

Dynamics of Wolf Social Groups and Wolf-Prey Systems Research in Denali National Park and Preserve

Biological Years 2007-2008
(May 2007-April 2008, May 2008-April 2009)

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Research in BY '07 and BY '08 again focused on groups, the primary functional units for wolves. The broad objective of this research, which began in 1966, is to learn more about wolf social groups, their evolutionary underpinnings and variations, and how they interact with prey, ultimately for improved management of wolf-prey systems and a better understanding of societies and systems in general.

Figures 1-4 and Tables 1-2 summarize highlights of the BY '07 and BY '08 field information; Tables 1-2 appear at the end of the report because of their length. Group numbers in the text correspond to the group numbers in these figures and tables. An accompanying Web site, www.alaskawolves.org, provides additional detail and numerous scenes of the study groups in action, usually in the form of photo essays. [Print this report only in color, to interpret Figures 1-4. Viewing the PDF file (available at alaskawolves.org, Reports2 page) will allow zooming to better distinguish between the multi-colored locations in Figures 1-4.].

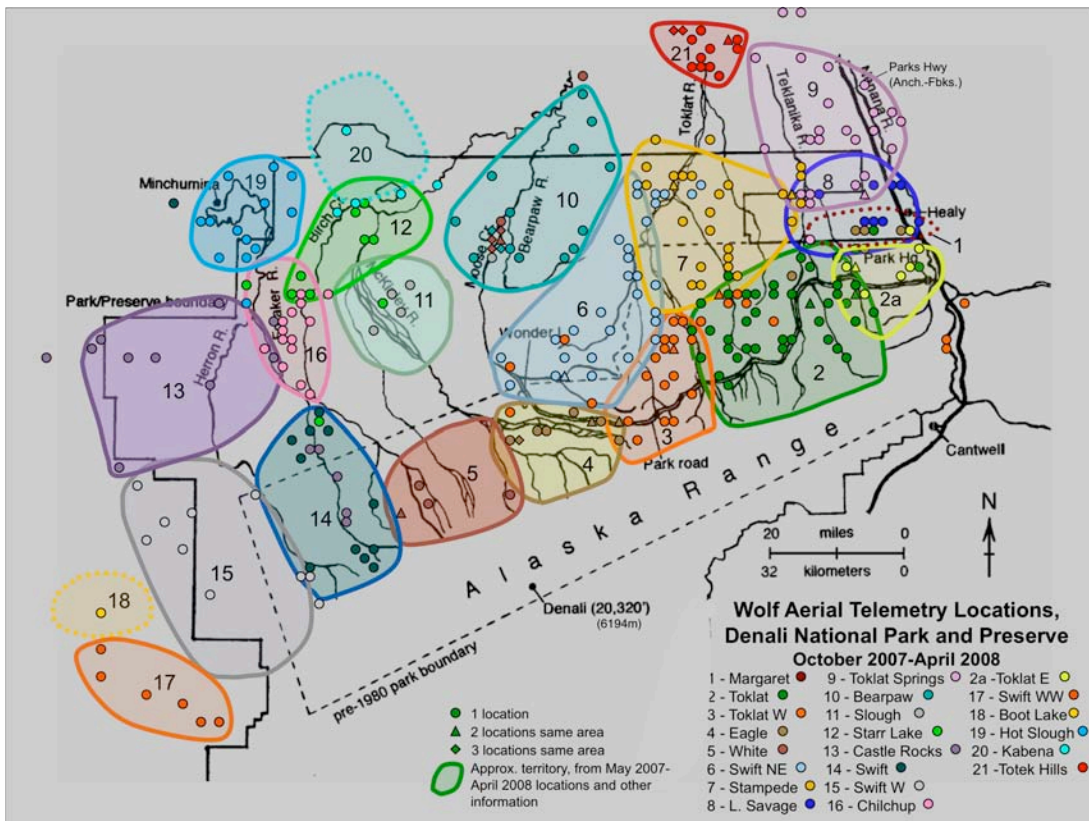
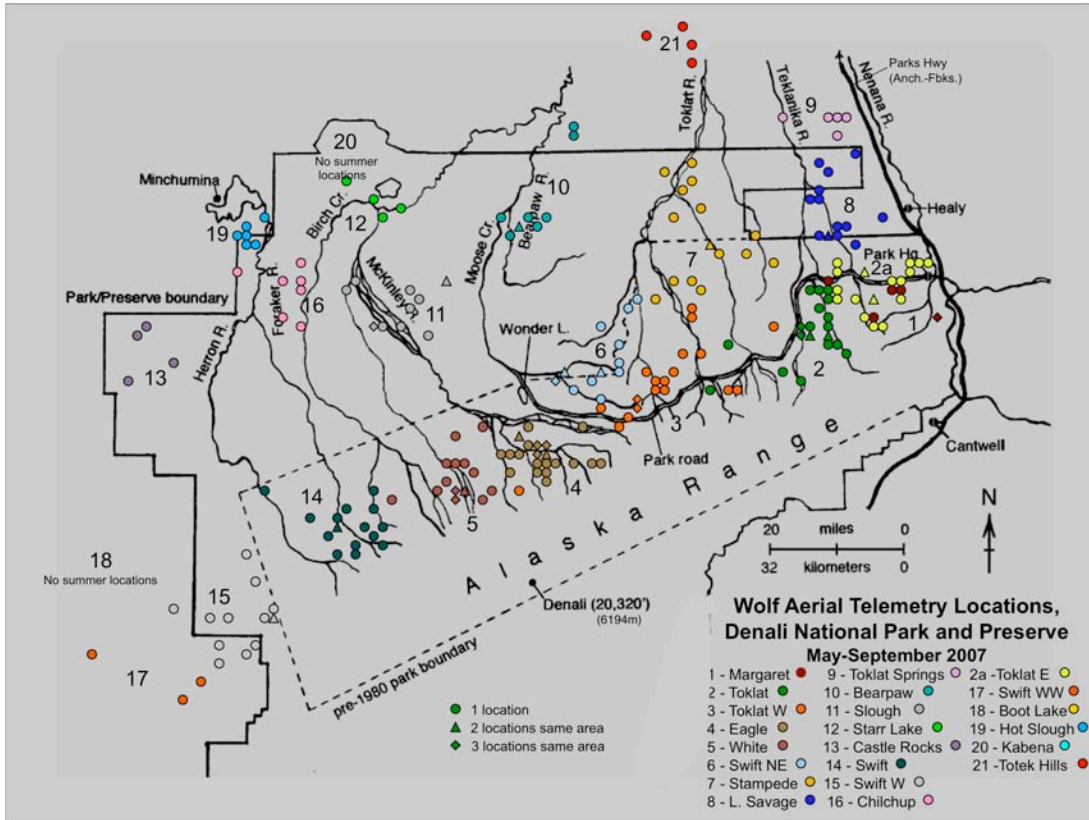
Haber (2007a) summarizes the recent history (BY '06 and earlier) of wolves in most of the areas used by the BY '07 and BY '08 study groups. Haber (1977, 2002, 2007b) describe my field methods.

The National Park Service (NPS) and I use different names for some of the study groups. Tables 1-2 provide all of the names. NPS does its own research via aerial radio-tracking and satellite upload from GPS collars. Denali National Park wildlife biologist Tom Meier and I exchange field information; I thank him for his information, some of which I have included here as personal communication.

