction next season?		
		Yes	No	Unknown
1–3	F	5	7	1
	M	4	2	2
	Multiple	0	0	0
	None	0	10	0
4–6	F	7	6	0
	M	6	6	0
	Multiple	1	0	0
	None	1	3	0
7–9	F	7	3	1
	M	5	5	2
	Multiple	1	0	0
	None	0	3	0
10–12	F	5	4	3
	M	8	6	0
	Multiple	1	0	0
	None	1	4	0

^a Excluding 10 cases where neighboring packs usurped territories and 4 cases with missing data.

breeders ($\chi^2 = 2.67$, $df = 1$, $P = 0.10$, $n = 94$). However, the proportion of dissolving groups differed ($\chi^2 = 30.01$, $df = 1$, $P < 0.001$) between cases where breeders remained (25.8%, $n = 97$) versus cases where breeders were absent (84.6%, $n = 26$). Group size influenced the frequency of group dissolution ($\chi^2 = 37.77$, $df = 5$, $P < 0.001$, $n = 115$; Table 8). Group size after breeder loss was smaller where groups dissolved ($\bar{x} = 2.36$, $SD = 3.18$) versus cases where groups did not dissolve ($\bar{x} = 5.75$, $SD = 4.74$; Mann–Whitney: $U = 660.00$, $Z = -5.10$, $n_1 = 42$, $n_2 = 73$, 1-tailed $P < 0.001$).

When we excluded cases where neighboring wolves usurped territories after breeder loss, wolves became reestablished in territories after an average time of 2.72 years ($SD = 1.88$, $n = 25$). After breeders were lost, group size differed between groups that budded or split ($\bar{x} = 9.43$, $SD = 5.74$, $n = 7$) and groups that did not bud or split ($\bar{x} = 5.36$, $SD = 4.50$, $n = 66$; Mann–Whitney: $U = 114.500$, $Z = -2.20$, $n_1 = 7$, $n_2 = 66$, $P = 0.03$).

DISCUSSION

We attempted to quantify and test hypothesized effects of the loss of breeding wolves on pup survival, reproduction, and wolf social groups and territories from data collected

under a variety of environmental conditions over varying periods in widely spread geographic localities. In addition, the resolution and coverage of data vary from study to study, which also imposed limitations on our analyses and conclusions. In spite of these drawbacks, our results have given us important insight into the responses of territorial wolves to the loss of breeders, which may be useful for managers that must consider wolf removal as a management tool in recolonizing populations.

Pup Survival

Evolutionary advantages associated with wolf social organization (Mech 1970, Mech and Boitani 2003, Packard 2003), fecundity (Mech 1970, Fuller et al. 2003, Packard 2003), juvenile precociousness and hardiness (Mech 1970, 1993; Packard et al. 1992; Packard 2003), and kin selection (Schmidt and Mech 1997, Mech et al. 1999) may explain why pups often survived breeder loss events, even from an early age. In most cases, >1 pup survived loss of breeders, even though litter sizes diminished afterward. Factors relating to the number of adult-sized wolves, along with pup age, seemed to influence the ability of pups to survive breeder loss events. Differences in pup survival between sexes of remaining breeders seemed to be related to differences in group size.

We found that the number of adult-sized wolves (including remaining breeders) and the presence of auxiliary nonbreeders positively influenced pup survival. Auxiliaries, or helpers, provide food and care for pups through kin-directed altruism (Harrington et al. 1983, Mech 1995b, Mech et al. 1999, Packard 2003). The positive influence of auxiliaries was illustrated in the Yellowstone Delta Pack where 7 pups were reared by 6 adult and yearling wolves after the mother died a few weeks after pups were born (Smith et al. 2001). Ballard and Stephenson (1982) found that pup survival was lower in packs with only one adult compared with packs with ≥ 2 adults. Helpers have been shown to increase offspring survivorship in other group-living species, including black-backed jackals (*Canis mesomelas*; Moehlman 1979), mongoose (*Mungo mungo*; Hedge 2005), and meerkats (*Suricatta suricatta*; Clutton-Brock et al. 2001).

Pup age was only a minor component in explaining why pups survived breeder loss. Juveniles are able to scavenge and hunt smaller prey and survive harsh weather conditions (Messier 1985, Mech 1993). Juveniles develop rapidly and they are sufficiently mobile to join packs on hunts by the age

Table 7. Time intervals (months) to breeder replacement ($n = 98$) and to next reproduction ($n = 92$) in pack territories by population type and size in Europe and North America, 1970–2003.

