Chapter 6

Outcomes of Hard and Soft Releases of Reintroduced Wolves in Central Idaho and the Greater Yellowstone Area

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Prior to European settlement, gray wolves (*Canis lupus*) were present over most of North America and virtually all of what would become the contiguous 48 states, including the northern Rocky Mountain region (Young 1944). By about 1930 they were eradicated from the American West (Lopez 1978; McIntyre 1995; Hampton 1997). Restoration of wolves to portions of the northern Rocky Mountains, particularly Yellowstone National Park (YNP), was advocated for several decades (Leopold 1945; Weaver 1978; Klinghammer 1979) until the U.S. Fish and Wildlife Service (USFWS) reintroduced a "nonessential experimental population" to central Idaho and YNP (Figure 6.1).

Gray wolves have been relocated under a variety of circumstances (Merriam 1964; Mech 1966; Henshaw and Stephenson 1974; Weise et al. 1975; Henshaw et al. 1979; Fritts et al. 1984, 1985; Bangs et al. 1995, 1998; Klein 1995), but no large-scale restoration attempt using wild wolves had occurred prior to this program. Although two fundamental strategies are available—

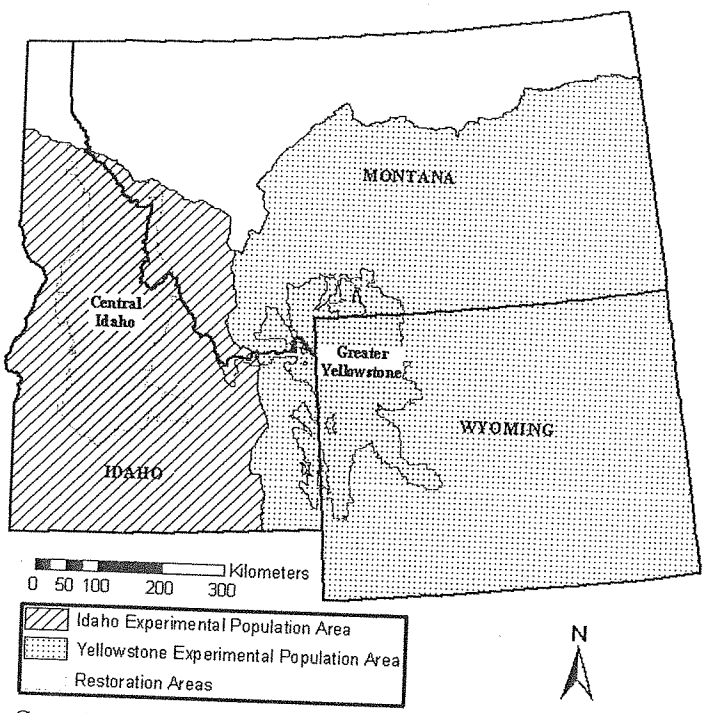


Figure 6.1. Central Idaho and Greater Yellowstone gray wolf restoration (shaded) and experimental population areas.

"hard" release and "soft" release—both were unproven for establishing a wild population. Hard release is an immediate and direct release into the new environment; soft release is a delayed release from a temporary enclosure (Fritts 1993). The degree of stimulation by humans at the time of release is a major variable that distinguishes these approaches. Soft release involves construction of acclimation pens and temporary husbandry. The two approaches differ as well in their demands of personnel, facilities, and cost. Hard releases have been the most common technique for wildlife reintroduction throughout North America, though with variable success (Griffith et al. 1989).

The objective of the authors and the agencies we represented was to establish populations of wolves in central Idaho and the Greater Yellowstone area as quickly as practical. In doing so we tested both methods, hard and soft release, to refine and optimize subsequent releases and to gain information that will benefit future wolf reintroductions. In this chapter we examine wolf reintroduction design and the outcomes of the hard and soft releases in central Idaho and YNP.

Restoration Areas

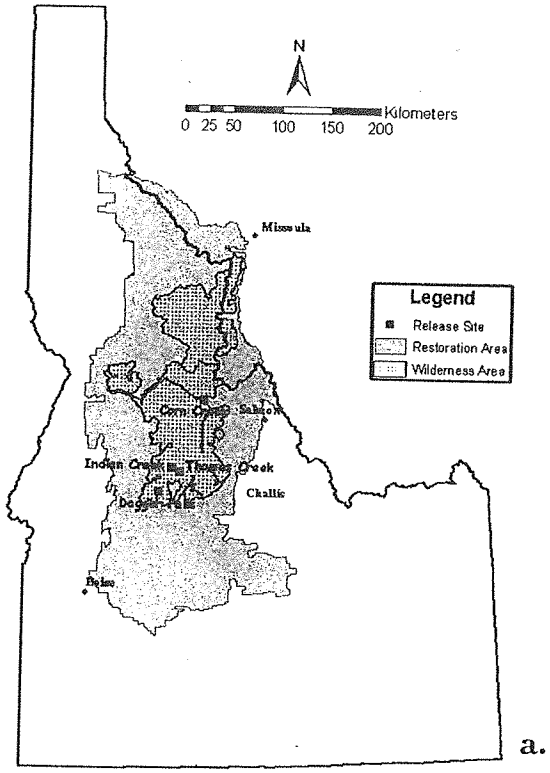
The central Idaho area is about 53,613 km^2 of rugged mountains (99 percent federal ownership), with almost 16,200 km^2 of designated wilderness and a human density of 1 person/km^2. Wild ungulates in the area include mule deer (*Odocoileus hemionus*), white-tailed deer (*O. virginianus*), elk (*Cervus elaphus*), mountain goat (*Oreamnos americanus*), bighorn sheep (*Ovis canadensis*), and moose (*Alces alces*). Mountain lion (*Puma concolor*), black bear (*Ursus americanus*), and coyote (*Canis latrans*) are sympatric. Virtually all motorized activity in wilderness areas is prohibited.