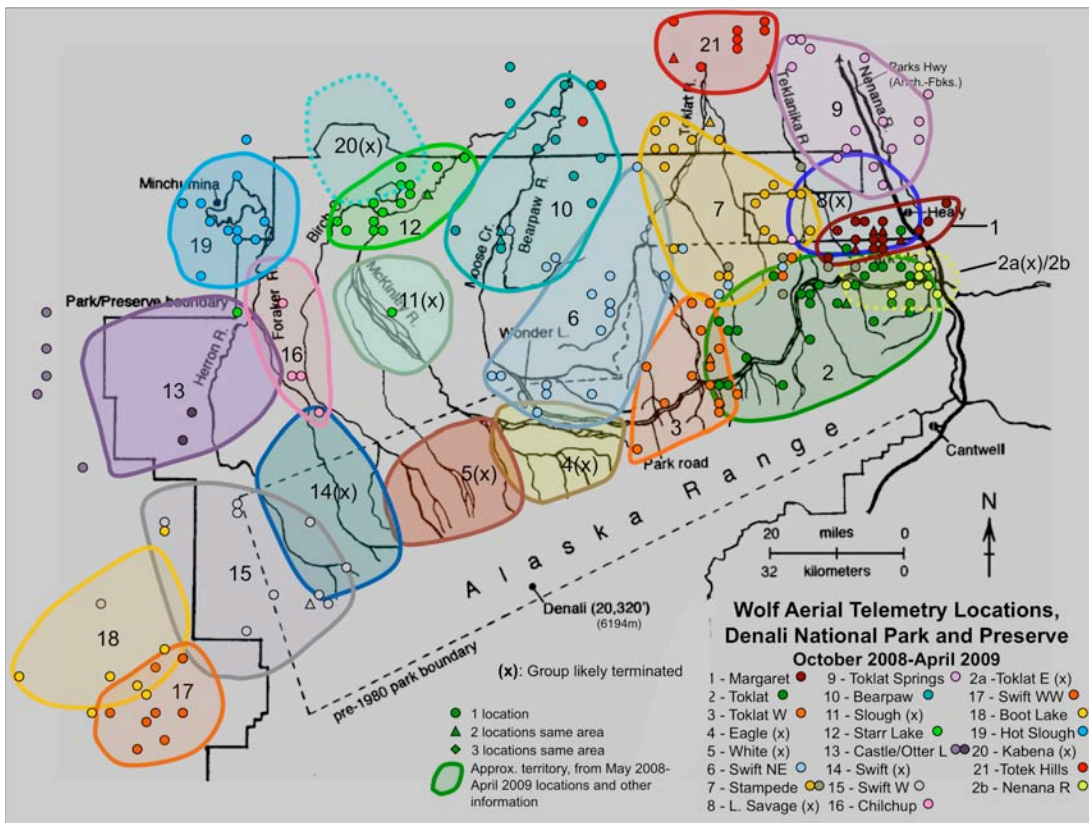
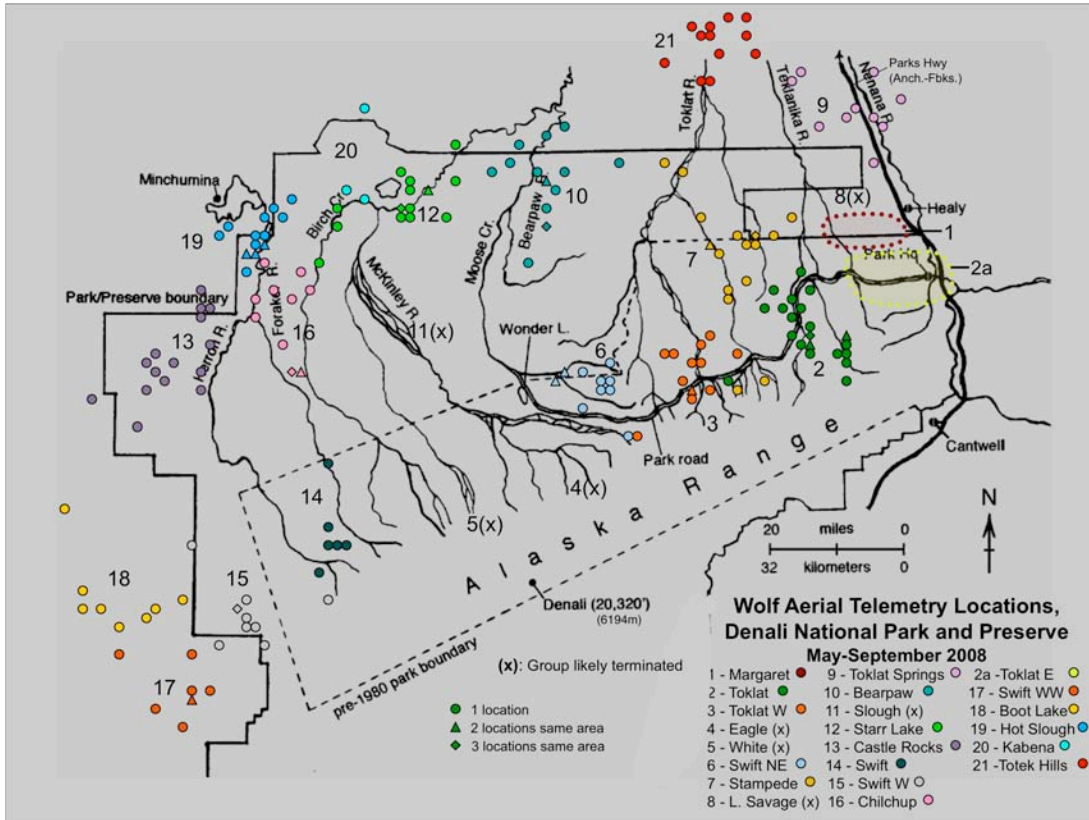
The first section provides an overview of the study groups. Their winter travels beyond territorial boundaries are turning out to be of greater significance than previously understood, so the second section considers some of these details from the last two winters. Reproductive bonds drive much of what happens in a social group; the third section summarizes recent variations observed in the study groups. The fourth section updates the Toklat (East Fork) study group's responses to the major trapping and shooting losses of 2005. The last section summarizes recent human-caused wolf losses for the entire study area.

Group Overview

I monitored 22 groups of wolves in BY '07, including two, #s 18, 20, that apparently did not originate or move into the study area until late in the biological year. Of the remaining 20 groups, at least 15 began BY '07 as reproducing families. A new pair, #2a – likely siblings, may have produced pups that died early in the biological year. There were no indications that four other groups produced any pups. One of these – a new pair, #17 - may not have formed until after the mating period. In another, #14, the dominant wolf appeared to be an old female without a mate. Another “group,” #16, consisted only of a single wolf, a young male. The estab-



Figures 1-2. Summer and winter wolf locations and territories, BY '07 (color-coded).



Figures 3-4. Summer and winter wolf locations and territories, BY '08 (color-coded).

lished breeding female of the fourth group, #1, was killed while pregnant near the end of BY '06; her mate and four other wolves seemed to split apart soon afterward (he was with at least two adults and two pups in another area by September, but most likely the pups were not his).

