

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

Investigator's Annual Report,
NPS Research Permit #670 (DENA-2004-SCI-0008)

Wolf Observations in Biological Year 2006 and Recent Group Histories

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Wolf research in BY '06 (May 2006-April 2007) again focused on groups, the primary functional units for this species. Figures 1-2 show the 16 groups of wolves that I studied during all or portions of BY '06. This included at least nine families (#s 1, 2, 3, 6, 7, 10, 11, 13, 15), two families (#s 8, 9) that suffered shooting and trapping losses with an apparently related reproductive failure (#8) and a dissolution/reformulation (involving both), a triplet of a male and two females without any known reproductive history prior to BY '06 (#4), a yearling male who was sometimes with another wolf (#16), and three groups whose BY '06 reproductive status I was unable to determine (#s 5, 12, 14). There were approximately 66-88 wolves in the 16 groups at or near the end of BY '06, with a likelihood of several additional small, as yet uncollared, groups ranging primarily in the western two-thirds of the northside park/preserve, in the gaps between the territories shown in Figures 1-2.

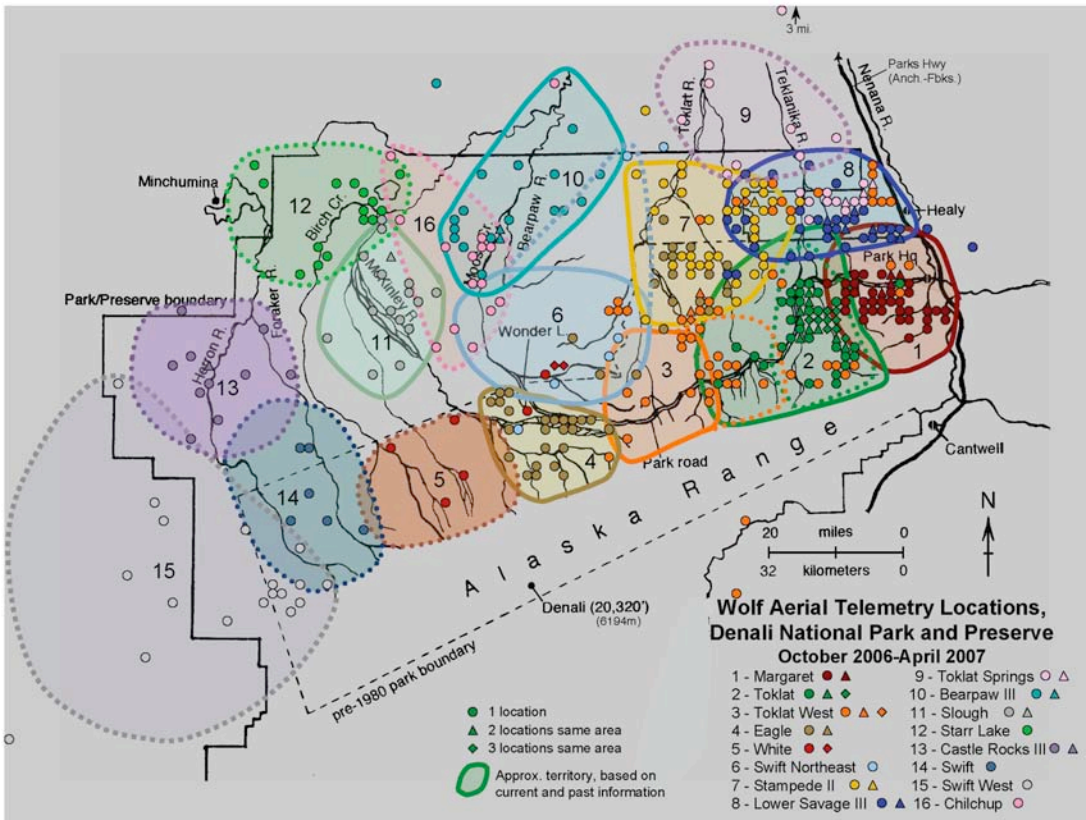
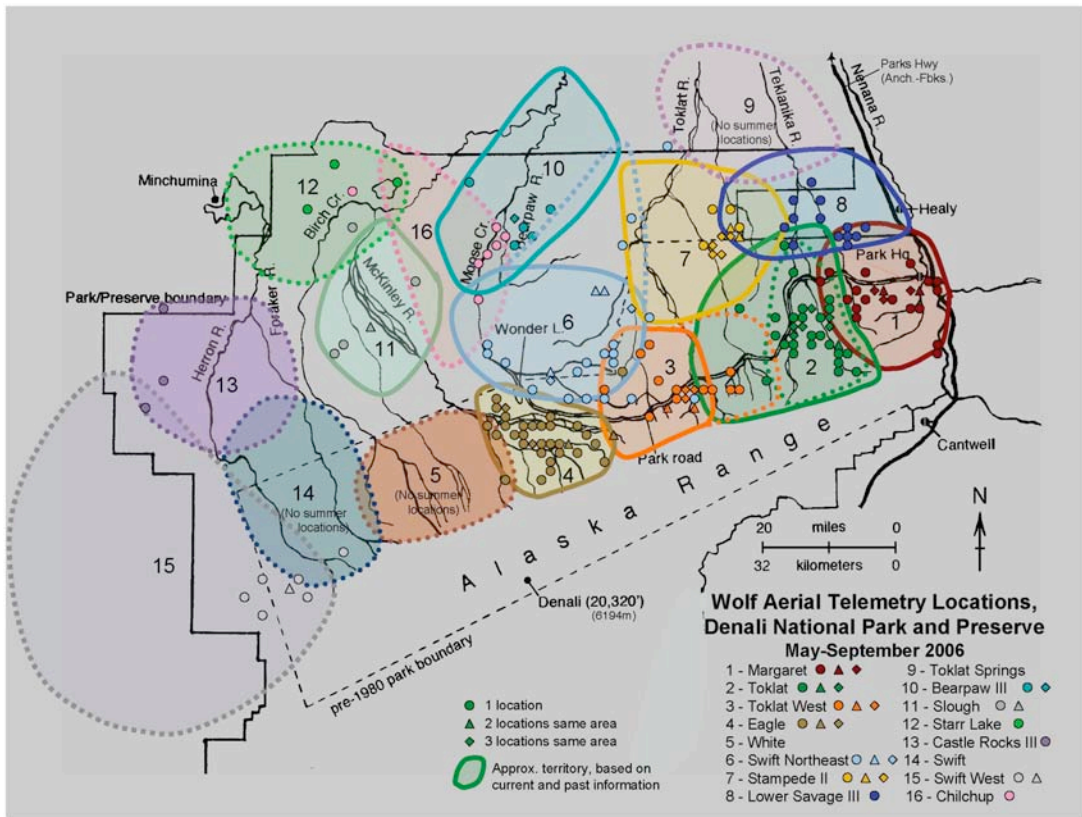
Figures 1-2 include my aerial radio-tracking locations for the 16 groups, divided into two intervals: May-September and October-April. Family groups generally attend their pups at homesites (dens, rendezvous sites) from May-September and usually hunt over lesser areas at that time of the year. From May-September I also studied three groups, #s 1-3, via ground observation, mainly at homesites. Figure 1 does not show any of the numerous radio-tracking and other locations associated with these observations.

Following are summaries of my BY '06 observations of the 16 groups and highlights of their recent histories, interspersed with related behavioral vignettes and management comments. The National Park Service (NPS) and I use different names for some of these groups. The NPS name appears in parentheses in the section subheads. NPS does all radio-collaring and other handling of Denali wolves (e.g., for necropsy), undertakes separate aerial radio tracking flights, and obtains locations via satellite upload with GPS collars on about two-thirds of the groups. 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.

1. Margaret

Margaret is the fourth major family group to occupy the eastern park area since I began this research in 1966. Savage was well established in 1966 and lasted until winter 1982-83 when the 12 Savage wolves disappeared, most likely due to illegal aerial hunting (based on strong circumstantial evidence). Trapping/shooting losses outside the park and radio-collaring mishaps inside played a major role in terminating the succeeding Headquarters and Sanctuary families. Margaret originated in a neighboring area in 1999 and recolonized the Sanctuary vacancy in 2001. The Margaret alpha male and possibly two others were snared just outside the park in 2004. Absent the human impacts, a much older family lineage would likely occupy this area at present ("family lineage" refers to social as well as genetic continuity).