The Greater Yellowstone area covers 64,750 km^2 (76 percent federal ownership). YNP at the center is 9000 km^2 and is surrounded by six national forests. Average human density is about 2 persons/km^2. Wild prey include elk, mule and white-tailed deer, moose, bighorn sheep, bison (*Bison bison*), pronghorn (*Antilocapra americana*), and mountain goats. Black bear, grizzly bear (*Ursus arctos*), mountain lion, and coyote are sympatric.

The cores of both the central Idaho and Greater Yellowstone areas do not support livestock and are some of the most remote lands in the United States outside of Alaska. Low human densities, public landownership, and large size make them refugia for large carnivores. Hunting and livestock production do not occur inside YNP, and the number of people in the park fluctuates seasonally. Lamar Valley in the northeastern part of YNP was selected for initial releases because of the high density of ungulates, presence of an access road, and records of wolf activity before wolves were eradicated (Weaver 1978).

Approach

In early 1993 we surveyed 53 biologists who had experience with wild or captive wolves and asked them how a reintroduction might be carried out. Although most recommended some form of soft release, the span of opinions in the 31 responses, together with the scarcity of reintroduction experience, made it clear that whatever approach we selected would follow an adaptive management strategy. Any perception of insurmountable problems or inadequate planning was likely to bring pressure to terminate the project by those already opposed to it (Fischer 1995). Hard release of individual wolves was planned for Idaho; soft release of small family groups was used in YNP. Wild captured wolves were translocated from Canada in areas with habitat similar to restoration areas (Bangs and Fritts 1996; Fritts et al. 1997) and were free of rabies, tuberculosis, and brucellosis (see Case 2 in this volume), and contained few livestock.



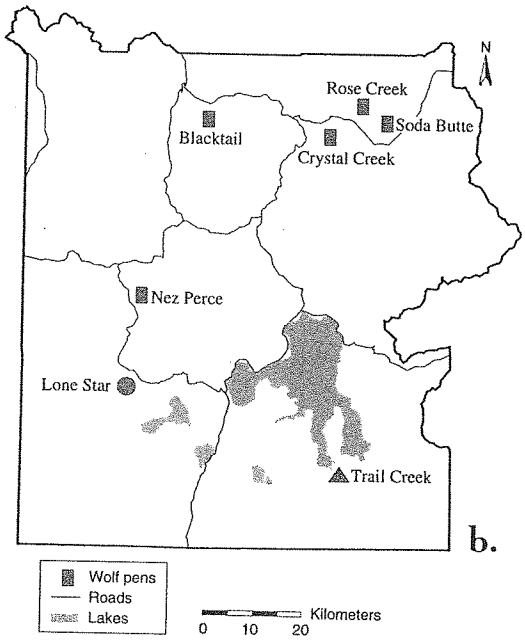


Figure 6.2. *a.* Locations of hard-release sites in central Idaho in 1995 and 1996. *b.* Locations of acclimation pens where wolves were soft-released in Yellowstone National Park in 1995 and 1996. The dot represents a temporary enclosure from which the Lone Star pair was released. The triangle represents a pen used for the second release of the Soda Butte pack. After denning on private land north of the park, the wolves were captured, returned to the park, acclimated, and released again.

Release sites in central Idaho offered aerial or ground access and had year-round populations of elk and deer (Figure 6.2a). Wolves brought to Idaho generally were nonbreeding adults and yearlings from the same Canadian packs that provided wolves for YNP. We did not view the relatedness of some wolves as an advantage or disadvantage so long as they were from several packs.

Three pens were constructed in YNP in summer 1994 using a 3-m-high, 9-gauge, chain-link fence with an inward overhang and a 1.2-m ground apron (Figure 6.2b). These pens were 0.4 to 0.8 ha in size and were built at least 8 km apart (Phillips and Smith 1996). Two additional pens were constructed for 1996 releases. All sites but one were accessible by roads.

1995 RELEASES. In January 1995, 29 wolves were captured by helicopter darting, net-gunning, and live-snaring near Hinton, Alberta, and transported to central Idaho (1000 km) and YNP (1100 km) via cargo aircraft and ground transport (Fritts et al. 1997). All wolves were radio-collared, marked with plastic numbered tags in both ears, and also marked with PIT tags (passive integrated transponders) (Bangs and Fritts 1996; Fritts et al. 1996, 1997). All wolves were treated identically during transport regardless of release method.

Fifteen wolves from seven Canadian packs were sent to the Idaho release sites in January 1995 and immediately released. Four wolves spent nearly 90 hours in their crates due to bad weather and a delay caused by an American Farm Bureau legal challenge to the program. The first four Idaho wolves were released at Corn Creek along the Main Salmon River. The eleven that followed were set free at Thomas Creek and Indian Creek along the Middle Fork of the Salmon River (Figure 6.2a). No food was provided at the release sites.

Fourteen wolves in three groups (from four Canadian packs) were shipped to YNP in January 1995. The first eight spent approximately 40 hours in their crates due to the Farm Bureau's legal challenge. YNP groups consisted of three, five, and six wolves and were held at the Rose Creek, Soda Butte, and Crystal Creek pens, respectively (Table 6.1; Figure 6.2b).