Four groups probably terminated in BY '07: #11 due to natural causes, #8 due to human causes, and #s 4-5 due to interacting human and natural causes. The female of group (pair) #2a was snared in late November 2007. The male was likely snared with her but escaped and is probably the same male with a snare around his neck (removed by NPS in May 2008) that paired with another female by late February 2008. There was no known contact with any wolves of the original group #1 in BY '07 after June 2007 other than the alpha male (direct observations in September 2007, via GPS satellite locations [Meier, pers. commun] the rest of the year). After shifting largely out of core areas of his established territory in early BY '07, he associated with wolves in a southeastern area (above) but then settled in an adjacent area to the north and paired with a new female.

I monitored 19 groups in BY '08. At least 16 of the 19 groups likely began BY '08 as reproducing families, although the female of one pair, #18, appeared to be raising pups on her own (an adult male of unknown origin joined her and the pups in mid-late BY '08). Two groups, #s 13, 17, seemed to base at natal dens, but I did not see any pups. Another, #1 – the same male that paired with the new female mentioned above, probably produced pups that died, based on the male's localized summer GPS locations and indications when the female was collared in November 2008 that she had lactated (Meier, pers. commun.). There were no indications that the three other groups produced any pups. One, #14, consisted only of an old female at the beginning of BY '08. Another, #20, seemed to be transient to the study area. The third, #2b, may not have originated until mid-late BY '08.

At least three groups, #s 2a, 7, 14, probably terminated in BY '08, # 2a following the human-caused death of the adult female, #7 due to interacting natural and possibly human causes, and #14 due to a natural cause. It remains to be determined if two females radio-collared in late February 2009 (Meier, pers. commun.) are survivors of group #13 or recolonizers; I lost contact with this group in December 2008 after the alpha female and the two other radio-collared wolves died, apparently from natural causes. Group #20 disappeared early in BY '08 most likely because these wolves were transients from well north of the study area. The only wolf observed from group #21 as of late BY '08 was the alpha male, and he was with and near group #10 in #10's territory during the last observations, April 18-20. There were only 3-4 wolves in this group after mid BY '08, at least one of which was trapped.

An estimate of north-side park/preserve wolf numbers should be calculated from *late* biological year group sizes (Tables 1-2) and allow for the likelihood that there are at least 3-4 unidentified small groups of wolves, especially pairs, in the open spaces of Figures 2 and 4. It should also be assumed that pairs or other small groups have already recolonized (or are recolonizing) at least several of the vacancies resulting from the group terminations indicated above and in Figures 3-4 and Tables 1-2. I question the value of Denali wolf "population" estimates and related averages (e.g., of pups per group), given that the park/preserve bounds only a small portion of the actual, i.e., biological, population (Haber 2007b). I will leave it for any readers who are interested to calculate their own estimates.

Extraterritorial Forays

Movements of established groups are usually constrained from May-September, while the wolves are provisioning their immobile young at dens and rendezvous sites. During the rest of the year, groups range inside their territories without any bases. But they also go outside for varying intervals, distances, and reasons. Some of these extraterritorial forays/migrations are predictable in the sense that there are few if any alternatives because of low prey availability. Traditional caribou wintering grounds in the northeast park boundary area are a foraging magnet for groups living in low-prey areas as far as 60-80 miles (100-130 km) away. Salmon concentrations in the warm and hot springs segments of certain river systems in north-central and farther northeastern areas attract wolves in a similar way.

Resident and multiple migrant groups of wolves are at high risk of mortal conflict in these areas (Haber 2007b), but the migrations are probably still adaptive because of higher odds of eating while there than in the home territory. This helps to explain the greater longevity, and perhaps higher sociality, of groups like Toklat (#2) that are afforded a richer year-round prey base apparently devoid of major foraging magnets. These groups likewise embark on extraterritorial forays, but less predictably and even while eating above their maintenance requirements (Haber 1977). Responding to neighbors in territorial boundary areas, probing to determine occupancy of other areas, and general explorations appear to be of more direct importance than foraging in motivating these trips. Some of the forays between Toklat and its former neighbor, Savage, were reciprocal (“tit-for-tat”); others seemed to be premeditated aggression (Haber 1977).

The BY '07 and BY '08 field observations again included a wide range of these behaviors. There is a history of distant winter foraging for groups in central areas of Denali in particular (Haber 2007b). The locations in Figures 2 and 4 indicate that group #s 3, 4, and 6 each embarked at least once on a northeastward or eastward foray, into or toward an active caribou wintering area. In winter 2007-08, group #5 went northward instead (Fig. 2), and in 2008-09 group #6 went westward as well as eastward (Fig. 4). The northward and westward forays were to a prominent warm springs area in group #10's territory where salmon concentrate and wolves are able to catch them in shallow water.

Wolves from other study groups living in low-prey areas were also attracted to these foraging magnets. Group #9 shifted its activities into a portion of the vacancy resulting from the shooting-trapping demise of group #8 but went on at least two additional southward and southwestward forays as well (Figs. 2, 4), further into the caribou wintering area. Group #11 went northeastward to the group #10 salmon area at least once (Fig. 2). There is a second major salmon area further to the northeast, at a hot springs in group #21's territory. Group #21 relied heavily on these salmon; many of the group #21 locations in Figures 2 and 4 were at the hot springs and in associated side drainages. It is likely that if more of the surrounding groups were radio-collared and monitored regularly the data would reveal at least as much competition over these salmon as in group #10's territory.

Most of the other indications of winter extraterritorial forays in Figures 2 and 4 likewise involved groups living in areas of relatively low winter prey availability, although the motivations are more speculative. Among these forays, group #12 went to southward areas and #13 to westward and southeastward areas. Group #20 appeared for several months and then most likely returned to a home base well to the north. The south-

westward foray that the locations indicate for group #21 in Figure 4 involved only the #21 alpha male, who may have been the only remaining group #21 wolf. He appeared to be trying to join the breeding female and others of group #10, following the death several months earlier of her mate, the #10 alpha male. A series of secondary locations shown in Figures 3 and 4 for group #7 mostly in southern and eastern areas of the territory and somewhat outside are of a young male, not the group, as he was apparently dissociating and beginning to disperse.

Two almost identical extraterritorial forays by group #2, Toklat, to the northeast park boundary area seemed much more likely to be probes or explorations than hunting trips. Toklat lives in one of the best year-round prey areas of the region. Both forays were brief (2-3 days), and on at least the second one the 11 Toklat wolves likely chased group #1, the latest Margaret pair, over a major segment of the route. There did not appear to be any caribou in the area during the first trip. The wolves either did not see or ignored a band of caribou less than a mile (km) away early on the second trip.

[To interpret the northeastern locations shown in Figures 2 and 4, it should be understood that wolves seldom cross over the top of a rugged east-west mountain range that lies inside the northeast park boundary southwest of Healy, between Nenana River and Savage River, north of the park road - roughly along the intersection of the group #s 1, 2, 2a, 2b, and 8 territories. When Toklat and the other southern groups show up in the northeast boundary area, it is usually because they have traveled around the west or east end of this range. This requires a much more deliberate effort than the short north-south distances between some of the northeast locations (on opposite sides of the mountain range) might suggest].