Margaret consisted of at least nine wolves as of April 17, 2006, in late BY '05. Nine began sporadically visiting and cleaning out an established den in early March 2006 but as of mid April localized and then settled at another established den six miles to the east. At least five pups were produced at this den in May and were attended there through at least June 24. In early July (by 7/4), at least 5-6



Figures 1-2. Summer and winter wolf locations, May 2006-April 2007 (color-coded).

adults/subadults moved the pups to the den visited in March and attended them at this site and a rendezvous site about a mile away through at least September 10. There may have been short-term moves to one or more other areas during the latter few weeks of this period, and there was further short-term use of the above den and nearby rendezvous site through the first week of October. Margaret's use of homesites ended by October 27. Five or six pups were together with 5-6 older wolves at the second den on July 9; 5-6 pups were still at this den on August 2, 3-5 of which were then at the nearby rendezvous site on September 10. Another observer saw five pups about seven miles to the east (within the Margaret territory) on about October 10. Pups could no longer be distinguished reliably from older wolves based on size after this observation.

The winter observations indicated there were 10 wolves in the group through mid February but that 1-2 uncollared wolves (not necessarily the same individuals each time) were often separated from the others. Two of 14 observations from October 27 through February 17 during which good counts were possible (e.g., when the wolves were not in heavy forest cover and there were good flying conditions) were of 8-9 wolves together, six were of nine wolves together, and six were of 10 wolves together, the last on February 13. Four subsequent observations through February 23 during which good counts were possible were of 6-7 wolves together. Three observations from March 8 through March 19 were of six wolves together. Six remained at one location for at least a week, April 14-21. I could not count them at this location but did observe five wolves departing on April 21. A dead radio-collared female remained behind, as indicated by the onset of the rapid, "mortality-mode," beat of her radio collar on April 19.

K. Beckmen, Alaska Department of Fish and Game, necropsied the dead female (T. Meier, pers. commun.). She was six years old, weighed 85 pounds, and was pregnant with three full-term male pups weighing 600-800 grams; she had also produced pups in one or more previous years. She died from peritonitis - probably with a high fever - secondary to a ruptured uterus caused by blunt trauma, most likely because she was kicked by a moose or hit by a car (she died near the park road). She was almost certainly the only Margaret breeding female in BY '06, thus it is not surprising that the other five wolves remained with her until she died and for two days afterward. There has not been any indication of more than one breeding female in this family group since it originated in 1999.

2. Toklat (East Fork)

Toklat is one of the oldest-known family lineages for any non-human social vertebrate in the wild. As such, it is a goldmine for insights about the cooperative underpinnings of a successful society, among the most important areas in all of scientific inquiry. Toklat was a well-established family when I began my research in 1966. It is likely the same family that Adolph Murie (pers. commun.) studied formally in 1939-1941 and informally until 1967.

Over the past 10 years in particular, Toklat has suffered a series of losses of key individuals and other disruptions due to trapping, shooting, during radio-collaring, and from other human impacts. Toklat currently appears to be in an unusual phase of its long history, following the trapping and shooting losses of the experienced adults in early 2005. Only six young wolves – almost certainly siblings born in 2003 and 2004 (3 from each year) – are known to have remained together within the established territory as of March-April 2005. They have reproduced well (8 pups in 2005, 6 in 2006) with high levels of cooperation (e.g., at least two cooperatively nursing females at the natal den in both 2005 and 2006). They continue to use the same natal den that Toklat has used annually since 1999 and during earlier intervals, albeit in different ways. But they have yet to exhibit other major, longstanding Toklat learning-dependent territory and hunting traditions. They and their young are also much less cohesive as a group during the winter than Toklat was for at least the previous decade.

A review of BY '05 observations indicates that sometime during summer 2005 – probably May or

June – another wolf joined the six young wolves and helped raise the eight pups. This may have been a yearling that was trapped in early February with at least two other Toklat wolves but broke loose from an experimental anchor cable (C. Wallace, pers. commun.); a wolf was observed once, shortly thereafter, within the Toklat territory, dragging a trap on its foot. Fourteen wolves were still together near the end of BY '05, on April 17, 2006, and 12-14 as of April 23. This total and the mix of colors indicate that seven of the eight pups, all six of the subadult survivors in spring 2005, and the additional wolf were likely still together at the beginning of BY '06. The missing pup disappeared under unusual circumstances on July 22, 2005, when the eight pups were alone at the natal den and it ran off toward a distant howl (several miles away).

The identity of the breeders became clearer in BY '06. A female radio-collared by NPS in late BY '05 (4/17/06) was the likely mother of six pups produced in BY '06. Examination during radio-collaring (T. Meier, pers. commun.) indicated she was 2-3 years old, weighed 92 pounds, and had previously nursed pups but was inconclusive as to current or past pregnancies. My subsequent observations at the natal den prior to first emergence of the pups indicated she was inside the den or just outside the burrows more than any other adult or subadult. After first emergence, she and at least one other, somewhat larger, female nursed the pups cooperatively, as in BY '05; it is possible the second lactating female also nursed the pups prior to first emergence.

A large male - the dominant, largest wolf of the group - mounted the above, radio-collared, female on February 23, 2007 and interacted with her sexually in other ways. These were the only two wolves that I observed interacting sexually, and during that period in late February-early March he behaved in the typical highly assertive manner of a breeding male. It was obvious from the way they often rested together closely and from other behavior that they had bonded at least several months earlier, a closeness that continued after the mating period and is still obvious. There were no comparable observations in 2005 or 2006 due to the interruption in regular contact after the previous radio-collared alpha male and female were shot and trapped. Some confusing observations of a black female nursing together with the above female and dominating two other blacks at the den in 2005, before it was clear that a fourth black wolf had joined or rejoined the group, led me to think, erroneously, that the large, dominant (black) male was actually a female and another high-ranking male was her mate. Based on a reexamination of the earlier observations and photographs, it is likely that the current closely-bonded pair has been the alpha/breeding pair since 2005.

Adults moved the six pups from the BY '06 natal den to a series of rendezvous sites in an area 4-5 miles eastward in late July, in at least two stages. I observed four of the older wolves, including the likely mother, in transit with two of the pups on July 31, scenting the ground intently along the way as if following the route of an earlier move. However, instead of joining these two pups with the others, the older wolves went only to the general area and then took them in other directions. Over the next three weeks, I saw two pups of the same description and of normal size and condition with eight older wolves and another observer saw two with at least two older wolves, at widely separated locations. On August 24, the six pups were back together at a rendezvous site about five miles east of the natal den. Since July 31, the two pups had accompanied adults on a route covering at least 35 miles first to the east, then southward, then northwestward, then back eastward. The adults continued to attend the pups together in the eastward area through at least September 10, but as of September 6 and 10 one of the pups was missing. By mid-late October the pups were traveling regularly with the older wolves and could no longer be distinguished easily based on size alone.

I observed 17 wolves together on November 24 and 16-17 on February 4. There were still at least 15 as of my April 21 observations (14 together and a radio-collared female at another location, possibly not alone). These totals and the mix of colors indicate that at least three of the pups were still present on both November 24 and April 21, that likely all but 3-4 of the 20 wolves present (14) and born (6)

at the beginning of the biological year were still together as of at least November and February, and that all but 5-6 were together near the end of the biological year. They indicate that all but 6-7 of the wolves present near the beginning of BY '05 (7, including the wolf that joined) and the pups they produced in BY '05 (8) and BY '06 (6) were probably still together near the end of BY '06. One of the missing wolves, a radio-collared young adult female, dispersed in early March 2007. She was shot shortly thereafter, on March 13 just outside the park, near Cantwell (T. Meier, pers. commun.).