Wolf husbandry is described by Phillips and Smith (1996, 1997) and by Johnson (Case 2 in this volume). In most instances wolves adapted to the pen within one week, and no significant conflict between wolves was known to occur. Some wolves damaged their teeth biting the fence when humans approached the pens. Tooth damage occurred primarily among adult wolves of both sexes, but there was no indication that killing ability or survival in the

Table 6.1. Basic Information on Packs of Wild Wolves S in Yellowstone National Park in 1995 and 1996

Pack	*Number of individuals*	*Natural pack?*[a]	*Bred in captivi before release?*
1995: Crystal Creek	6	natural	no
Rose Creek	3	artificial	yes
Soda Butte	5	natural	yes
1996: Nez Perce	6	natural	yes
Lone Star	2	artificial	yes
Chief Joseph	4	artificial	no
Druid Peak	5	artificial	no

[a] "Natural pack" means that all members were part of the same wild pa in Canada. "Artificial" means that pack members were from different v were penned together and released together in Yellowstone.
[b] A pup separated from the breeding pair after six days.
[c] A pup separated from the group the first day after release.
[d] After several weeks with the pack, the alpha female began making lo and began traveling alone in mid-August.

wild was affected. The wolves ate the food provided, howled, bred in captivity. Acclimation time averaged 67.9 days in wolves took an additional 2 to 10 days (a mean of 5.7 days) t they had been opened by opening the gate or removing a sec

1996 RELEASES. Wolves were captured in January by helico the vicinity of Fort St. John, British Columbia. Altogether, eight packs were transported to central Idaho (1400 km) and Y (Bangs and Fritts 1996; Fritts et al. 1996). Twenty wolves snowmobile to a single release site at Dagger Falls along the the Middle Fork of the Salmon River in Idaho (Figure 6.2 included three 9-month-old pups, two of which were litter n released with an adult female from the same wild pack.

Deliveries of eleven and six wolves were made to YNP on 27 January. Seventeen wolves from four packs were placed i YNP during January 1996. Group sizes were two, four, five, (Table 6.1). The Nez Perce pack included the breeding male a a wild pack; the other three groups (Lone Star pair, Druid Pe Joseph pack) included breeding female wolves and breeding a from different packs.

The Druid Peak pack and the Nez Perce pack were allowed to exit the pens in which they were acclimated: one in northern YNP (the old Rose Creek pen) and the other in the Firehole River–Nez Perce Creek area (Figure 6.2b). We chose not to release the Chief Joseph pack and the Lone Star pair from their pens inside the territories of packs released in 1995. After being acclimated in the Crystal Creek pen, the Chief Joseph pack was transported to the recently vacated Nez Perce pen, 53 km to the southwest, and then allowed to exit after recovering from the anesthesia. The Lone Star pair was immobilized and left to awaken in an incomplete temporary enclosure 61 km to the southwest (Figure 6.2b). In 1996 the acclimation time was 72 days, and the wolves took an additional 0 to 12 days (mean 4.2) to exit the pens.

Monitoring

Most radio-tracking in Idaho was done in a Cessna 206 fixed-wing aircraft. All locations were recorded with GPS units. Funding limitations restricted the frequency of flights to about one or two per month. Wolves were located from the ground as well during routine fieldwork. Wolves in YNP were located by aircraft as often as weather permitted for two weeks, then twice per week until midsummer, and then once per week thereafter. Some packs were observable from vantage points in the park.

Data Analysis

We examined initial and ultimate travel direction from release sites and distance moved from release sites by 25 June, 15 September, at home range establishment, and at the "ultimate" location. "Initial direction" was the first known location away from the release site (or from a point within 2 km of the release site) that was followed by a pattern of movement away from the site (Fritts et al. 1984). "Ultimate direction" was the compass bearing from the release site to the site of mortality, recapture (management action), last known location, or the approximate center of an established home range (Fritts et al. 1984). Ultimate distance was the straight-line distance between those points. Each wolf was treated as a separate and independent observation in the statistical analysis even though many appeared to be traveling together.

We examined ultimate distance with analysis of variance using three factors as independent variables at two levels: year of reintroduction (1995, 1996), restoration area (Idaho, YNP), and sex. We did not use an age variable in the ANOVA model because the number of known yearlings in Idaho was small and visual comparison of adults and yearlings suggested no difference

between the groups. Moreover, a *t*-test revealed no difference in ultimate distance between YNP adults and yearlings.

Variance in ultimate distance between wolves at different factor levels (1995 vs. 1996), for example, was unequal due to outliers. To meet the ANOVA assumption of homogeneity of variances among groups (assessed using a Levin's test), the square root of ultimate distance (SQRTD) was used as the dependent variable. ANOVA was not performed on the June and September measures because those metrics were too similar to the ultimate distance to warrant separate statistical analysis. We compared distances from release sites to centers of territories established in the two restoration areas by using a Mann-Whitney *U*-test. Variances for the two groups were equalized using a $\log_{10}$ transformation.

Directions from release sites were evaluated using statistics for circular distributions (Batschelet 1981; White and Garrott 1990). We calculated mean angles, mean bearings, and angular deviation (*s*) for the initial and ultimate azimuths of wolf travel (Batschelet 1981). We evaluated the extent that directions deviated from a uniform circular distribution by calculating *r*—a measure of concentration of azimuths scaled from 0 (bearings dispersed) to 1 (highly concentrated)—and compared them with critical values (Batschelet 1981). If wolf movements were nonrandom, we further tested the hypotheses that initial and ultimate directions of wolf movements were toward the capture site in Canada using a *V*-test (Batschelet 1981; White and Garrott 1990). We used direction to a point halfway between the two capture sites in Alberta and British Columbia for those analyses.

We tested for associations between directions (both initial and ultimate) and year, restoration area, and sex by using log-linear analyses. This initial step was used to determine differences in the direction of wolf movements at different levels of these three factors. Where movements were significantly ($p < 0.05$) associated with a factor (direction varied by restoration area, for instance), we calculated circular statistics separately for each level of the respective factor (Idaho separately from YNP, for instance). For that analysis, initial travel directions were grouped into two categories: north (271–90°) and south (91–270°).