There were 7-8 known or likely natural deaths associated with the observed BY '07 and BY '08 extraterritorial forays. The alpha female and 1-2 pups of group #5 were killed by other wolves at the warm-springs salmon area in group #10's territory in March 2008; I watched 10 wolves of group #10 hotly pursuing her there earlier in the winter. Her mate was trapped, perhaps with others of the group, 30 miles (48 km) further northeastward in late December 2007 or early January 2008. All six wolves of the group may have been together on this more distant foray, but the female and at least 1-2 others were at the salmon area by January 9 and remained there until at least two were killed in March. The alpha female of group #11 died (was likely killed by wolves) at the same (salmon) location in late December 2007 or early January 2008 (by Jan.10); her mate died naturally (details undetermined) inside the #11 territory a month or two earlier. There was no further contact with any surviving young.

The alpha male of group #7 died near the east side of his territory sometime between January 21 and February 7, 2009, probably killed by trespassing wolves of group #9. NPS (Meier, pers. commun.) and I observed group #9 on two forays in this area and to the southwest in late February and early March 2009, and group #9 trespassed in the same area at least once in winter 2007-08. The group #7 alpha female died inside the #7 territory shortly before April 18, 2009. She was probably killed, while alone, by the 11 trespassing wolves of group #6; I observed the #6 wolves hunting caribou less than a mile (km) away on April 20. She and 4-5 young were at or within 10 miles (16 km) of the northeastern hot springs salmon area in late February. There was a second-hand report that four wolves were trapped in the hot springs area about then. She was subsequently alone to the south and seemed to be hurt and in poor overall condition. There may have been a trapping or

shooting encounter but her proximity to the salmon area also raises the possibility of a hostile interaction with other wolves.

The alpha female and at least one other wolf of group #13 died three miles (5 km) apart about 10 miles (16 km) west of the #13 territory in November and December 2008. Both deaths were most likely natural. There were no indications of trapping or other human activities on the ground. This is in an active state aerial wolf-killing area, but the circumstances (poor tracking conditions, etc.) also leave that as an unlikely cause.

Reproductive Bonds

Reproductive bonds are at the heart of social organization, and in BY '07 and BY '08 the Denali study groups again illustrated the importance, complexity, and rich variety of these relationships.

Group #1 seemed to vacate the core of its established territory and dissolve within weeks after the pregnant alpha female was killed in late BY '06. Raising new pups at a den is like a social glue for wolves, without which individuals seem more likely to split apart and disperse, at a time of the year when some of the young adults are already predisposed to disperse. The group #1 alpha male was with other adults and pups by September 2007 – perhaps including a female who also lost her mate - but then ended up with another female in a third area, apparently producing pups with her in BY '08 but losing them by November 2008. He was trapped there a month later. The female remained in that area, paired with a new male in February 2009, and was still with him in late April 2009.

A young pair, #2a, Toklat East - the female and almost certainly the male from neighboring group #2, Toklat (i.e., likely siblings), moved into the vacated core of the original group #1 territory in early BY '07 and localized as if producing pups, although no pups were ever seen. The female was trapped just outside the territory to the northeast in November 2007. The male was likely trapped with her but escaped and is probably the same male – initially wearing a snare – that produced five pups with a new female in the original territory #1 in BY '08. This female was struck and killed by a vehicle in an eastern area of the territory in November 2008. He was observed nearby for another week or two, but I am not aware of any confirmed observations since then (he is not radio-collared but would be easily identified by a prominent neck scar from the snare wound).

Group #2b, the Nenana River pair, has ranged in the original #1 territory since at least February 2009, when NPS collared them. Group #2 extended its movements into much the same area in winter 2008-09 (Fig. 4). This and other indications of tolerance suggest that #2b is a second pair of Toklat dispersers. It is nothing new for Toklat dispersers to recolonize adjacent areas to the west; the Wonder Lake and Toklat West/Grant Creek (#3) groups originated as western offshoots in 1971 and 2003 (Haber 1977, 2007b). Continuing human-caused losses are now allowing this to happen frequently on the east side, where the year-round prey base could otherwise support a second long-lasting group such as Savage (Haber 1977, 2007b).

The same male and female have maintained a strong bond as the primary breeders of group #2 since the experienced adults were trapped and shot in 2005. They are almost certainly siblings, in this case with an impressive history of producing surviving offspring. At least 27-28 pups were present at the primary natal den in early BY '05, '06, '07, and '08 combined, excluding the pups mentioned below that were likely attended at a separate location in early BY '08. At least 21-23 of the 27-28+ pups survived through mid biological year.

Seven of eight pups present at the den in early BY '05 survived through the end of BY '05, as did 5-7 of the eight pups in BY '08 (no "late" pup counts for BY '06 or BY '07).

I observed an additional lactating group #2 female at the natal den in 2005 and 2006, i.e., a female that I saw nursing the pups cooperatively with the alpha female. What appeared to be the same, secondary-lactating female closely attended the pups at the natal den in 2007 as well; there were indications that she nursed, although I did not actually see her nursing. It is possible but unlikely that these were double litters. I did not see any indications of a second lactating female at the primary natal den in 2008. The foregoing secondary female was one of the wolves that turned up missing after group #2's three-day trip into the northeast park boundary trapping area in February 2008.

In 2008, a group #2 female likely produced pups at a separate location and then combined 1-2 survivors with the primary litter of seven (from 8+ born) at a late-summer rendezvous site. A second female appeared to be sexually active along with the primary female during the 2008 courtship activities, and the alpha male seemed interested in both (see the April 8, 2008 blog entry at alaskawolves.org - the 4-photo sequence and caption from March 2 near the bottom of the photo section). There were no indications of interest from any other males. In 2002, I observed cooperative polygyny involving the previous group #2 primary breeding pair and that female's mother, i.e., the current alpha male's parents and grandmother (Haber 2002).

Group #3 underwent major changes centered around the primary breeders in BY '07 and BY '08, among other things likely illustrating a sibling reproductive bond that did *not* endure. The original breeding female was killed by group #2 in October 2006 (Haber 2007a). Later during winter 2006-07, her mate, the original male (the current group #2 alpha male's uncle), separated from the remaining offspring for a lengthy period, then separated again during most of summer 2007. He rejoined them a second time but was killed by wolves (group #2?) in September 2007. Two of the others produced a seemingly healthy litter of five pups in BY '07, but most if not all of the pups were missing by January 2008. The male separated from the female and two younger wolves in early January 2008 and was trapped less than two weeks later 40 miles (65 km) to the east. In late February 2008, a new adult male (origin unknown) joined the female inside the #3 territory, and by the end of March both of the younger wolves were gone; I watched him attack one of the younger wolves repeatedly, prior to the departures. He and the female produced six pups in BY '08, four of which were still with them in late April 2009.