Population type	Breeder replacement			Next reproduction		
	<i>n</i>	\bar{x}	SD	<i>n</i>	\bar{x}	SD
Recolonizing (≤ 75 wolves)	34	19.09	19.50	33	22.58	19.47
Recolonizing (> 75 wolves)	33	9.27	12.11	30	12.08	11.70
Recolonizing (total)	67	14.25	16.90	63	17.57	16.97
Saturated	31	10.42	14.95	29	15.31	15.58
Total	98	13.04	16.33	92	16.86	16.49

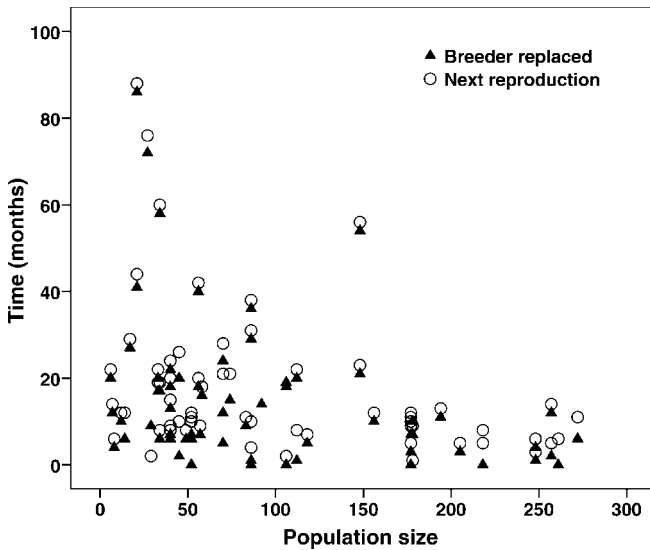


Figure 1. Relationship between size of recolonizing wolf populations and time intervals to breeder replacement ($n = 67$) and next reproduction ($n = 63$) in Europe and North America, 1970–2003.

of 4 months (Packard 2003). Our data include instances where solitary parents (2 F and 1 M) successfully raised pups from an early age without the assistance of other wolves (Boyd and Jimenez 1994). The youngest pups included in our study that survived the loss of both parents were 5 months old; pups aged ≥ 5 months survived the loss of both parents in 71% of cases ($n = 7$). Elsewhere, pups have been shown to survive without parents from the age of 4 months (Fritts et al. 1984, 1985; Packard 2003).

Food availability has been shown to positively influence pup survival (Fuller et al. 2003), and Harrington et al. (1983) suggested that it was more important than the presence of auxiliaries in packs. However, the ability of packs to kill prey also should influence the ability of pups to survive, and our results indicated that the number of adult-sized wolves in packs benefited pup survival. Sand et al.

(2006) suggested that the ability of wolf packs to effectively kill prey may be dependent upon the presence of the breeding pair, because pups do not contribute substantially to the outcome of hunts (Mech 1966, Haber 1977, Mech and Peterson 2003). Similarly, Funston et al. (2001) demonstrated that large groups of adult female lions (*Panthera leo*) were more successful than smaller female groups with subadults large cubs, or both in killing medium-sized prey. In addition, small groups may have to compete to a large extent with scavengers (Peterson and Ciucci 2003, Vucetich et al. 2004), which may, in turn, have adverse effects on survival of pups.

Reproduction

We found that wolves only reproduced in 47% of cases in the season after breeder loss. In contrast, wolf pairs normally produce pups every year in thriving populations (Fritts and Mech 1981, Mech and Hertel 1983, Peterson et al. 1984, Mech and Boitani 2003). The loss of one breeder was more easily mitigated than the loss of both, in terms of breeder replacement and subsequently the ability of wolves to reproduce the next summer.