We used two-tailed Fisher's exact tests to validate the log-linear analysis. Expected cell counts used in calculating chi-square statistics for log-linear analysis should be five or greater, but ours were usually less than five. We applied Fisher's exact tests to all possible 2 × 2 contingency tables generated from combinations of restoration area, sex, and year to identify any two-way or three-way interactions that remained undetected in log-linear analysis.

Due to a small sample of pups released in Idaho, we did not use wolf age

as a variable in the analysis. However, we were able to test for differences in travel direction by age (adults versus pups; north versus south) for YNP releases using a two-tailed Fisher's exact test prior to the log-linear analysis. Pups were captured in Canada at eight or nine months of age and released before their first birthday. These individuals were either pups (Idaho) or yearlings (YNP) when their initial directions were measured. Typically, wolves captured as pups in Canada were yearlings when their ultimate distances were measured.

We also compared survival and mortality causes, sociality (persistence of packs released in YNP and ability to form packs in Idaho), home range establishment, reproduction, and livestock killed. Information on depredations was collected in coordination with USDA/APHIS, Wildlife Services. When wolves were relocated to acclimation pens because they killed or threatened livestock, ultimate distance and ultimate direction were measured using the site of recapture.

Results

We analyzed two release protocols in different areas, both of which ultimately succeeded. Comparing behavior of wolves in the two areas was not straightforward, especially in view of the well-documented individualistic behavior of wolves (Fritts et al. 1984; Mech 1987). Nonetheless, there were certain commonalities among wolves and restoration areas and also some distinct differences. Although wolves that were hard-released into central Idaho and soft-released into YNP established populations, behavioral processes for achieving population status were dissimilar in many respects, corresponding to the challenges the wolves had to overcome.

Direction and Distance Moved

Fifty of the 65 wolves (77 percent) initially moved northward (271°–90°). Initial direction was not known for one Idaho wolf. Mean travel direction for all wolves was 36° and was concentrated about 50° east of the homeward direction (Figure 6.3).

In YNP, there were no significant differences between adults and pups in initial travel direction ($p = 0.45$). Because the initial movements of three Idaho pups did not appear to differ from those of Idaho adults, we pooled wolves by age in subsequent tests. Log-linear analysis indicated that directions varied by sex (partial association chi square: 4.1; $p = 0.043$), but not by year, restoration area, or three-way interactions ($p > 0.15$). Analysis of 2×2 tables using Fisher's exact tests supported this result with one exception:

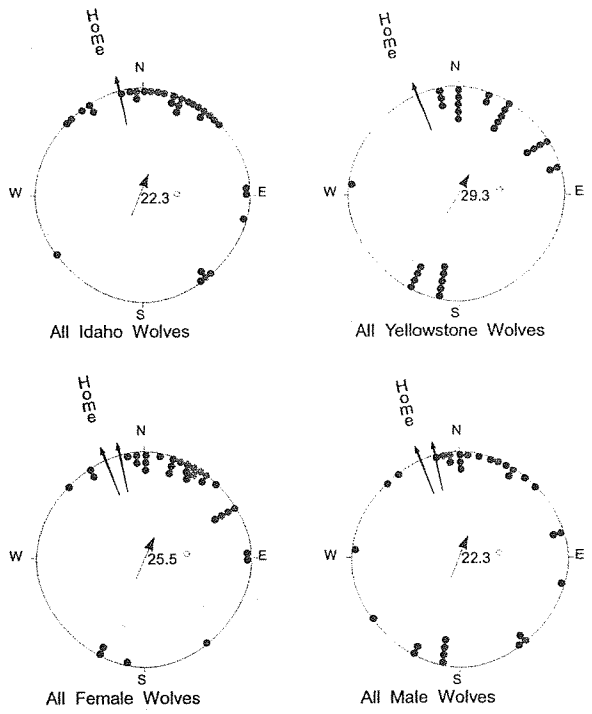


Figure 6.3. Direction of initial movement from release sites by wolves released in central Idaho and Yellowstone National Park in 1995 and 1996. Different release sites were used in each restoration area; release sites were standardized for measurement of directions and distances. Arrows indicate mean azimuths (travel direction). Differences between sexes were significant, whereas there were no significant differences by restoration area.

Idaho wolves initially moved northward more than YNP wolves in 1995, although this association between restoration area and direction was weak ($p = 0.08$). Thus we calculated separate sets of circular statistics for males and females, pooling restoration areas and years (Table 6.2).

Initial direction moved by females in Idaho and YNP was nonrandom ($p < 0.001$) and directional ($p < 0.0001$) toward home in Canada (Figure 6.3). Direction taken by males was random ($p = 0.084$) with a weak trend ($p = 0.047$) toward the capture site (Figure 6.3). This finding applied to males during both years and at both restoration areas, except that Idaho males tended to move slightly more northerly than YNP males in 1995 (Table 6.2a).

Wolves released in Idaho traveled extensively within a few weeks of

Table 6.2. Analysis of Circular Statistics

A. INITIAL AZIMUTH (INITIAL DIRECTION TRAVELED FROM RELEASE SITE) OF ALL RELEASED WOLVES

	Mean bearing	*Angular deviation*	*r (p value)*	*V test u (p value)*
Females	25.5°	53.5°	0.65 (<0.001)	3.81 (<0.0001)
Males	22.3°	91.9°	0.28 (0.084)	1.68 (0.047)

B. ULTIMATE AZIMUTH (DIRECTION FROM RELEASE SITES) OF ALL RELEASED WOLVES

	Mean bearing	*Angular deviation*	*r (p value)*	*V test u (p value)*
Idaho	29.6°	73.1°	0.443 (0.001)	2.73 (0.0032)
Yellowstone	168.7°	94.5°	0.257 (0.132)	no test

release. Most moved a short distance immediately after release and then remained in one area for one to three weeks before exploring widely. There was considerable variation in the timing of movements away from release sites. Male B-2 remained near the site for several weeks, for example, while female B-10 moved dozens of kilometers immediately after release. Female B-13 moved 88 km east of her release site in nine days before being illegally shot. By June, Idaho wolves averaged 84 km from release sites in 1995 (range: 35–223 km) and 79 km from their release sites in 1996 (range: 6–236 km).