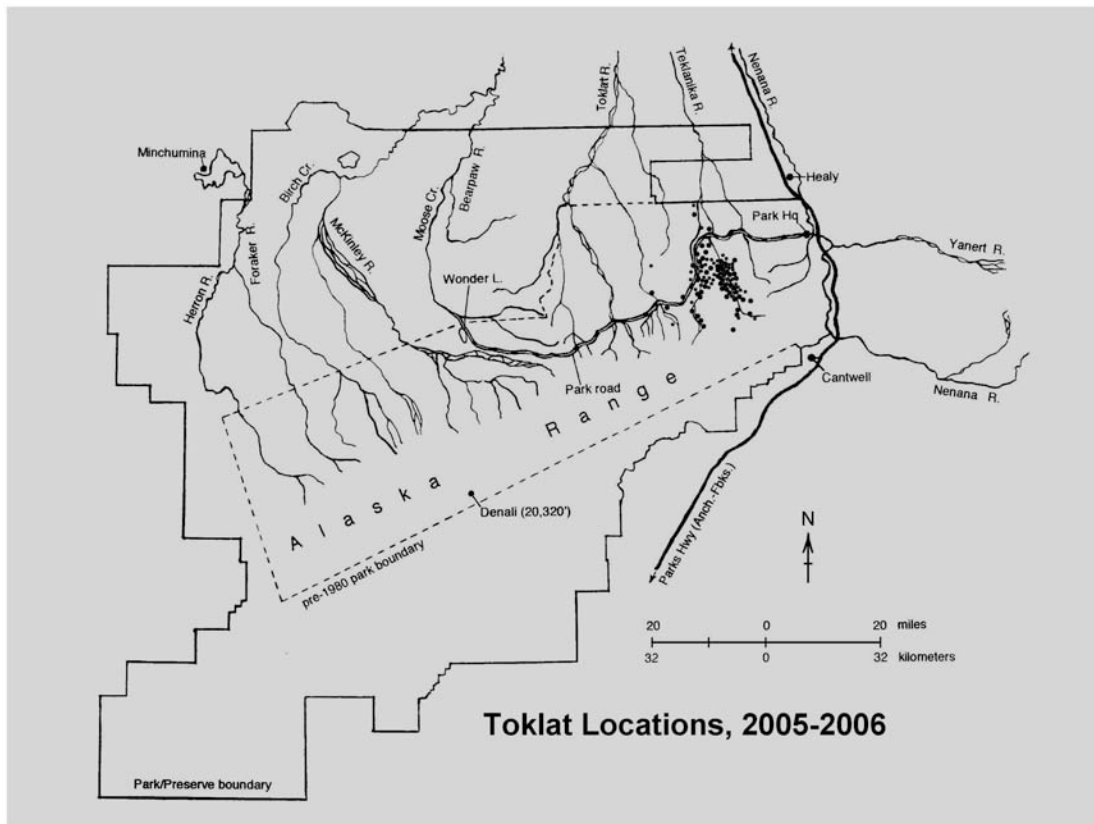
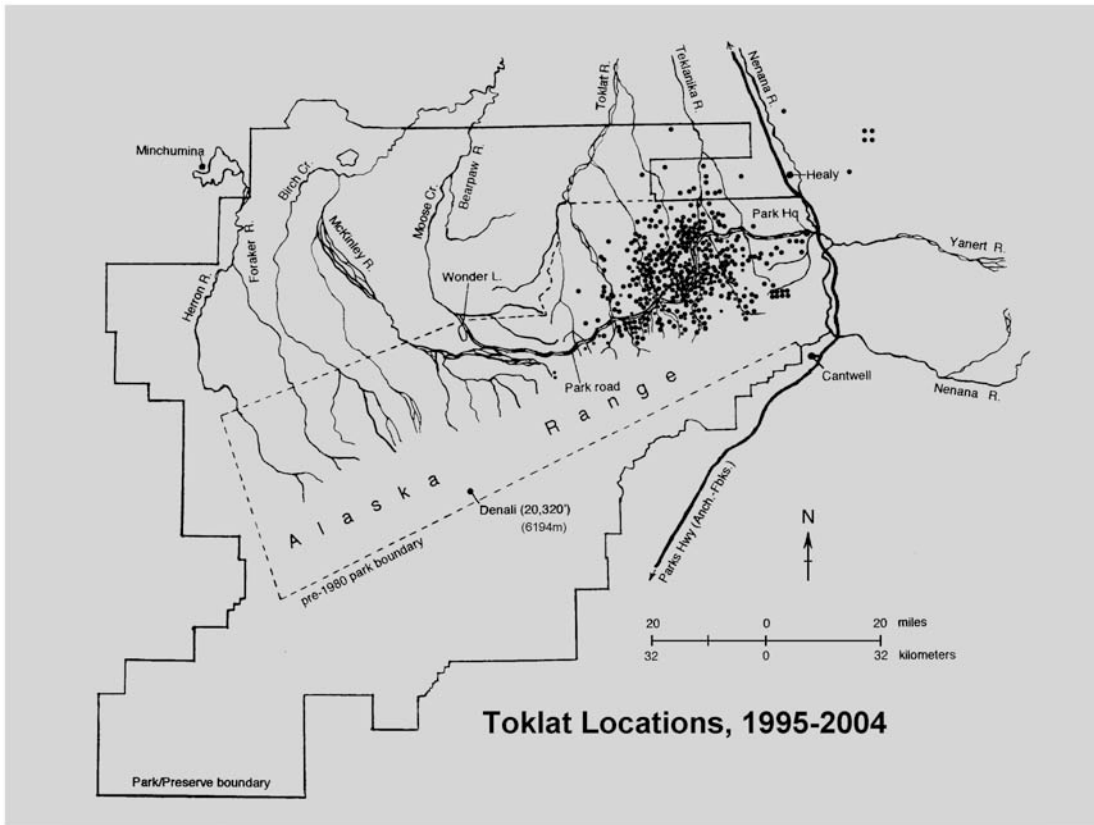
There was much temporary winter splitting. For example, in 37 of my aerial locations of the radio-collared breeding female from October 2006-April 2007 where counts were possible, group sizes, in sequence, were as follows (“+” indicates a possibility of up to several additional wolves that I did not see because of vegetation, poor snow cover, etc.): 14, 7, 15, 14+, 11+, 6+, 13, 17, 15, 13+, 5+, 11+, 12+, 6+, 6, 13, 8+, 2-3+, 14, 16-17, 5-6+, 9, 14, 3+, 6+, 7, 9, 2, 1, 2, 1, 1, 5, 3, 7+, 4, 14.

The winter foraging routine was highly unusual. Instead of hunting and scavenging continuously as a group throughout hundreds of square miles or more of the territory and traveling extensively outside now and then as they did during the pre-2005 winters of my research, and as most of the other study groups continue to do, the Toklat wolves regularly lounged around within the same relative few small areas for long intervals. Figures 3-4 show the major overall reduction in use of the established Toklat territory and in forays outside (refer also to the green solid and dotted territory boundaries in Fig. 2). Figure 4 shows locations only through December 2006, but it can be seen from Figure 2 that the distribution remained about the same through the final four months of BY '06.

Although they are regularly using only a portion of the established territory, the Toklat wolves continue to display normal territorial behavior in defending this reduced area. The neighboring group to the west, Toklat West (Grant Creek), began probing the unused western half of the Toklat territory, particularly within the orange dotted line in Figure 2, shortly after the first of the Toklat adults were trapped just outside the park, as the young were withdrawing to the smaller area and the alpha male (who was later shot) was occupied near the trapping area and elsewhere. Only one of my 15 winter 2004-05 Toklat West locations prior to the Toklat losses was within the Toklat territory, versus 10 of 17 afterward. The eastward trespasses continued in BY '05, now all the way to the far east side of the Toklat territory. Ten of my 21 winter 2005-06 Toklat West locations were within the Toklat territory.

On March 18-19, 2006, three wolves of uncertain identity but probably Toklat aggressively tracked the six Toklat West wolves from at least 10 miles away to a caribou kill 21 miles east of the Toklat West territory, within the Toklat territory near its east side. The three approached the kill with highly aggressive behavior as the Toklat West six slept out of view about 200 yards away. However they ran off when Toklat West awoke and gave short pursuit, after which Toklat West went back to sleep near the kill. Toklat West returned to its own territory on March 26 after two days of apparently unchallenged sheep-hunting – resulting in one sheep kill - inside western areas of the Toklat territory.

Toklat West continued to trespass deeply into the Toklat territory in BY '06. On October 27, 2006, I located 15 Toklat wolves well west of the reduced area, on a rare post-2/2005 trip within the western half of the established territory, heading up the East Fork River a short distance downstream from the East Fork bridge. Meanwhile, 10-11 Toklat West wolves were 16 miles inside the Toklat territory, sleeping in a high valley where they had been hunting sheep, at the head of Calico Creek. They were within the reduced area of the Toklat territory, 12-13 miles *eastward* of the Toklat 15 at 2:30 p.m. (locations included in Fig. 2, in westcentral and southeastern areas of the Toklat territory). When I returned at 12:30 p.m. the next day, the Toklat and Toklat West wolves were in the same area, in and near Refuge Valley several miles eastward of the previous day's Toklat West location. Fourteen Toklat wolves were resting about a mile north of a site where they had killed the Toklat West alpha female and one of her pups. The Toklat West alpha male was a mile eastward, looking back at the 14



Figures 3-4. Toklat locations before and after the experienced adults were killed in early 2005.

as he fled further eastward. An hour and a half later he was back southwestward in the area of his dead mate and pup, then climbed into the steep, snowy 5,000-6,000-ft mountains above. Tracks, the onset of mortality-mode of the dead female's radio collar, and other evidence indicated that the Toklat wolves approached the Toklat West wolves more-or-less directly up Calico Creek, then chased them several miles through the 5,000-6,000 ft mountains eastward into Refuge Valley where they caught and killed the female and pup probably that morning (10/28), in the same general area where they confronted the Toklat West wolves in March 2006. Most of the other Toklat West wolves had scattered in the high mountains, during the chase. The next day (10/29), the Toklat West alpha male gathered six of these remaining offspring and led them at a rapid pace at least nine miles back westward, toward his own territory.