Group #4 reformulated from an adult triplet without any surviving pups in BY '05 or BY '06 into a disparate-aged pair that in BY '07 raised two pups in good condition through mid January 2008. However, the 8-9-year old female died of an undetermined natural cause in mid January 2008. Her 4-5-year old mate went to the northeast park boundary caribou wintering area by late January (as was usual for this group), but the pups were missing and not seen again. He was trapped along the northeast boundary in late February 2008. In 2004, the previous male likewise continued to the northeast boundary caribou wintering area after the death of his mate enroute. He found a new mate in the northeast area several months later (from neighboring group #5, which was also on a northeastern foray), then brought her back to his established territory 40 miles (65 km) to the southwest. Had the latest male not been trapped, there is a good chance he would have found a new mate

and extended group #4's history in a similar manner (a good winter foraging area is also likely to be a good place to find a new mate).

In BY '07, group #6 produced two litters (6+5) at separate natal dens, but I do not know how the four adults were paired or if there was any polygyny. The four combined the 11 pups in late September 2007, and at least 14 of the 15 total wolves were still together at the end of the biological year, in late April 2008. There was probably only one litter in BY '08, and 11 of the 14 total wolves together at mid biological year were still together in late April 2009.

Group #8 lived in an area with a long history of human-caused losses. The alpha male had lost two successive mates in late BY '05 and BY '06. In late BY '06, the alpha female from neighboring group #9, which had also suffered major human-caused losses, joined him in his territory, as did a subadult of unknown origin. These three raised a litter of eight pups in BY '07 – the largest pups I observed anywhere in the study area in BY '07. All 11 were still together and appeared to be in excellent condition through mid biological year. Shortly afterward, the male was missing and his radio collar was in a river just downstream from a bridge near the east side of the #8 territory; the circumstances indicated that someone probably threw his collar in the river after shooting him elsewhere in the territory. Then the female was trapped. There was no way to determine for certain if others survived and remained in the #8 territory (the female wore the only other radio collar), but probably not. The group #1 male paired with another female (not from group #8) in this area soon thereafter.

Group #9 suffered a series of additional trapping losses in BY '08, apparently leaving only one survivor, the alpha male, at the end of the biological year.

The established reproductive bond of group #10 ended in early 2009 with the death of the aging alpha male, due to an undetermined cause. In late April 2009, the alpha male of nearby group #21, who may have been the only survivor of his group, was in the group #10 territory apparently trying to join the #10 female and four of her young (he was traveling with them in one of my observations).

The group #16 male and female produced three pups in BY '08. The five were still together and appeared to be in excellent condition as of late February 2009, when NPS recollared the adults (Meier, pers. commun.). But then the pups disappeared, without any clue as to what happened. A human cause is suspect; it is legal for residents from nearby Lake Minchumina to trap and shoot wolves and other wildlife in this area of the park, and there is at least one well-established trapline in the area. The #16 male was orphaned as an 11-12-month-old in April 2006 after the group #12 wolves killed his parents and took over (and are still occupying) most of their territory. He spent most of BY '06 inside group #10's territory, often near - and apparently dodging - the #10 wolves in the warm-springs salmon area. He was occasionally with another wolf (of undetermined sex) while in the group #10 area but by May 2007 was alone in a new area 25 miles (40 km) to the southwest, where 5-6 months later he met his current mate and subsequently produced the three 2008 pups with her.

In contrast, so far the group #17 pair has not produced any pups that survived beyond mid biological year. Nearby, something happened to the #18 male by early BY '08, leaving the female on her own to raise at least two of their pups successfully through late 2008 or early 2009. An adult male of unknown origin joined the female and two pups by late January 2009, and they continued to do well together. An aerial hunter probably shot at them in mid April 2009; as of this writing I have determined only that the male was unhurt.

The group #15 breeding female and #19 breeding male apparently died natural deaths in BY '08. Not much has been determined about any replacements. A newcomer joined group #19 in February or March 2009. This wolf appears to be a subadult or young adult (male?) unlikely to be involved in a reproductive bond yet.

Toklat Responses

Following the trapping and shooting losses of the Toklat adults (group #2) in early 2005, the six survivors – three yearlings and three two-year-olds – and others have continued to reproduce well with impressive cooperation and high natural survival. But there were also major changes in BY '05 and BY '06, particularly in the winter patterns of behavior (Haber 2007a). There was less group cohesion – the wolves split into small subgroups and singles more often. They used less than a third to a half of the established territory, lounging around much of the time without a regular travel routine inside the territory and without the usual forays outside now and then – although they strongly defended this core area from intrusions by neighboring groups (#s 1 and 3). They relied primarily on snowshoe hares (*Lepus americanus*), coincident with a major high in the hare population, instead of hunting and scavenging ungulates.

Toklat returned in large measure to the pre-BY '05 patterns in BY '07 and BY '08:

- Winter cohesion increased markedly. In BY '07, Toklat consisted of 17 wolves at the beginning of the winter (October-April) and 8-9 at the end, with a high likelihood that most of the missing wolves were trapped during an extraterritorial foray into the northeast park boundary trapping area in February 2008. At the 41 winter aerial radio-tracking locations where counts were possible, group sizes, in sequence, were as follows (the alpha male and female – the only collared wolves – were present at all of these locations; “+” indicates a possibility of up to several additional wolves that I did not see because of vegetation, poor snow conditions, etc.): 16, 16, 16, 16, 16, 14, 15, 17, 16-17, 11, 8+, 15, 14, 13, 13, 6+, 4-5+, 17, 16-17, 13-14+, 10, 10, 8+, 6, 6+1, 7, 7, 9+, 8+, 7+, 9, 9, 9, 9, 2, 9, 9, 9, 8, 8, 4. In BY '08, with 17 wolves at the beginning of the winter and 11 at the end (and no known trapping losses), the sequence of group sizes from the 23 counts that were possible was: 15, 14+, 13-14+, 16, 9+, 12-13, 13+, 16, 15+, 14+, 15+, 15, 14-17, 13-14+, 9, 9+, 11, 11, 11, 11, 10, 11, 11. Refer to Haber (2007a: 5) for the BY '06 winter sequence; there were 17 wolves at the beginning of that winter and 14-15 at the end. There were no comparable winter group-size data (or hunting data, below) for BY '05 because there was no telemetry contact until February and April 2006, when NPS first radio-collared wolves of the reformulated group.

- Winter movements expanded dramatically, once again extending across most of the established territory but with a major eastward shift in BY '08 (compare the Toklat locations in Figs. 2 and 4 of this report and Figs. 2, 3, and 4 of Haber 2007a). Not surprisingly, the basic routine picked up as well, to a more continuous travel schedule – something closer to the routine observed previously for wolves in this area under a wide range of winter conditions (Haber 1977), when they averaged 10.1-17.8 miles/day (16.2-28.6 km/day). Human causes – the continuing series of eastern vacancies and a failure of the young Toklat wolves to fully learn the established Toklat territory (before the experienced adults were killed) - are among the leading candidates in explaining the eastward shift.

- There was decreasing reliance on hares and a return to moose- and sheep-hunting during the winter.

Below is a summary of Toklat winter foraging data for BY '01 (Haber 2002), prior to the latest peak in hare abundance and loss of the experienced adults, BY '06 (Haber 2007a), at or near the peak in hare abundance, after the loss of the experienced adults, and BY '07 and BY '08, as hare abundance decreased and the alpha male and others were now 4-5 years old:

M = moose, S = sheep, C = caribou

Biol. yr. and # wolves at beginning and end of winter	Observable locations	Hare-kill locations	Ungulate-kill locations			Ungulate-scavenge locations
			M	S	C	
BY '01 (7→7)	53	0	2	3	0	5 (5M or 4M+1C)
BY '06 (17→14-15)	39	14	0	0	0	0
BY '07 (17→8-9) (up to 7 trapped)	41	4	1	3	0	0
BY '08 (17→11)	27	3	1	0	0	1M (or kill?)