For the first two weeks after release, most YNP wolves stayed near their pens and remained grouped. All packs but one tended to linger near their pens before traveling more widely. By June 1995, some 12 free-ranging Yellowstone wolves averaged 22 km (range: 3–34 km) from their release sites. Movement from release sites was higher in 1996 (average in June: 55 km; range: 22–125 km) because the breeding female and three female siblings from the Nez Perce pack (the only intact pack brought to Yellowstone in 1996) traveled 48 km the first day. They continued traveling to the northeast for four days, averaging 53 km/day before temporarily restricting movements to an area near Red Lodge, Montana. From there, the adult female continued northward, leaving the younger wolves behind.

Postrelease behavior and movements of the 1995 YNP wolves were categorized into three periods: exploration near release pens (2–14 days); wide-ranging exploration (3–35 days); and return to the area around the pen and home range establishment (more than 35–40 days). During week 3 of 1995, all three groups made exploratory moves to the northeast and north that extended for 80, 60, and 32 km. Movements of three of the four 1996-

released groups were similar, with the exception of the Nez Perce pack. Five of the seven groups that survived the early release period established territories in the vicinity of their acclimation pens, including one (the Rose Creek pack) that was recaptured and returned to the park (Phillips and Smith 1996, 1997). The Lone Star pack (a pair) had no chance to establish nearby because of the female's death and the male's dispersal.

As in late June, measures of distances from release sites at later periods were consistently greater and more variable for Idaho wolves than for YNP wolves. By mid-September of the release year Idaho wolves averaged 88 km (range: 17–224 km) from their release sites compared to 31 km (range: 3–120 km) for YNP wolves. For ultimate distance, averages were 98 km (range: 9–282 km) for Idaho wolves and 59 km (range: 2–166 km) for YNP wolves. Following initial northerly movements, Idaho wolves moved randomly (sometimes in a zigzag fashion through heavily dissected drainages) for the first three months. For several individuals, movements encompassed much of the central Idaho restoration area. Although patterns of movements by single wolves appeared to be random and unpredictable in direction and purpose, they often re-used travel routes to and from familiar areas separated by great distances. Single wolves moved long distances in short time periods to areas used by other wolves (related or not). Wolves visited familiar areas repeatedly. Those visits were often brief (a matter of days) and separated by extensive movements between visits.

The movements of female B-10 were the most extensive: a minimum of 800 km accumulated over 14 radiolocations in five months. Male B-2 moved only 200 km over a similar period. Only one wolf completely left the Idaho experimental population area: male B-14 traveled throughout central Idaho for almost three years before joining a nonreintroduced resident female and her two pups 258 km away in western Montana. A separate analysis, using all radio-fixes, showed that wolves drifted farther from their release sites in the first five or six months of freedom (Mack and Laudon 1998).

Movements of unpaired wolves in Idaho were similar to the wide-ranging movements of lone wolves elsewhere in North America (Fritts and Mech 1981; Mech 1987). The area used by male B-14 covered at least 18,130 km^2 from 1995 to 1998 (Mack and Laudon 1998). Most long-range movements took wolves well north of release sites but still within the experimental population area. After four to six months, the extensive and unpredictable movements became more localized as pairs formed. The change in pattern after pairing was typically abrupt, as is true for newly formed pairs elsewhere (Rothman and Mech 1979; Fritts and Mech 1981). By November 1996,

Idaho wolves were distributed over 47,170 km^2 (Mack and Laudon 1998) whereas Yellowstone wolves were found within 12,690 km^2.

We found no differences in ultimate distance between YNP pups and adults (p = 0.83), so their data were pooled in the ANOVA. That analysis indicated there were significant differences (p = 0.01) in ultimate distances between restoration areas, but no differences between sexes and years (p > 0.24; Figure 6.4). A significant area-year interaction (p = 0.042) indicated that the differences in restoration area were contingent on the year. There were significant differences in ultimate distance by reintroduction area (p = 0.004) in 1995 and no difference by sex (p = 0.62). There were no significant differences in ultimate distance between areas and sexes in 1996 (p > 0.61). Removing the outlier Nez Perce pack from these analyses resulted in a highly significant difference between Idaho and YNP wolves (p = 0.0021) (Figure 6.4).