The time interval for replacement of breeders and next reproduction was much longer for small recolonizing populations compared with either larger recolonizing or saturated wolf populations. The shorter time interval in larger recolonizing and saturated populations may be due to the supply of dispersing wolves or nonterritorial floaters, which is presumably higher in larger populations and is probably a key factor influencing replacement of breeding wolves (Fuller et al. 2003). Breeders are usually replaced by unrelated adults (Peterson et al. 1984, Messier 1985, Stahler et al. 2002); in some instances, pack members can usurp breeder positions (Mech and Hertel 1983, Mech 1995b). Although wolves generally avoid incestuous mating, it can occur (Peterson et al. 1984, Mech 1995b, Smith et al. 1997, Mech and Boitani 2003). In Scandinavia, incestuous breeding occurred when packs were isolated and the

Table 8. Group and territory cohesion relative to the number and sex of remaining breeders and postloss group size in Europe and North America, 1970–2003 ($n = 123^a$).

Variable	Group dissolved			Group remained		
	Territory abandoned ^b	New group formed	Territory usurped ^c	Territory intact	Territory split	Territory shifted
Surviving breeder						
F	3	4	2	32	5	1
M	2	10	4	30	1	0
Multiple	0	0	0	2	1	0
None	7	11	4	4	0	0
Postloss group size						
0	4	6	4	0	0	0
1	3	6	3	8	0	1
2	0	2	0	9	0	0
3	1	1	1	8	1	0
4	1	2	0	11	1	0
≥ 5	3	4	1	29	5	0
Unknown	0	4	1	3	0	0

^a We excluded 2 cases involving packs taken into captivity.

^b Includes 3 cases where all wolves were removed.

^c Through territory expansion by neighboring wolves.

population was very small (Wabakken et al. 2001, Vilà et al. 2002, Liberg et al. 2005).

We have seen that population size influences replacement of breeders and subsequent reproduction in territories. It is probable that proximity of other wolf territories, along with the number of solitary, dispersing wolves, will influence the frequency with which lost breeders will be replaced. Fuller et al. (2003) indicated that isolated packs generally had a lower chance of persisting than those near other packs. In Alaska, USA, and in Canada, local wolf populations that had nearly been eliminated through intensive control measures rebounded within 2–4 years through the immigration of breeding wolves from surrounding areas (Gasaway et al. 1983; Ballard et al. 1987; Potvin et al. 1992*a, b*; Hayes and Harestad 2000). In contrast, the Scandinavian wolf population was relatively isolated from the larger source population in Finland and Russia (Wabakken et al. 2001, Vilà et al. 2002, Flagstad et al. 2003, Liberg et al. 2005, Linnell et al. 2005), and during the early phase of recovery dispersers sometimes settled long distances from established territories through leaping presaturation dispersal (Wabakken et al. 2001). Wolves displayed similar dispersal patterns in recolonizing populations in Montana (Boyd et al. 1995) and Wisconsin (Wydeven et al. 1995). In such situations, it may take years for solitary adults to find new mates.

Groups and Territories

Removing breeders may disrupt packs and scatter remaining wolves or subdivide existing wolf territories with the effect of increasing wolf densities locally (Ballard and Stephenson 1982). In our study, wolves remained in territories after breeders were lost in 62% of cases. Of those territories that dissolved, wolves later became reestablished in 74% of cases, either through recolonization or invasion by neighboring territorial wolves. We found that budding or splitting occurred in larger packs, which was similar to results reported previously (Hayes et al. 2000, Mech and Boitani 2003). Mech and Boitani (2003) speculated that packs split when 2 related breeding pairs are present in the same pack. Splitting of related wolves into new territories ensures a division of resources such that competition between kin is avoided (Mech 1970, Mech and Boitani 2003).

MANAGEMENT IMPLICATIONS

At some point, managers of recolonizing wolf populations may need to remove wolves to reduce conflicts with local human populations. We recommend that managers carefully evaluate the possible impacts of lethal control on territorial wolves relative to ethical and biological considerations. From a strictly humanitarian viewpoint, managers should prioritize removal of solitary wolves or territorial pairs because it can be difficult to selectively remove nonbreeders from packs. However, where management goals dictate that packs with pups must coexist in proximity to humans and their activities, conflicts may be reduced by allowing removal of some pack members. Because there is a risk that breeders can be removed in such scenarios, managers should attempt to minimize pup mortality, social disruption, and breeding

interruption when managing reproductive packs. Therefore, we recommend that managers only remove wolves from reproductive packs when pups are >6 months old and packs contain ≥ 6 members (including ≥ 3 adult-sized wolves). Ideally, such packs should be close to neighboring packs and occur within larger (≥ 75 wolves) recolonizing populations.

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