The BY '07 and BY '08 summer foraging observations indicated there was scattered caribou hunting, in addition to continuing heavy use of hares. The only summer moose or sheep hunting that I recorded for the Toklat wolves was on June 6, 2007, when the alpha pair and two others killed one of *three* calves accompanying a cow moose, an unusual, relatively easy opportunity for the wolves. Emphasis on caribou in the summer and moose and sheep in the winter is the traditional pattern for this group (Haber 1977, 2007b).

The earlier research (Haber 1977: Chapters 8-9) showed that eastern Denali wolves – the Toklat and Savage groups - were able to hunt caribou even as yearlings but generally needed 2-3 winters of learning in the presence of experienced older wolves for proficiency at hunting moose and sheep, consistent with the documented order of difficulty in hunting these three species. The earlier research determined that Toklat and Savage scavenged, rather than killed, almost half of their winter ungulate meals, and that the young wolves needed extended learning in the presence of adults for proficiency at this aspect of foraging as well.

Observations over the last two biological years have answered questions that I asked in Haber (2007a) and elsewhere as to how soon and to what extent Toklat wolves would reestablish past ungulate hunting patterns, especially the important winter use of sheep: As noted above, Toklat was already returning to significant use of ungulates in BY '07, including sheep. Hares were still relatively abundant through late 2008, albeit down sharply from the major high of BY '05 and BY '06. The Toklat wolves continued to hunt hares prominently through November of BY '08, but less often, at least in the winter, than during the high. I did not see any hare hunting (or many hares) at 17 observable Toklat winter locations after November 25, 2008 (when 14+ wolves caught eight of the nine hares they found in a willow patch during a 20-minute period).

Three of the six young Toklat wolves, including the alpha male, had spent a winter and a half foraging with the experienced adults when they were orphaned in early 2005 (they were born in May 2003). When they began hunting moose and sheep in BY '07, it was with the benefit of two more years of overall experience and probably enough additional intelligence as mature adults to figure out other essentials that would normally be

acquired earlier, from more time with adults. In between, they were able to rely on a coincidental high abundance of easily exploited prey.

However, the Toklat wolves have not yet shown much expertise in scavenging their winter meals, a possible artifact of their incomplete early learning. As indicated, scavenging contributed about half of the ungulate winter meals for Savage and Toklat in the past, and young Savage and Toklat wolves did not show much ability to find these carcasses on their own. Wolves commonly dig to frozen carcasses buried under the snow, as deep as 5-10 ft (1.5-3 m) or more into hard-packed drifts and avalanches.

The Toklat wolves adapted their hare-hunting tactics to changes in hare tactics as hare abundance declined, and they taught their pups how to hunt hares when the pups were only 3-4-months old (e.g., Feb. 3 and Oct. 1, 2008 blog entries at alaskawolves.org). Their hare-hunting behavior was impressive, to say the least. But none of it was destined to be of much value for more than a few years. And by withdrawing to only a portion of the established territory during the feast, they risked losing other areas – and a long-term supply of ungulates - to neighboring groups.

There was no evidence of any comparable reliance on hares or a switch from ungulates by Toklat or other study groups during earlier hare highs or by other groups during the latest high. Heavy use of hares by the young Toklat wolves beginning in 2005 was the result of unusual circumstances. It seems best characterized as a necessary rather than an optional variation from normal foraging behavior.

Trapping, Shooting, and Related Impacts

In BY '07, wolves were trapped and/or shot from at least seven of the study groups - #s 2, 2a, 4, 5, 7, 8, and 15. Group #s 4, 5, and 8 probably terminated due to these and interacting natural losses.

In BY '08, wolves were trapped and/or shot from at least four study groups - #s 1, 9, 19, and 21. The group #2a breeding female died after being struck by a vehicle. The pups disappeared from group #16 most likely due to trapping or shooting, and from group #7 possibly due to trapping. Trapping cannot be excluded in the death of the group #10 alpha male. An aerial hunter likely shot at the group #18 wolves, though I have not yet been able to determine if there were any related deaths. Group # 2a probably terminated due to the human-caused death of the alpha female and interacting natural events. Although the pups of group #7 may have been trapped, that group likely terminated because of natural deaths of the alpha male and female. Trapping reduced group #9 to one wolf, the alpha male, as of late BY '08. The alpha male also appeared to be the only survivor of group #21, and trapping may have played a major role in that case as well.

Much more is known now about the territories and movements of Denali wolves and the distribution and movements of their prey than when the park boundaries were drawn. It is clear that these boundaries are not very ecological, especially in the northeastern area where Denali's most important wildlife wintering area is left largely unprotected. It might not be possible to change the park boundaries, but much more could be done to protect Denali wolves with adequate no-wolf trapping-hunting designations in adjacent state areas and inside the 1980 park additions (details at alaskawolves.org). The state and National Park Service have provided full protection to Denali caribou since 1972. It would be a sound move from biological, scientific, ethical, esthetic, educational, visitor-viewing, and other standpoints to do the same for Denali's highly valued wolves.

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Tables 1-2 follow this page

Table 1. Wolf study group sizes, reproduction, and related information, May 2007-April 2008. From best observations early, mid, and late biological year (May-April). "Total / pups" = total group size and number of surviving pups in total. Other names in parentheses for groups with 2+ names.

Group (see Figs. 1-2)	<u>Early biol. yr.</u> Total / pups	<u>Mid biol. yr.</u> Total / pups	<u>Late biol. yr.</u> Total / pups	Comments
1 Margaret	5 / ?	4+ / 2	1-2+ / ?	Pregnant alpha female killed (by vehicle or moose?) late 4/07. 5 survivors largely vacated core of territory by 5-6/07 and Toklat East pair (#2a) began occupying core. Alpha male with 1+ adult and 2 pups of unknown identity near SE corner of territory in 9/07, then settled in NE park boundary area by winter (alone? – based on GPS locations; Meier, pers. comm).
2 Toklat (East Fork)	19-20+ / 5-6+	17 / 2-3+	8-9 / ?	Adults split litter of 5-6 pups into 2 groups (2+ sites) late 8/07-9/07 after leaving natal den. Still 17 thru at least 1/30/08, but 7 missing after trip into NE park boundary trapping area 2/20-23. One returned by 3/14 with snare around his neck; missing by 3/28. Nine seen together thru 3/29, then 8 on 4/16-18.
3 Toklat West (Grant Creek)	9-10 / 5	5 / 2+	2 / 0	Alpha male separated from others mostly in territory until rejoining them between 8/9 and 8/23/07; then killed by other wolves (Toklat?) between 9/22 and 9/27. Four wolves remained in early 1/08 – young adult male and female (likely sibling parents of the pups) and 2 subadults or pups. The male adult separated from the others and was trapped 40 mi (65 km) east, along E park boundary, mid 1/08. Newcomer adult male joined the female and 2 younger wolves inside territory 2/25-26, then began punishing at least one of the younger wolves (a male?). That wolf gone by 3/14, the other young wolf gone by 3/18-28.
4 Eagle (Turtle Hill)	4 / 2	4 / 2	0-2 / 0-2	Aging female and prime male produced first pups (2) 5/07. Female died naturally 1/11-12/08. Male and 2 pups with her then, but by next observation, 1/30, male had migrated 45-50 mi (75 km) to NE boundary area, as is usual for this group. Pups not with him or seen anywhere else after 1/12/08. Male ranged in NE area until trapped there 2/25-26.
5 White (Straightaway, McLeod L.)	6-9 / 2-3	6 / 2-3	0-1 / 0-1	Six wolves raised 2-3 pups and ranged inside territory thru at least 12/8/07. Alpha male (and others?) dead on trapline 60 mi (97 km) NE of territory on next obs., 1/9/08. Alpha female and 1-2 pups near hostile residents and other trespassers at a salmon-rich warm springs (#10) 30 mi (48 km) NNE of territory on 1/9 and in all later observations. The female and at least one pup dead there on 3/4 and ~3/25.