The locations in Figure 2 indicate there is also much potential for trespassing and other interactions between Toklat and its neighbor to the east, Margaret. On several occasions I observed Toklat wolves scent marking aggressively in the heavily used interface between the two territories. On February 3, 14 Toklat wolves pursued 10 Margaret wolves at least eight miles eastward on the park road within the Margaret territory, just after Margaret returned via the road apparently from trespassing in the Toklat territory. Initially the Toklat 14 were miles behind, strung out in a long line, following Margaret's tracks at a full run with tails and hackles up as Margaret moved casually eastward at a normal single-file travel pace, unaware of the pursuit. When the Toklat 14 could finally see the Margaret 10 a mile or so ahead on the road, the front-runners acted even more aggressive and seemed to run even harder toward them.

Remarkably, the Margaret 10 remained completely unaware of the Toklat 14 bearing down on them from behind until the Toklat front-runners actually caught right up to the Margaret tail-enders. It took a short interval even after that for the Margaret leaders to realize what was happening a hundred yards or so behind. It seemed to my pilot and me that there was about to be a bloody 24-wolf melee. There was much milling around together on the road – wolves of the two groups within a few feet of each other - but no actual contact. Some of the Toklat wolves quickly turned and ran back westward and some of the Margaret wolves ran eastward. Several young Toklat wolves further back in the long line of pursuit stopped and ran back westward well before arriving, as if they had enjoyed the chase until realizing what they were chasing.

All of the wolves at the point of contact remained on the road, but then one of the Margaret wolves ran off into brush. This triggered an attack by the Toklat alpha male and alpha female, who caught the wolf in the brush and pummeled it violently for several minutes. By this time most of the other Toklat and Margaret wolves were running westward and eastward, respectively. But a large, uncollared Margaret male came back to a point on the road above the area where the Toklat alpha male and female were pummeling the Margaret wolf. The Margaret male stood there, huffed up, as if ready to jump in. The Toklat pair then ran off, westward. The two remaining Margaret wolves disappeared in the trees. We could not see any blood in the snow and little if any fur; surprisingly, the pummeled wolf seemed to depart without serious injuries. The next day, 16-17 Toklat wolves were together 13-14 miles to the west, hunting snowshoe hares (*Lepus americanus*) inside their own territory, and nine Margaret wolves were 3-4 miles southward, resting. The tenth Margaret wolf re-joined them by about a week later. None of the 10, nor any of the Toklat wolves, showed indications of injury.

Especially noteworthy in my observations of Toklat wolves since 2005 is the absence of any winter sheep-hunting, even within the reduced area of the established territory. Sheep have been a longstanding mainstay in Toklat's winter diet, as they were for Savage. Both groups were at ease in the high, treacherous ridges and peaks of sheep country and developed impressive search and pursuit

tactics. The territories of these two groups include(d) most of the northside park/preserve's only major area of sheep habitat. This is likely a key reason for the relative longevity of the eastern "road-corridor" groups of wolves. Sheep provide an alternative to following caribou to extraterritorial wintering areas, where there are additional survival risks from interactions with resident and migratory wolves.

Toklat wolves appear to have hunted snowshoe hares and little else since 2005, coincident with the latest peak of abundance in the hare population cycle. I observed Toklat wolves hunting hares at 12 of the above 37 radio-tracking locations, and at two others, without any indication that they hunted or scavenged other prey at these 39 or the other 38 winter 2006-07 locations (77 Toklat winter locations total). It was not unusual to see several dozen or more hares hopping around in a patch of willow brush a hundred yards or so in diameter. Typically the wolves fanned out abreast of each other when they entered a willow patch, then stopped at short intervals to look and listen ahead intently. The closest wolf or wolves immediately began leaping after any fleeing hares, zigging and zagging with them through the brush with impressive quickness, agility, and skill. Sometimes a willow patch exploded with 8-10 or more wolves zigging and zagging in different directions in pursuit of a dozen or more fleeing hares. Ravens and red blotches in the snow from hares already eaten commonly followed the wolves among willow patches even at the locations where I did not directly observe the hunting.

Two hare hunts provide an indication of their success. On December 10, 12 Toklat wolves moved through several willow patches with the usual line-abreast driving tactic. During a 38-minute period there were 6-7 hare chases resulting in 4-5 hares killed and eaten by 4-5 different wolves. On February 4, 16-17 Toklat wolves entered a willow-spruce thicket with the driving tactic. During a 15-20-minute period there were 8-9 hare chases resulting in six hares killed and eaten by six different wolves. A seventh fleeing hare ran into 3-4 wolves, two of which likely ate it together. In both observations, each wolf ate its hare without any challenges, attempts to take it away, or other obvious aggression by other wolves, regardless of rank differences. In one case (February 4), a wolf leaped playfully at another that had just caught a hare, but then the leaping wolf walked away.

The wolves sometimes also ignored nearby hares, apparently because they were eating well. On March 14, the breeding female and one of her young were alone, resting 200 yards apart in willows where from above I could see at least 50 hares milling around like ants in a colony, many within 30-40 feet of the female. On September 6, this female, six other adults and subadults, and five pups were moving through willow brush between rendezvous sites. The female caught a hare and immediately carried it to the smallest pup, who ate it. Another pup was soon eating a second hare that it apparently caught by itself. The other wolves, including the other pups, continued moving along steadily, paying little attention to hares leaping nearby or to the two pups that were eating hares (both pups had to catch up to the group after eating). On February 23, a single wolf headed toward six others, including the breeding female and her mate (the alpha male). The single wolf was carrying a hare. A hundred yards or so before joining the others and within view, it buried the hare in snow. The others greeted this wolf when it joined them a little later, but in a rather aggressive way. None went to the hare-cache location.

Much of the unusual winter splitting, the reduced movements, reduced use of ungulates, and other changes can be related directly to the abundance of snowshoe hares. But has the Toklat wolves' behavior changed in these major ways simply in response to hare abundance, to take advantage of a short term opportunity? Or is this primarily the result of broken traditions due to the loss of the experienced adults in 2005? How could temporarily abandoning large areas of an established territory, risking annexation by neighboring groups, be adaptive in the long term, given the

implications for reduced ungulate resources and a sharp reduction in the sustainable group size?

Three points warrant emphasis in considering these and other questions: (a), I saw no indications of comparable or even significant reliance on hares by any other study group this winter and none by Toklat or other study groups during earlier periods of hare abundance, including during research on Savage and Toklat that was at least as intensive as the present research; nor has other wolf research reported it; (b), in the earlier research (1966-1974), I found that young wolves in moose-sheep areas of Denali – specifically young wolves of the Savage and Toklat families – generally required 2-3 winters of learning from the adults for hunting proficiency; and (c), the current Toklat wolves were orphaned as yearlings and two-year-olds, with a maximum of only one and a half winters of learning from the adults. A family group of eleven wolves with 7-8 years of experience (the age of the adults that were trapped and shot) was suddenly converted to six inexperienced young wolves coincidentally during the latest snowshoe hare peak.

The forthcoming hare crash, probably within the next year or two, will provide key opportunities to understand what has happened.

3. Toklat West (Grant Creek)

Toklat West is probably most accurately viewed as a western offshoot of Toklat. Individuals and subgroups have occasionally budded from Toklat and formed new groups within and adjacent to the western side of the Toklat territory since at least the early 1970s. Most recently, in both 1990 and 1996, young females were either known or likely to be raising pups in this area, with occasional friendly visits from core Toklat adults but apparently no lasting associations. In April 2003, the Toklat alpha male's younger brother left Toklat and within a few weeks paired with a female of unknown origin in this area (the brothers were ear-tagged in a group 170 miles away before ending up in Denali in May 2001 and taking over the Toklat family, following the March 2001 radio-collaring death of the established Toklat alpha male).

Thus the Toklat West male is almost certainly the uncle of the six young Toklat wolves that were orphaned in 2005; his (older) brother was shot in April 2005. However, I have not seen any indication that the six, who were born after he left the family, recognize him as closely related or vice versa. Most of the interactions I have observed were hostile (e.g., previous section). During one observation in BY '04, Toklat and Toklat West ended up less than a mile apart where their territories meet. Toklat did not seem to know Toklat West was nearby but Toklat West saw Toklat and fled westward, deeper into its own territory.