There were no significant differences between adults and pups in ultimate

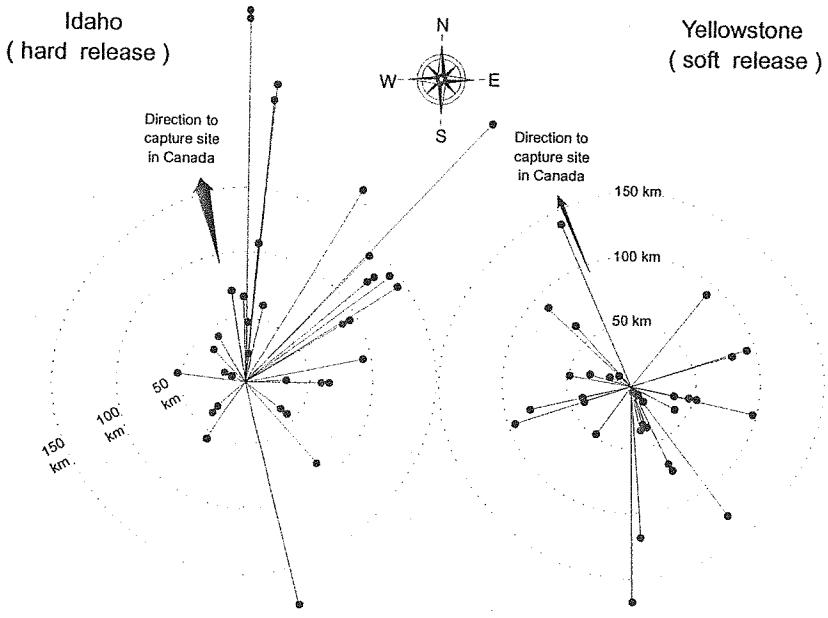


Figure 6.4. Ultimate direction and distance for wolves released in central Idaho and Yellowstone National Park in 1995 and 1996. Multiple release sites were used in each area; release sites are standardized for measurement of directions and distances.

direction of Yellowstone wolves ($p = 1.0$) and no differences in Idaho adults and pups based on a subjective inspection of the data. Log-linear analysis indicated that ultimate direction varied by restoration area (partial association chi square = 14.1; $p = 0.0002$), but not by sex, year, or three-way interactions ($p > 0.34$). Analysis of 2×2 tables using Fisher's exact tests supported this result. Therefore we calculated circular statistics separately for the two sites, pooling data by sexes and years. The results indicate that ultimate directions for Idaho wolves were nonrandom ($p < 0.001$) and significantly ($p < 0.0032$) toward the capture site in Canada (Table 6.2b; Figure 6.4). Ultimate directions for YNP wolves were random ($p > 0.132$). (Thus, no V test was made for movement toward the capture site). Based on angular deviation, directions of YNP wolves were more variable than those of Idaho wolves.

Survival and Mortality

All but two wolves survived handling, holding, transport, and reintroduction. One was killed by an errant dart during capture in Alberta and the other was euthanized for mandatory rabies tests after biting the thumb of a biologist. Because they were not confined in pens, Idaho wolves entered the wild with less tooth damage than those in YNP.

We were able to account for the fates of all YNP wolves and all but two Idaho wolves. This was possible due to the intensity of monitoring, communication with local residents, and coordination between the various government agencies involved in the program. One pup starved in Idaho; the other two associated with an adult and survived. Including YNP, the other 65 wolves found sufficient food despite the unfamiliar environment. At least 31 of 35 Idaho wolves (88.6 percent) and 25 of 31 YNP wolves (80.6 percent) survived for 12 months after their release. Three years after their release, a minimum of 29 Idaho wolves (82 percent) were still alive, whereas 13 Yellowstone wolves (42 percent) were alive.

There were 21 known deaths after three years: 4 in Idaho and 17 in YNP (Table 6.3). Illegal shooting and depredation control were more common in the greater Yellowstone area. Fourteen of the 21 deaths (67 percent) were human-related, mostly due to illegal shooting and government livestock depredation control. Differences in accessibility by humans probably accounted for the difference in illegal shooting between the two areas. Because wolves were released in remote areas where contact and conflicts with humans were less likely, humans caused a lower proportion of all mortalities in both areas than was the case with naturally recolonizing wolves in Montana (Bangs et al. 1998).

Intraspecific aggression among established packs increased mortality in

Table 6.3. Causes of Mortality Among Reintroduced Wolves During the First Three Years

Cause of mortality	*Central Idaho*	*Yellowstone*
Illegally shot	1	7
Depredation control	1	4
Vehicle collision	0	1
Other wolves	0	2
Accident	0	2
Starvation	1	0
Cougar	1	0
Other natural cause	0	1

YNP. The alpha male from the Crystal Creek pack and a yearling and two-year-old female with a litter from the Rose Creek pack were killed by the Druid Peak pack. In addition, the Druid Peak pack likely killed a litter of the Crystal Creek pack.

Sociality

In Idaho there were nine instances in which several pack members (two to six) were released from the same Canadian pack. We documented subsequent associations between former pack members in five of these nine related groups. Interactions were intermittent, lasting only a few days, occurred more often within nine months of release, and rarely occurred between more than two former pack members at one time. No Idaho wolf paired with a former pack member. The most frequent and long-term interaction was between an adult female and two pups that remained in contact through October of the release year. Later, two of these three wolves were known to have pair-bonded with wolves that originated from other packs.

Wolves in Idaho formed pairs in as little as 16 days in 1995. By the end of September 1995, three pairs had exhibited localized movements. The first pairing of Idaho wolves in 1996 occurred 63 days after release, and this pair established a territory less than 60 days later. Eight pairs formed in 1996 included two pairings of animals released in 1995. Pairs produced litters in their first breeding season after pairing in 82 percent of the cases. The number of pairs and packs producing pups increased to ten in 1998 (Figure 6.5). By fall 1998, all the surviving females of breeding age had paired and formed packs. Idaho packs increased from 11 in November 1996 to 14 in 1998. Pairs in Idaho were permanent unless one member died.