6	Swift NE (McKinley Slough)	15+ / 11+	15 / 11	14 / 10-11	Two litters (6+5) raised at separate natal dens, then combined 9/22-28/07. All 15 present thru at least 1/30/08, 14 by 2/26.
7	Stampede (Chitsia)	10-13+ / 4+	11 / 4-6	4-6 / ?	Possibly 2 litters raised at separate natal dens; one group by late 8/07. 11 total on 10/27/08, 10 on 11/18. 1+ trapped 12/8-25 on 20 mi (32 km) foray NE of terr. 7 total by 1/10/09, 6 by 4/19, 4-6 on 4/29.
8	Lower Savage (Pinto)	11+ / 8+	11 / 8	0?	Two adults and a subadult and the 8 large pups they raised still together through at least 9/29/07. Adult female and 6 pups observed on 10/27, but male's radio collar was in a nearby river after he was likely shot (also others?) and his collar discarded. Female trapped in same (NE park boundary) area between 11/2 and 11/18. No further contact with any survivors. Lower Savage territory subsequently occupied by Margaret male (#1) and Toklat Springs (#9).
9	Toklat Springs	9-10+ / 6+	9 / 6	4-6 / ?	6 total by 1/08 thru mid 3/08, 4-6 by 4/08. No info on losses; in trapping area. Alpha male injured ~3/17/08 - likely kicked by a moose; unable to move much for ~1 week, then OK.
10	Bearpaw	10+ / 3+	10+ / 3+	8 / ?	10 total thru 1/12/08, 9-10 on 3/2; only 8 seen 3/6-4/19. Heavy winter use of salmon in major warm springs area in territory. Close hostile contact with White (#5), Slough (#11), previously Chilchup (#16), and likely other trespassing groups attracted to these salmon. Slough and White alpha females and 1-2+ others dead there in 1/08 and 3/08 (saw 10 Bearpaws chase White female on 1/12).
11	Slough (McKinley R.)	7+ / 4+	7 / 4	?	2 adults and likely 1 subadult raised 4 pups thru at least 10/28; adult male dead by 11/1 (apparently natural cause). Still 6 total 11/23-12/9/07. Adult female dead at above springs (#10) by 1/10/08 (last collar; no more contact).
12	Starr Lake	4-5+ / 2+	7 / 3	2-3+	7 total thru at least 11/23; 1 adult dead (likely natural) by 1/11/08. Only 4 seen by 3/5, and 2-3 as of 3/10-4/19.
13	Castle Rocks	7-8+ / 3+	7-8 / 3	7 / ?	Outside territory well to the W and SE for long winter periods. 7 total thru at least 4/16/08.
14	Swift (Hawke)	3 / 0	4 / 0	1 / 0	Aging female and 2 younger adults joined by another adult in 10/07. All 4 together thru 2/1/08, but only the female and 2 others by late 2/08. A male dispersed in early 3/08, and another wolf (male?) disappeared by late 3/08, leaving the old female alone in the territory thru the end of the biological year.

15 Swift West (Somber, 100 Mile)	7-8+ / 4+	8 / 4	3-7 / ?	9 total as of late 8/07 (includes 1 newcomer?). 8 by 9/28 (1 shot by hunter in 9/07). 8 thru at least 3/10/08, 7 by 3/29, and 3+ on 4/19.
16 Chilchup (Kantishna R.)	1 / 0	1 / 0	2 / 0	Young adult male shifted 25 miles (40 km) SW to new area as of 5/07, after spending much of winter 2006-07 in hostile salmon area of Bearpaw terr (#10). Lost his previous terr (as an 11-12-month-old) to Starr Lake (#12) after Starr L killed his parents there in 4/06. Paired with young adult female in new (5/07) terr sometime between 9/29 and 11/18/07.
2a Toklat East	2? / 0?	2 / 0	2 / 0	Young adult Toklat (#2) female dispersed 4/07 to adjacent eastern area (vacated by Margaret wolves - #1), apparently with a male Toklat sibling. Localized as if denning but no den or pups seen. Female snared just outside NE corner of park in late 11/07. Male likely snared with her but escaped; probably same male (with a new female) from which NPS removed snare on 5/2/08.
Swift WestWest 17 (Tonzona)	2 / 0	2 / 0	2 / 0	A Swift West (#15) female dispersed 20 miles (32 km) SW between 1/12 and 2/3/07. Joined adult male in that area by 3/14/07. They remained together there, but no successful reproduction.
18 Boot Lake			1-2 / 0	Began observing adult Boot Lake female in 4/08; possibly with an adult male.
19 Hot Slough	7-8+ / 4-5+	7-8 / 4-5	5-6 / ?	7 total seen thru 11/1/07, but 8+ on 2/2/08. One dead as of 2/26 (killed by other wolves?); 7 total thru 3/10. 5-6 seen together 3/29-4/19.
20 Kabena			6 / 1-3	Began observing 3/2/08. 3 total (subadults?) together 3/5-10, then 6 on 4/16, and 4+ on 4/19. Ranging in Starr Lake territory as a trespassing group from the N (Table 2)?
21 Totek Hills		7 / 2-4+	5+ / 0	Began observing 8/07. 6+ total thru at least 2/2/08 and 5+ as of 4/16. Heavy winter use of salmon in major hot springs area in territory, especially 1-3/08.

Table 2. Wolf study group sizes, reproduction, and related information, May 2008-April 2009. From best observations early, mid, and late biological year (May-April). "Total / pups" = total group size and number of surviving pups in total. Other names in parentheses for groups with 2+ names.