The new (2003) Toklat West pair remained in the western area and produced pups in 2004 (6) and 2005 (2-3). They began BY '06 with four of their 2004-2005 offspring and seven new pups at the same natal den they used in 2004 and 2005. All six attended the seven pups during the homesite period, apparently with cooperative nursing by two females – the alpha female and a daughter that other observers determined was lactating. By late July, the older wolves began moving the pups back and forth between the natal den and other sites within a mile or so. Between August 19 and 24 they moved them to a rendezvous site four miles to the south, and by August 28 to a site almost four miles northwest of that site, two miles southwest of the den. The six older wolves continued attending the seven pups at and near the latter site through at least September 24 but no longer appeared to be using any homesites as of early October. At least 12 of the 13 total were still together on October 2, including at least five of the pups.

My next observations, described in the previous section, were on October 27-29, when the Toklat wolves caught 10-11 Toklat West wolves trespassing deeply and killed the alpha female and one of her pups. The alpha male was able to gather up six of his surviving offspring afterward – it looked

like three of the 2007 pups and three of the 1-2-year-olds - and led them hastily out of the area back toward his own territory. The seven were still together within the Toklat West territory in early November. By November 24, there were nine together, indicating that two more – likely including another 2007 pup - found their way back westward 20-30 miles to the others after the October 27-28 confrontation with Toklat (the 11/24 total and colors were consistent with 11 minus the dead female and pup). I saw nine of the same colors and other characteristics on December 12 and January 13 and at least 7-8 during three interim observations. Eight observations indicated at least 6-7 were still together February 1-18 but only six by February 18-20.

The deep forays into Toklat's territory ended after Toklat killed the alpha female and pup, but that did not stop the Toklat West male from taking his surviving offspring far and wide on other extraterritorial forays. It remains an open question as to how much of this behavior was triggered by the loss of his mate. The Toklat West wolves struck out together on distant winter forays in 2005 and 2006 as well – once to the south side of the Alaska Range and once eastward into the heart of Margaret's territory, each time for a week or two in April and despite what seemed to be good sheep-hunting success in the home territory. I saw no indication that the death of the Toklat West male's mate in October 2007 affected him to the extent that the trapping loss of the Toklat alpha female in early 2005 affected his brother. Over the next few months, before he was shot in April 2005, his brother abandoned the six surviving Toklat young and the Toklat territory while searching obsessively outside for his dead mate (now taken away by the trapper) and then engaging with two successive females, both of which he soon lost, the first after she was separated in a likely trapping incident and the second when she was shot.

From at least February 1-13, 6-7 or more Toklat West wolves were at a winter killed moose carcass several miles outside the northwest area of their territory, in an area often hunted by Swift Northeast (#6). They were inside the southeastern area of their territory on February 17, but six were 12-13 miles northward, just outside again, on February 18. The next day, the six were 18 miles further northeastward, where they chased at least 5-6 of the nine resident Stampede II wolves from a mostly-eaten moose kill and took it over. They remained at this kill and in the general area for three days, choosing mostly high vantage points when they rested, at times with nine Stampede wolves 5-6 miles to the southeast and at least 5-6 Toklat Springs wolves 5-6 miles to the northeast.

The alpha male led them from this area on February 23. But instead of returning southward to the home territory, he took them at a rapid pace eastward along a well-used snowmachine/sled dog/ATV trail, toward a mostly-uneaten winter killed calf moose 9-10 miles away, inside the Lower Savage II territory, where earlier in the day we found at least one of the Toklat Springs wolves. The next day (T. Meier, pers. commun.), he was at the calf moose carcass, the radio-collared Toklat Springs wolf had left the carcass and was a half mile away, and at least four of his five remaining offspring were scattered within the previous day's area 8-10 miles westward. The Toklat West wolves may have become separated from each other during a confrontation with the nearby Stampede wolves.

The alpha male ranged within the Lower Savage territory for several weeks, through March 14, mostly alone; this is an especially dangerous place for wolves due to roads, residential subdivisions, essentially unrestricted wolf trapping and shooting, and other groups of wolves. One of the young wolves with him on February 23 disappeared. First three and ultimately four others, apparently the oldest a radio-collared 22-month male, found each other and by the end of February and early March were 30-40 miles southwestward, at locations back inside the Toklat West territory. From about March 6-10 they were outside again a short distance to the northeast at a mostly-eaten caribou or moose kill or winter kill in the Stampede territory. From March 12-16 they were back within the northeastern area of their territory, mostly resting at two locations without any kills or winter kills. On March 14, the alpha male was in the northeastern area of the Lower Savage territory, some 35

miles northeast of the four young wolves. The next day he was in the Stampede territory on his way back toward them, only about 15 miles northward of their location by late in the day. His route extended further west than was required for a direct return, likely because he was circumventing the Stampede wolves who were on the direct route and only 5-6 miles away.

He reunited with the four young wolves late the next afternoon, March 16, after a 21-day separation. They were resting on a high rocky ridge along the east side of the Toklat River valley, about a thousand feet above him and a mile and a half away as he came upriver and reached a point just downstream from their location. It was obvious that he knew they were somewhere in the area but not exactly where. As he approached, he began loping excitedly, then stopped several times to howl and listen while looking intently in their general direction. Likewise they looked around intently in his general direction and perhaps howled but apparently did not see him. Ultimately he continued about a mile further upstream until downwind of their scent in the brisk northeast wind, at which point he turned sharply and climbed almost two miles northeastward to their location. I was not present for the actual greeting, but when we returned shortly afterward the five were curled up sleeping together near that location. All five appeared to be in good, normal condition during this and the preceding and subsequent observations.

With the alpha male leading most of the time, the five hunted sheep inside their territory during my March 17 and 19 observations. But on March 20 they departed their territory again, this time southward across the Alaska Range (apparently through Anderson Pass), much as they did in April 2005. Tracks indicated that earlier they successfully crossed an extremely dangerous, crevasse-filled section of the Muldrow Glacier, which I had also observed this group do in previous winters. High winds and other prohibitive flying conditions limited contact with the five while they were on the south side of the Alaska Range. Nonetheless it was clear that they ranged widely through the rugged, snowy mountains of that region, including into some heavy, dangerous snowmachining areas, at one point only 9-10 miles westward of the Hurricane Gulch bridge on the Parks Highway (outside the national park boundary).

They returned to the north side of the Alaska Range sometime between April 4 and 13. All five were still together and apparently in good condition on April 14. But once again they were outside their own territory, now in the northern area of the Toklat territory. Next, from April 16-21, they were in the heart of the Margaret territory, for the most part within 2-3 miles of the six Margaret wolves while the Margaret breeding female was dying from an unrelated cause (#1) and for at least two days afterward. Strangely, it did not seem that either group was aware of the other's nearby presence. Whenever I could get a good look at the five Toklat West wolves they were sleeping or resting casually. When the five Margaret wolves left the area where the female died and I could finally see them all, they were relaxed and showed no awareness of the Toklat West five, who were sleeping and resting on an open ridge less than two miles away in the opposite direction.

My next observation of Toklat West was not until May 16. At least two wolves – the radio-collared alpha male and young adult male - were back in their own territory but not at or near any known dens.

4. Eagle (Turtle Hill)

I first observed Eagle in 1999 as an uncollared pair in the Eagle Gorge area, 7-8 miles west of Wonder Lake. This pair was subsequently radio-collared and recolonized the current territory just to the east in 2000 after the previous occupants of that area, Beaver Fork, budded a small offshoot group to the northeast in late 1998, failed to reproduce in 1999, and the three remaining wolves died and/or dispersed. The Eagle pair produced pups in most years but none survived beyond early winter.

As with its predecessors, Eagle is one of several groups in the central park area that is heavily

dependent on caribou and often migrates northeastward for varying intervals to traditional caribou wintering areas in Stampede Flats, from the east side of the Kantishna Hills to Healy. The Eagle female was killed by other wolves in December 2003 while the pair was migrating. A young female from neighboring White (Straightaway) joined the male apparently in May or June 2004, well after the normal mating period.

Another young female, who mated with the Toklat alpha male in early March 2005 following the trapping death of his established mate (the Toklat alpha female), dispersed westward after becoming separated from the Toklat male in mid March, apparently in another trapping-related incident. She attempted to join three White wolves 70 miles southwestward in April, in the White territory; the dominant White male seemed to accept her, but two others, both likely females, repeatedly attacked and pummeled her. She eventually left uninjured and was accepted by the neighboring Eagle pair in early June 2005, seemingly with more enthusiasm by the male than the young White female who had joined him a year earlier. The three were together at one of the male's established natal dens in early June but shortly thereafter he died at the den, apparently of old age (T. Meier, pers. commun.). I did not observe pups at this den or anywhere else with the two females, even though at least one of them had engaged in what appeared to be a normal copulatory tie (with the Toklat male). The two females continued ranging within the Eagle territory, albeit often separated by a few miles.