After release, six of seven YNP groups stayed together and five survived

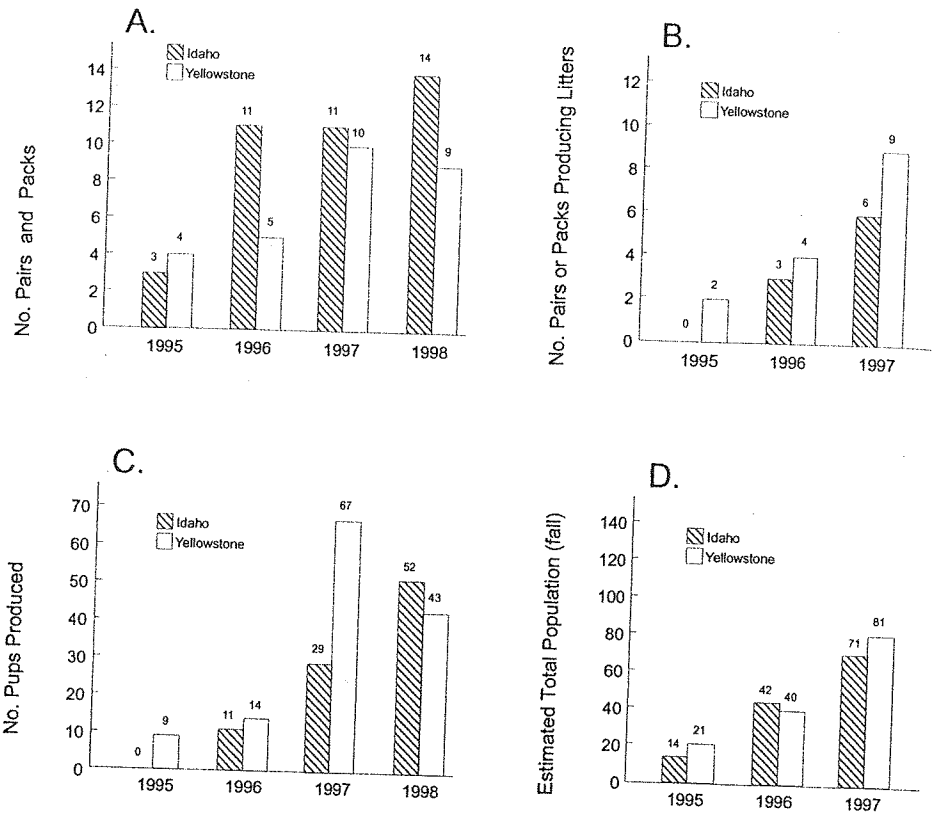


Figure 6.5. Performance of the newly established wolf populations in central Idaho and the Greater Yellowstone area through 1998: *a.* Number of pairs and packs in the populations. *b.* Number of pairs or packs producing pups. *c.* Number of pups produced. *d.* Estimated total population of wolves in each restoration area.

to establish actual or potential breeding units. One of our greatest concerns was that penned wolves, especially those from different packs, would separate and disperse after release. Nonetheless, the four groups that were made up of wolves from different packs remained together after release and two of them bred in captivity (Phillips and Smith 1996). Interestingly, the only group in which the alpha pair separated was the naturally occurring Nez Perce pack. In that instance, the alpha female and two younger females immediately departed the pen, leaving the males to exit later. Two subadults left other packs within a week after release. All other separations occurred after several months. Although we considered this normal behavior, it could have been hastened by confinement with conspecifics. Reintroduced wolves formed

three new pairs in 1996, and all packs reproduced in 1997. By the end of 1998, 9 of 11 packs in the Greater Yellowstone area were the result of reintroduced wolves; the other two packs involved the offspring of reintroduced wolves. Six other reintroduced wolves dispersed and failed to pair because of human-caused mortality.

Home Range Establishment

Both hard- and soft-released wolves settled into home ranges, but those that were soft-released established home ranges sooner. In Idaho, home range establishment coincided with pair formation; home ranges were established 27 to 256 km (mean: 92 km) from release sites. YNP packs that stayed together took about a month to settle into home ranges that became centered 4 to 23 km from release pens (mean: 14.5 km; five pack territories included their release pens). Median distances of home ranges from release sites were greater in Idaho than in YNP (Mann-Whitney $T = 0$; $p = 0.0003$). In YNP, individuals from the original groups paired with individuals from others to form additional territories in and near YNP, some of which were more distant from release sites.

The hard-release protocol in Idaho evidently contributed to a more widespread pack distribution. Yet, the fact that some Yellowstone wolves were recaptured and returned to the park also played a role. Entire or potential packs were confined to acclimation pens on three occasions after settling in unsuitable areas or threatening livestock. Each established a home range near their second release site; thus the second acclimation refocused home range selection. The only home range shifts occurred as a result of aggression by the Druid Peak pack toward the Crystal Creek and Rose Creek packs; the Crystal Creek pack was completely ousted from the Lamar Valley.

Reproduction

Of the initial reintroduced wolves, at least 22 Idaho wolves (63 percent) gave birth to or fathered pups through 1998, and two more did so by 2000. Reproduction and recruitment in Idaho were delayed compared to YNP because of the type of release. Releases there occurred only three to six weeks before the breeding season. None of the three original pairs reproduced in 1995, but all three produced pups in 1996. Twenty-four of the 31 YNP wolves (77 percent) gave birth to or fathered pups, nine of which resulted from breeding in acclimation pens. One of the four groups released in 1996 successfully produced pups. Altogether, four of seven groups that were acclimated in Yellowstone bred in captivity and produced litters. Yellowstone litter production grew from two in 1995 to nine in 1997. Three packs had multiple litters in

1997 and two did so in 1998. Multiple litters probably resulted from the soft-release protocol whereby a dominant male was combined with several unrelated females—thus relaxing the inbreeding avoidance characteristic of wolves in packs (Smith et al. 1997). Including the introduced wolves, Idaho and YNP populations grew at annual rates of 101 percent and 75 percent from 1995 to 1998, respectively. In this calculation the releases in 1995 and 1996 mask the effect of delayed start of reproduction in Idaho (Figure 6.5).