Group (see Figs. 3-4)	<u>Early biol. yr.</u> Total / pups	<u>Mid biol. yr.</u> Total / pups	<u>Late biol. yr.</u> Total / pups	Comments
1 Margaret	1-2+ / ?	2 / 0?	2 / 0	Margaret male's GPS locations (Meier, pers. comm) localized during most of 5-8/08, as if denning. Recollared by NPS in 11/08 with young adult female who reproduced in 5/08, but no surviving pups. Male trapped 12/08. Female still ranging in area - briefly with another adult or subadult in 1/09, then paired with an adult male by early 2/09.
2 Toklat (East Fork)	16-19+/8-10+	17 / 7-8+	11 / 5-7	Apparently a second litter of 2+ pups was produced 10 miles (16 km) westward of the primary natal den and then combined with the primary litter (8 pups, 7 survived) at a site 5-6 miles (9 km) eastward of the primary den on 8/22-24. 13-14+ wolves total thru 2/7/09, then 11 as of 2/24 thru at least 4/20. Two of the missing wolves may have recolonized the adjacent, overlapping eastern area, as the new Nenana River pair (#2b).
3 Toklat West (Grant Creek)	8 / 6	8 / 6	6 / 4	Two of the 6 pups disappeared between 9/25 and 10/18/08.
4 Eagle (Turtle Hill)	0	0	0	Likely terminated winter 2007-08 (Table 1). No information on any subsequent recolonization of area.
5 White (Straightaway, McLeod L.)	0	0	0	Likely terminated winter 2007-08 (Table 1). Two wolves observed in area 2/09 (NPS) – likely recolonizers.
6 Swift NE (McKinley Slough)	14+ / 3-6+	14 / 3-6	11 / ?	Still 13-14 total thru at least 11/25, then 11 by 4/18-20/09. Only 8-10 seen together 2/7-4/2.
7 Stampede (Chitsia)	9 / 5	8 / 4	0	Four older wolves produced 5 pups; 4 surviving pups by 10/18. A young adult male disassociated from the others between 8/12 and 8/21, ranging mostly just outside territory or in peripheral areas; not found anywhere after 4/2. The 4 remaining adults and 4 pups still together thru at least 1/21/09. Alpha male dead by 2/7, likely killed by trespassing Toklat Springs (#9) wolves (others also killed or separated then?). 4+ young wolves possibly trapped late 2/09. Aging alpha female ranged alone in territory thereafter, possibly injured. Dead by 4/18 near 11 trespassing Swift NE wolves; carcass still intact.

Lower Savage 8 (Pinto)	0	0	0	Likely terminated winter 2007-08 (Table 1). Area partially recolonized by Margaret (#1).
Toklat Springs 9	5-6+ / 1+	5-6 / 0-1	1 / 0	5-6 older wolves produced 1+ pup, but only 5 older wolves (0 pups) present by 11/2. 1-2 trapped by late 1/09; only 3 remaining by 2/24. 2 more trapped by 3/20, leaving only the alpha male, still ranging alone in established territory as of 4/20/09.
10 Bearpaw	9-10+ / 4-5+	9-10 / 4-5	5 / 1-3	Alpha male dead 7-8 mi (11 km) NW of terr. by 2/7/09 (trapped?, with others?); only 6-7 remaining. 5 remaining as of 3/7, but one often separated. Totek (#21) alpha male with Bearpaw alpha female and 3 other Bearpaws in Bearpaw terr. on 4/18; one young Bearpaw male 11 mi (18 km) away. Totek male alone 5 mi (8 km) from Bearpaw on 4/20/09; young Bearpaw male back with 4 other Bearpaws.
11 Slough (McKinley R.)	0	0	0	Likely terminated winter 2007-08 (Table 1). No information on any subsequent recolonization of area – probably none.
12 Starr Lake	3-4+ / 1+	3-4 / 1	3-4 / 1?	Only 1 pup seen; unusually small.
Castle/Otter L 13	7? / 0?	7 / 0?	2 / 0	Apparently the same 7 wolves present in 4/08 still together thru mid biological year, without new pups. 1 dead by 11/8/08, 1 missing by 11/25, and alpha female (last radio collar) dead by 12/12. Both deaths in the same area 7-8 mi (12 km) W of territory; both probably natural. 2 young adult females collared by NPS in the Castle territory on 2/23/09 (Meier, pers comm) may be Castle survivors, now called Otter Lake.
14 Swift (Hawke)	1 / 0	0	0	Old female continued ranging alone in established territory thru at least 7/25, after 3 others of the group died/dispersed in 2-3/08 (Table 1). Dead from a natural cause by 8/12/08. No info on any subsequent recolonization of area.
15 Swift West (Somber, 100 Mile)	8-10 / 3+	7 / 3	2-4 / ?	Alpha female died 7/08, a young male 11/08, both probably natural deaths. Six wolves remaining by 11/21-12/12/08, 4 by 2/24-late 3/09, and 2-4 by 4/2-18.
16 Chilchup (Kantishna R.)	5+ / 3+	5 / 3	2 / 0	Young adult pair in same territory occupied 5/07 (Table 1). Produced first pups (3) in 5/08. All 5 in excellent condition 9-11/08 and when NPS recollared 2/20/09 (Meier, pers comm). Pups then disappeared; possibly trapped/shot (established traplines in this area of park).

2a Toklat East	7+ / 5+	7 / 5	0?	Adult pair produced 5 pups in eastern, i.e., former Margaret, area; snare removed from male 5/2/08 (#2a, Table 1). Female died after struck by vehicle 11/27/08; male and pups disappeared soon thereafter (none radio-collared). Area used heavily by Toklat (#2) in winter 2008-09 and new Nenana R. pair (#2b) by late 2/09.
Swift WestWest 17 (Tonzona)	3+? / 1+?	2 / 0	2 / 0	Sporadic 6-8/08 locations at an established den, but adults alone by 9/27 – i.e., pups were likely produced but died by mid biol. year.
18 Boot Lake	3+ / 2+	3 / 2	4? / 2?	Female lost her mate by at least 6/5/08 (no details) but raised 2 surviving pups in good condition thru 11/21. Joined by adult male (origin?) by 1/21/09. All 4 still together and in good condition thru at least 4/2. Likely shot at by aerial hunter on 4/16. Male OK on 4/18; female (radio collar) present nearby but not observed (her condition?). No info on pups.
19 Hot Slough	8-9+ / 4-5	8+ / 4-5?	4-6 / ?	No observations of alpha male after 7/25; apparently died naturally. Young adult trapped 11/08. 6 total by 11//25 thru at least 2/7/09. Another wolf missing after 2/7. Newcomer young adult (male?) present by 3/31 - apparently began attempting to join in late 2/09 (Meier, pers comm). Newcomer still together peacefully with alpha female and the 4 others on 4/2 and with her and at least 2 others thru at least 4/20.
20 Kabena	3+ / 0	0?	0?	Still ranging in Starr Lake territory (#12) late 5/08-early 6/08 but 10 mi (16 km) N of terr on 7/3. Non-breeders on an extended southern extraterritorial foray? Collar not heard again.
21 Totek Hills	4-5 / 1-2	4 / 1-2	1 / 0	1+ wolf trapped late 1/09-early 2/09. Former disperser collared as a pup in 2007 returned to Totek area by late 2/09 (Meier, pers. comm). Observed only alpha male and possibly one other Totek together in Totek territory by 4/2. Alpha male in Bearpaw terr (#10) 4/18-20, first with Bearpaw, then alone.
2b Nenana R.	0	0	2 / 0	Adult pair ranging in Toklat East area (#2a) by late 2/09, following disappearance of Toklat East wolves in late 2008. Overlapping use of area with Toklat (#2) and other observations suggest one or both are Toklat dispersers, as was also likely for the Toklat East pairs.