In October 2005, they were joined by a large, young adult male of unknown origin. The three remained together in what seemed like a loose relationship, with no indication of any pairing during the subsequent courtship and mating period in late February-mid March 2006. They were still together at the beginning of BY '06, without pups and not using a den. Based on field examination of tooth wear and other physical features during radio collaring, T. Meier (pers. commun.) and others estimated that, as of May 2006, the male was about three years old, the first female (from White) was about seven years old, and the second female was 4-5 years old. From behavioral and other observations dating back to 2003, I concluded that the second female was more likely a Toklat pup of 2003 and thus was three years old in May 2006.

The loose relationship between these three wolves continued in BY '06. In the 16 summer (May-Sept.) aerial radio tracking locations where I could determine if they were together or separated by at least a mile, they were together 53% of the time. I observed the following summer combinations, in sequence (a question mark indicates the wolf was separated but its collar was not heard): 3, 3, 3, 2+1, 1+1+?, 2+?, 1+1+1, 3, 2+1, 2+1, 1+1+?, 2+1, 3, 3, 2+1, 2+1. In the seven cases of the 16 when one wolf was separated, the male was by himself three times, the older female once, and the other female three times. In the 37 winter (October-April) aerial radio tracking locations where I could make these determinations, the three were together 73% of the time. The combinations, in sequence, were: 3, 3, 3, 2+1, 3, 3, 3, 3, 3, 3, 3, 3, 3, 2+1, 2+1, 2+1, 3, 3, 3, 3, 3, 3, 3, 2+?, 2+?, 3, 3, 3, 3, 3, 3, 3, 3, 2+?, 3, 1+1+?, 2+1(dead), 2. The younger female was by herself in all eight cases when one was separated from the other two. Wolves of family groups are commonly separated from each other temporarily during the summer – more often than in winter - because of the different summer hunting routine while provisioning pups at fixed homesites; wolves regularly depart on and return from hunts individually and in small groups. The more frequent summer (vs. winter) separations are noteworthy in this case because Eagle did not reproduce or use summer homesites for any other reason.

Eagle embarked on three BY '06 caribou-related winter migrations 20-30 miles northeastward, to a traditional caribou wintering area (a portion of Stampede Flats) in the Stampede II wolf territory. The younger female was alone on the first migration, which lasted from approximately January 6-16, 2007. The other two wolves began the second migration on March 6 without her, but she rejoined them on March 8-9. The three were still together in the Stampede II territory on March 20, but the two were back in the established Eagle territory without her on March 31.

The three were together in their territory on my next observation, April 14, a day or two prior to departing on the third migration. The male and older female were at separate locations in the caribou wintering area when I next tracked them on April 16, but I did not locate the other female until April 19. She was dead 6-7 miles away but from the air and in photographs showed no obvious indication of a violent death and was still intact. T. Meier (pers. commun) landed via helicopter for an in situ examination on May 13. She had suffered massive muscle damage and hemorrhaging in the neck area (not obvious until palpating her), almost certainly from an attack by other wolves, probably the resident Stampede II wolves who were in nearby areas on my April 16 and 19 observations.

The male and surviving female were together at a location some 20 miles to the southwest on April 19, within the heart of the Swift Northeast territory. They were back in their own territory, still together, on April 21, my last observation of BY '06.

I observed mating activity in this reformulated triplet for the first time on March 17, 2007, while they were on a migration and in a prolonged (unsuccessful) standoff with a moose in the Stampede II territory. The male and older female tied for at least 18 minutes while the younger female was 50 feet away in a spruce thicket, apparently sleeping. By early June (BY '07), the mated female was denning inside a beaver lodge within the central portion of the Eagle territory.

I still refer to this group as "Eagle" despite the absence of any known genetic continuity. As noted earlier, social groups, including family lineages, are based on varying degrees of social as well as genetic continuity. The death of the original Eagle alpha male in June 2005 may have broken the genetic continuity, but the White female who joined him about a year earlier had an opportunity to learn at least some features of the territory, winter migrations, etc. from him, and the other two wolves have had 1-2 years to learn from her. This is unlike the earlier transition, for which the available information indicates the (Beaver Fork) occupants died and/or dispersed and were replaced by the pair from the west.

I am reminded of criticism in the 1998 book, *The Wolves of Denali*, of the idea that the current Toklat (East Fork) wolves are likely the same family lineage as the wolves that Adolph Murie studied in 1939-1941 because the original genes would now be so "diluted." For what social group do the original genes *not* become diluted? This is especially true for human families, into which newcomers are accepted at high rates by marriage and occasional adoptions. Would anyone dispute that the generations of McDonalds who have continuously occupied the same Nebraska farmstead for 150 years are a family lineage? Diluted as the current McDonalds are genetically, they still use the (several times renovated) farmhouse and barns that old McDonald built, bring the cows home on the same pasture trails, and celebrate the harvest with strong remembrances of the old man and the farm's trials and tribulations.

5. White (Straightaway)?

I began observing White in 1999 as a pair in the White Creek area within the current Swift territory (#14). A well established group, Muddy (McLeod), that occupied most of the area eastward to about Muddy River decreased for unknown reasons from 14 wolves in late winter 1996-97 to three by late January 1998 and 0-3 a month later. By fall 1998, 2-3 wolves were together in this area (one from West Flats, #13; the others survivors or recolonizers?), but apparently they did not reproduce in 1999 or 2000. There were three by June 2000, when they began shifting westward. Only one of the three, a female, remained as of September 2000, and she died or was killed by other wolves in October. The White wolves (one of which probably came from Beaver Fork, #4) shifted eastward and occupied the Muddy vacancy, including an established den, in June 2000. They produced six pups and were joined by two other adults/subadults in 2000, then maintained a late winter size of 9-12 wolves from 2001-2004. White is another of the central park groups that depends heavily on caribou and migrates

northeastward to traditional (Stampede Flats) caribou wintering areas in most years.

I lost regular contact in summer 2004 after a radio-collared White female paired with the neighboring Eagle male and the other collared White wolves died, probably from natural causes. In April 2005, I observed three wolves in this area, including a dominant nearly-white male, and in fall 2005 caribou researchers observed eight. In both cases, these were most likely White wolves. In March 2006, NPS radio-collared a dominant whitish male who was with seven others 50 miles northeastward; this, too, was most likely White, on a caribou-related migration. A month later, the Swift Northeast wolves intercepted the eight while they were heading back southwestward through the Swift Northeast territory toward the White territory and killed the dominant male, the only collared wolf in the group.

In March 2007, NPS collared a group of eight wolves within the previous White territory (T. Meier, pers. commun.), though it is not yet certain that this is the previous (White) group. When I began observing the newly-collared group on March 10, only six wolves remained and they were hunting 15-20 miles northeastward within the Eagle and Swift Northeast territories. At least five of the six were still together on March 20 shortly before they returned to a denning area within a central area of the White territory by March 31. My observations on April 14, 16, and 21 were all within the White territory but because of brush and poor snow conditions I could confirm only that at least four wolves were still together.

6. Swift Northeast (McKinley Slough)

Swift Northeast apparently formed (or was reformulated) in early 2002 when a male from Swift (#14) joined a female and another wolf 20 miles northeastward in the present Slough territory (#11) and produced 6-7 pups with them in spring 2002. In winter 2002-03, Swift Northeast shifted eastward into the present area (#6), where there is more access to caribou and moose. The previous small resident group of the eastward area appeared to dissolve naturally by February 2003, when one of the remaining two wolves died and the other disappeared. Swift Northeast maintained a late winter size of 6-10 wolves from BY '02 through BY '06.

Swift Northeast used a natal den on a tundra pond in what seemed like an inferior hunting area near the west side of the new territory in 2003 and 2004; this den was apparently also used in 2002, prior to the full eastward shift. In 2005 and 2006, the primary natal site was in a beaver lodge 18 miles eastward, in a better hunting area within the southcentral portion of the new territory. The original, oldest, female began each of these two years at two other dens 13 and 15 miles northeast of the beaver lodge den. She was periodically joined by 1-2 other adults or subadults but most often seemed alone. Apparently her attempts to raise her own pups failed, and in both years she was in attendance at the beaver lodge den within a month or two.

Ten wolves were still together in Swift Northeast near the end of BY '05, on April 18, 2006. Three pups were produced at the beaver lodge den in BY '06, all of which were only half to two-thirds the normal size of Denali pups on August 7. The female that produced three pups at the beaver lodge den in 2005 seemed only loosely associated with this den in 2006. As of early August, I began observing her and 1-2 other adults at and near an established den 17 mile to the northeast. I observed at least one pup at this second den on August 21, and NPS (T. Meier, pers. commun.) observed three on August 27. It was unclear as to whether this was a second Swift Northeast litter or the beaver lodge litter moved northeastward after August 7; I did not observe pups simultaneously at the two dens nor at all at the beaver lodge den after August 7. The last activity observed at or near the beaver lodge den – by at least five adults – was on September 28-October 7, although this may have represented a return rather than continuous use since early August. My last evidence of use of the other den was on August 27.