Depredation on Livestock

Five Idaho wolves (14 percent) were involved in depredations, although a total of 11 (31 percent) may have been associated with packs that killed livestock. From 1995 to 1998, Idaho wolves killed 15 cattle and 64 sheep (Bangs et al. 1998; Mack and Laudon 1998). In response, six wolves were translocated (two were translocated twice), and two were killed in control actions (Bangs et al. 1998). Ranchers were compensated more than $13,800 for livestock losses. Of the 31 wolves released in YNP, 6 (19 percent) were involved in depredations or were involved, implicated, or associated with packs that killed 8 cattle and 20 sheep during 1995–1998. Government agents killed four wolves. Fourteen reintroduced wolves and their pups were translocated to reduce conflicts with livestock and provide those wolves greater security (Bangs and Fritts 1996). Compensation to ranchers totaled $13,000. Hard-released wolves in Idaho killed a few more livestock than soft-released wolves despite a higher abundance of livestock near YNP (Bangs and Fritts 1996). Hard-released wolves might have been more prone to encounter livestock as a result of their wider-ranging tendencies. We saw no indication that reintroduced wolves were more inclined to kill livestock than naturally occurring wolves.

Conclusions

Both hard- and soft-release techniques established breeding wolf populations. Although our original plan was to release wolves for five years, pack establishment and reproduction allowed us to stop at the end of year 2 by which time 66 wolves had been released. Perhaps the most important components of success were the wolves' ability to endure the rigors of reintroduction and the suitability of release habitat. We learned that combining wolves from different packs did not hamper—and may even have improved—the soft-release procedure by promoting reproduction. All but one soft-released pack remained together, indicating that temporary captivity does not compromise pack cohesiveness. Further, the level of contact with humans needed to maintain captive wolves probably did not increase their tolerance of people. As has been found

elsewhere, hard releases seem to guarantee that wolves will not remain together, (Fritts et al. 1984, 1985; Bangs et al. 1995).

Most wolves in this and other studies appeared to move toward home after release even though translocated up to 1000 or even 1550 km (Fritts 1993). Nonetheless, homeward movement was not a significant factor in the outcome of the program because the restoration areas were very large. Such homing tendencies have been exhibited by translocated cougars (Belden and Hagedorn 1993; Ruth et al. 1998), black bears (Rogers 1988), other wolves (Henshaw and Stephenson 1974; Weise et al. 1975; Fritts et al. 1984), and a variety of mammals (Bovet 1992). The concentration of travel directions some 50° east of the homeward direction, apparent in both sexes and both restoration areas, had no ready explanation.

Why females initially moved homeward more than males is unknown. The pattern did not extend to home range establishment. The ultimate directions of hard-released wolves tended toward their capture sites, however, whereas soft-released wolves were distributed more randomly. We believe the shorter distances moved by YNP wolves resulted from the soft-release procedure. During acclimation, YNP wolves apparently lost some motivation to return home and were less likely to scatter from the release site. Evidently soft-released packs are likely to return to the vicinity of their release sites after a period of exploration. Thus soft releases give managers an element of control not possible in hard releases. Soft releases and occasional management actions to return wolves to captivity encouraged their establishment in the most desirable areas of the Greater Yellowstone area. Wolves released in Idaho generally moved well north of the center of the release area. The disintegration of the YNP Nez Perce pack was unexpected but may have been related to noise from snowmobiles. No other pack was subject to that disturbance. Based on this case, we suspect that the degree of stimulation by humans while wolves are penned and at the time of release could well affect the outcome. The release of the Nez Perce pack was far from a failure, though, as the divided pack became dispersers that ultimately produced seven litters.

The extremely rugged terrain of Idaho with its complex networks of ridges and drainages might have helped attenuate homeward movement and general exploratory activity. The ability of wolves to navigate through central Idaho suggests cognitive mapping that is tied to landscape features (Dyer 1998). Fritts et al. (1984) reported that some translocated wolves in Minnesota returned to the vicinity of previous locations and then moved away in different directions, apparently using those locations as reference points. Cases of wolves leaving territories, traveling great distances, and then return-

ing again are known (Fritts and Mech 1981; Messier 1985; Mech 1987; Fuller 1989). Merrill and Mech (2000) have documented the long-distance travels of four wolves that returned to territories after traveling up to 494 km away.

High survival (more than 80 percent the first year) contributed to early population establishment in both release areas and is better than translocations of canids elsewhere (Fritts et al. 1985; Carbyn et al. 1994; Bangs et al. 1998). Survival among the YNP wolves might have been higher if release pens had been more widely spaced. Future reintroductions might reduce intraspecific conflict by spacing release pens much greater than 8 km apart. No deaths from intraspecific aggression occurred among hard-released wolves through 1998.

Because of some breeding in captivity, reproduction occurred sooner with the soft-release technique. This enabled population growth to begin earlier in the Yellowstone area. But because of the ability of wide-ranging wolves in Idaho to find one another, pair-bond, and reproduce, the recruitment within that population was delayed only a year. By 1998, pup production had caught up to the YNP level. This result demonstrates the demographic advantage of having more breeding units early in a wolf population's history.

Both populations have continued to grow since 1998, and both appear well established today. By December 2000 there were about 192 wolves in central Idaho and 177 in the Greater Yellowstone area. Clearly, release technique was not the only factor that determined restoration success. It appears that if landscape conditions, prey availability, wolf restoration stock, and early release management are suitable (Phillips and Smith 1997; Mack and Laudon 1998; Smith 1998; Bangs et al. 1998), the choice of hard versus soft release seems to matter little. Nonetheless, hard releases may be advantageous if the size of the area can accommodate wolves wandering without encountering people or killing livestock. The technique is relatively inexpensive as well, and involves less husbandry. If the size of the area is restricted, however, then a soft release should be used to limit postrelease movements. Because few areas are as extensive as central Idaho, soft releases are likely to be preferred in future wolf restoration efforts.

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