The female who had been using the latter den was 13-14 miles northward of this den with two other adults on September 2. She was 13 miles further northward on September 10, possibly with one or more other wolves, just outside the park on state lands within a hundred yards of a cabin where at least one moose hunter was present at the time and it was legal to shoot wolves. Her fate after that and the fate of any pups she may have been attending to the south are unknown; despite extensive searches, neither me nor NPS ever heard or saw her radio collar again and it has not been returned to NPS (T. Meier, pers. commun.).

The other remaining collared wolf, i.e., the old original female, and eight other wolves were together 3-4 miles from the above (now unoccupied) cabin on October 28; two of the nine may have been pups. The next day the old female was alone 30 miles southward, and by November 4 she was dead 19 miles further southwestward in a northern area of the Eagle territory (#5). She was intact and appeared to have died while resting in a normal position. There were tracks of 2-3 other wolves at this location. At least two of the Eagle wolves were 4-5 miles south of the dead female on October 29, and all three were together nine miles east of her on November 4. T. Meier (pers. commun.) examined her in situ on December 11; blood underneath her still intact (albeit hollowed out) remains indicated she may have been wounded, perhaps from an earlier attack by wolves.

The death of the old female meant there were no more functioning Swift Northeast radio collars. The next regular contact with this group was in March 2007, when NPS recollared two of eight wolves (T. Meier, pers. commun.). I did not resume contact until early BY '07.

Swift Northeast has increasingly ventured on northeastward extraterritorial forays/migrations over its first three full winters in area #6, especially 2005-06, in much the same manner as Eagle, White, and the previous area #6 group. The loss of most winter contact precluded a determination of the extent of Swift Northeast's forays in BY '06.

Swift Northeast is especially vulnerable to legal hunting. Like other migratory groups and groups such as Margaret and Toklat whose territories extend somewhat outside the park, Swift Northeast ventures onto adjacent state lands where there is essentially unrestricted wolf hunting and trapping. The female that was last seen at the northern moose-hunting cabin in September 2006 is a case in point of this exposure. In addition, NPS allows a so-called subsistence hunt in the Kantishna area each fall from September 1-20, for special permittees primarily from the nearby communities of Cantwell, Denali Park, and Healy. The hunt area, which is virtually in the center of Denali National Park and Preserve and is easily reached via the park road, includes most of Swift Northeast's territory. While the hunters are mainly after moose, they are also allowed to shoot up to 10 wolves apiece of any age or sex, including pups, even though there is no reasonable subsistence use of a wolf at this time of the year. NPS allows them to drive their pickups to Kantishna via the park road and along a six-mile abandoned mining trail from the park road up Moose Creek (with repeated crossings through the creek itself) into a remote area less than a mile from the beaver lodge den that Swift Northeast has used since 2005. An area of about a half-mile radius around the den is closed to all entry. Nonetheless, the wolves regularly travel to and from the den outside the closure, including on the mining trail, and move their pups unpredictably to nearby rendezvous sites outside.

So far, hunters haven't shot any Swift Northeast wolves. But NPS is leaving this to chance and individual whims of the hunters, some of whom have track records of killing wolves elsewhere and of viewing wolves as their moose-hunting competitors. The Federal Subsistence Board authorizes the Kantishna hunt. However, NPS retains overriding authority to modify or close it and to more tightly regulate vehicle access into the hunt areas.

7. Stampede II (Chitsia)

An established area #7 group, “Stampede,” decreased from 7-8 wolves in October 1996 to 2-3 by May 1997 and did not produce any surviving pups in 1997. In 1998, the alpha male and a female who may have been his daughter produced three pups. One wolf disappeared and the alpha male died in April 1999, apparently from injuries sustained while killing a moose, leaving three wolves in the group by late April – his mate and probably two of their 1998 offspring. These three attended pups at a den in 1999, but none of the pups survived beyond June following abandonment of the den when a lightning-caused fire approached to within a hundred yards. Only a younger male remained with the female by April 2000. At least one pup was present with this pair in May 2000 but (together with any littermates) disappeared by September. The female then died of natural causes in summer 2001. The younger male remained alone until joined by a wolf of unknown origin in late January-early February 2002. The male was dead within his territory on my next observation, March 4, 2002; he was probably killed by nearby migrating/trespassing wolves, and his recent companion was gone.

Two wolves, one of which came from Stampede, occupied an adjacent area to the south by early 2000 and then expanded into the Stampede vacancy. This pair did not reproduce much if at all until 2003 when it produced at least two pups at an old den in the southwestern area of the Stampede territory. The male died a natural death (details unknown) in late June-early July, after which the pups died and the female began ranging primarily in areas southwest of the Stampede territory. She was still alone and ranging primarily in the southwestern area when I lost contact with her in late October 2003.

The current resident family group, Stampede II, probably recolonized area #7 in 2004. I began observing Stampede II in March 2005. The 4-5 adults and subadults produced four pups in BY '05, at an established den that Stampede had used. The seven adults and subadults present a year later produced at least six pups in BY '06. In early August, they moved the six pups to a rendezvous site 8-9 miles to the north, in a northcentral area of the territory. They moved the pups again by August 27, to a site five miles to the south-southeast (4-5 miles northeast of the natal den) where adults had been harassing a grizzly bear with a cached moose or caribou kill since at least July 31. I observed only five pups at the new site, where the bear was still present on August 27 but departed four days later. In early September, the adults provisioned the pups at this site in part by regurgitating from a skinned grizzly bear carcass that moose hunters had shot three miles eastward. Stampede adults ate at this carcass on repeated visits, even though it was only 150-200 yards from the still-occupied moose-hunter's camp. The adults may have moved the pups back to the natal den by September 10. They continued provisioning them through at least October 2 but by October 28 no longer used homesites.

All seven of the adults and subadults present at the beginning of BY '06 were still together through October 2. There were 11 wolves total in the group through November 24, including at least four pups. At least 10, including three or more pups, were still together on December 9, and at least nine, including two or more pups, through March 19. There were few opportunities for good counts after that, but my April 14-21 and early BY '07 observations indicated there were at least six Stampede II wolves through the end of BY '06.

At least twice, trespassing wolves routed the Stampede II wolves from moose kills inside their own territory. On November 25, the Stampede wolves were voraciously eating a yearling or adult moose they had just killed on the ice of a small creek in a southeastern area of their territory. Poor light and brush did not allow me to get a good count, but at least 5-6 of the 11 wolves I had observed elsewhere the day before were present. Meanwhile, the five Lower Savage II adults and subadults were only 1-2 miles downstream, romping together playfully as they approached the kill; neither group showed any indication it was aware of the other. Oncoming darkness forced us to fly off at this point, prior to the actual confrontation. When we returned the next afternoon, the five Lower Savage wolves were eating and playing at the moose carcass, much of which was still uneaten. Seven of the Stampede

wolves, including the alpha male and at least several pups, were five miles to the northwest, heading westward, but I was unable to find the alpha female and three others. The five Lower Savage wolves did not leave the moose kill and return to their own territory until November 28. The Stampede wolves remained in areas of their territory further to the northwest through December 9, at which time the alpha female and at least two others were back together with the seven.

The second eviction was in the northeastern area of the Stampede II territory on February 19, when six Toklat West wolves chased at least 5-6 (of 9) Stampede wolves from a mostly-eaten moose kill, as noted in the Toklat West section (#3). In this case, the Toklat West six diverted several miles to the kill from their route of travel, apparently after scenting the kill and/or the Stampede wolves. They studied the oblivious Stampede wolves intently from an adjacent ridgetop for a minute or two before charging down the slope aggressively, in a line abreast. The Stampede wolves saw them coming about half way down the slope and fled in several directions, without any attempt to challenge them. The Toklat West six remained at the kill for three days. The nine Stampede wolves were back together by February 22 but apparently did not return any closer than 5-6 miles to the kill while Toklat West was there.

8. Lower Savage III (Pinto)

Area #8, like area #7, is within a traditional (Stampede Flats) Denali caribou wintering area and thus attracts wolves from near and far. Resulting winter competition and strife among the areas #s7-8 resident groups and various migratory groups has likely been a major factor in the high rates of turnover observed for these groups. Trapping and shooting – to which they are unusually vulnerable because of proximity to Healy and its western subdivisions - also contributes heavily and in recent years appears to have been the primary cause of the turnovers in area #8. Lower Savage III is probably the fourth major group to occupy this area since 1987 alone.

The previous group, Lower Savage II, occupied the area by March 1998 and by July-August included at least one wolf from Sanctuary, Margaret's predecessor in area #1. Lower Savage II consisted of four wolves in April 1998, eight in April 1999, 8-13 in April 2000, then 17 in fall 2000, five of which were shot in a single late-October incident. Despite sporadic known or likely trapping and shooting losses, Lower Savage II continued to maintain a size of 12-15 wolves. I was circling low overhead on November 3, 2002, watching six adults and five pups of this group (3-4 were elsewhere at the time) when one of the most powerful earthquakes ever recorded in North America struck – 7.9 on the Richter Scale, with the epicenter only about 70 miles eastward. Perhaps it was symbolic of Lower Savage II's resilience to previous shooting and trapping losses that during this earthquake all 11 remained stretched out on their sides, asleep, showing not the slightest response.

But the losses continued to mount later that winter and during BY '03, until the group probably dissolved in winter 2003-04. I was still seeing 11-12 wolves together as of February 19, 2003 but not more than eight by late March. On April 10, the radio collared male was out of view in trees just off the west side of the Parks Highway, a half mile north of Otto Lake, essentially within the Healy town limits. I suspected that others were with him and that they were shot or trapped.

The two collared wolves were back together and with a third wolf in a safer area of the territory four days later (albeit with the male's collar transmitting very weakly), but after that there were just the two collared adults. They produced three pups at a den in a southeastern area of the territory in May 2003 and by early August moved the pups to a rendezvous site 15 miles to the west. I last saw the five together on August 29, traveling along Savage River. On September 6, a hunter shot the adult female. I could hear the male's malfunctioning radio collar in the general area but it was too weak and nondescript to track; I never heard or saw it again.

On February 17, 2004, the Eagle male, who had not yet found a new mate following the death of his established mate in December 2003 (see #4), was with two wolves in the Lower Savage area, about a hundred yards from an active trapline. On March 3, I observed him in the same area, again near the trapline, with a wolf that NPS had since radio collared. However, by March 6 the Eagle male was alone in other areas and by April 10 the second collar was transmitting from the trapper's house, 7-8 miles to the east. The two wolves with the Eagle male on February 17 and the newly collared wolf with him on March 3 could have been Lower Savage II survivors from fall 2003. Whatever their identity, at least one and likely both were trapped in late winter 2003-04, and Lower Savage II was probably terminated by that time.

In March 2006, NPS radio collared a group of wolves that had most likely recolonized area #8 since 2003. There were six in the group when I began my observations in March 2006. There were still six on April 22, and both collars were present when I last checked on April 23. Sometime over the next week, someone legally shot the radio collared female and later returned the collar to NPS. This was the wolf that NPS determined at the time of collaring to be the likely breeding female (T. Meier, pers. commun.). NPS did not learn she had been shot until well after the fact, so there was no opportunity to determine her current breeding status via necropsy or field examination; the individual who shot her (not identified to me) apparently provided little if any useful information. The five surviving wolves continued to range within the established territory, but there was no reproduction or use of a den in BY '06.

There were still five in the group through at least November 28, 2006. When I was next able to obtain a good count, on January 6, 2007, the collared male was alone with a new wolf, a smaller black that was likely a female (the male and the four others were tan-gray). It was not possible to determine whether the four separated from him naturally or were trapped/shot; they were not with him in any of my subsequent observations. The black wolf limped most of the time with an injured right front paw, but he was attentive in what seemed like a close relationship that lasted through February, after which the black disappeared. The male continued ranging within his established territory and by March 8 was accompanied by two other wolves – a radio collared adult female who was previously the breeding female of neighboring Toklat Springs (#9) (T. Meier, pers. commun.) and a wolf - possibly a subadult - of unknown origin. These three were together during all of my remaining opportunities for good counts through April 21 and at an established Lower Savage natal den in early BY '07.

9. Toklat Springs

NPS has monitored Toklat Springs since 2004, but my contact did not begin until December 2006. This is another group with a recent history of heavy hunting and trapping losses, including of the alpha male who was shot in fall 2005 in a northwestern area of the territory, a pup and young adult female shot in fall 2006 in northwestern and eastcentral areas (T. Meier, pers. commun.), and two young adults trapped in early 2007 in a central area of the Lower Savage III territory.

There were still at least a half dozen wolves in this group in late February 2007, based on my observations of seven together in a northeastern area of the Lower Savage III territory on February 20 and at least 5-6 at a winter killed moose in a southeastern area of their own territory on February 22. As indicated in the preceding section, by March 8 the Toklat Springs breeding female joined the Lower Savage III male in his territory. My subsequent eight observations through March 20 were of only the one remaining Toklat Springs wolf with a functioning radio collar, a young adult male. As of February 22, this wolf ranged primarily within the Lower Savage III territory and seemed to be mostly alone. When I observed him next, on April 19 and 21, 2007 (my last observations of BY '06), he was 10-15 miles north of the Toklat Springs territory.

On December 15, 2006, I found the above male together with at least 3-4 other wolves at Toklat

Springs, in the northwestern area of the group's territory. At least one of the 3-4 appeared to be a pup (I actually saw only one or two; tracks leading to an adjacent forested area indicated there were 3-4+). Simultaneously six adult/subadult Toklat Springs wolves, including the other functioning collar, were at a mostly-eaten winter killed moose six miles to the southwest. The additional 3-4+ wolves at the first location were probably the 2006 pups that T. Meier (pers. commun.) found alone in the same area in March 2007, heavily infested with lice but otherwise healthy (~85 lbs). Whether they were an abandoned or otherwise separated Toklat Springs litter or orphans from somewhere else has not been determined.

Toklat Springs and Lower Savage III interacted closely within the Lower Savage III territory in January-March 2007, ultimately with the Toklat Springs breeding female joining the Lower Savage male. Perhaps there was a prior relationship between these groups. Whatever the case, it is not surprising that breeding adults from such hard-hit neighboring groups who had lost their respective mates would end up forming a new pair.

Groups 10-16:

Although the areas of Denali National Park and Preserve north and west of Wonder Lake are far from the road system and most of the groups (other than #s 5-6) do not migrate seasonally to high-risk northeastern areas, these areas have nonetheless seen a long history of wolf trapping – by, among others, trappers based at Lake Minchumina (current), the mouth of the Bearpaw River (as recently as the late 1990s), the Kantishna River (current), Kantishna (near Wonder Lake) (as recently as the early 1980s), Swift Fork River (possibly current), and the Tonzona River (as recently as the early 1980s). Current Minchumina trappers alone maintain traplines extending through portions of areas used by at least four northwestern and western groups - #s 11-14, and at times #5, via at least two cabins they built inside the park/preserve in the early 1990s with NPS permission. This trapping activity in combination with the remoteness of the area (and thus its lower-intensity research coverage) makes distinguishing between natural and trapping causes of observed group turnovers and mixing at least as difficult as anywhere else in Denali.

10. Bearpaw III

A group that used a major portion of the current Bearpaw territory beginning in 1989 - i.e., Chitsia (not the same NPS "Chitsia" in #7) - may be the same group that I followed in 1996-1997, until in early 1997 a single trapper based at the mouth of the Bearpaw River trapped 11-12 of the 13 wolves present at that time. A group of 5-7 wolves, Otter, used an area coinciding more closely with the current territory by at least 1999 but seemed to die out in 2001 or shortly thereafter (including from at least one radio-collaring mortality). I began my observations of Bearpaw III in 2004, shortly after NPS radio collared the current residents, though it is uncertain if Bearpaw III is actually a new group or a regeneration from Otter survivors.

There were 2-5 wolves in Bearpaw III at the beginning of BY '06. They produced at least 5-6 pups at an old den in a central area of the territory, and this den was occupied through at least August 9. My opportunities for good counts were limited; I observed 10 wolves total on November 25, eight total on February 17, and at least 5-6 on March 12. Five consecutive locations from October 27-November 25 and two others – on December 12 and January 12 - were along and near the same open leads in a hot springs section of Moose Creek, indicating that the wolves may have been attracted by the salmon fishing of this area.

11. Slough (McKinley River)

A well established group, East Flats, that used this area and surrounding areas decreased from 9-10 wolves in fall 1997 to 1-3 by April 1998 with an active trapline extending through its territory (as in most winters) There were five wolves in the area during fall 1999 but I did not determine their

identity or status after 1999. Slough apparently succeeded Swift Northeast (# 6) in area #11 after Swift Northeast shifted eastward in 2003. I began my observations of Slough in 2004, shortly after NPS collared a pair of wolves in this area. This pair produced pups at the same, well established slough-area den in 2004 and 2005 that East Flats had used, but apparently none of the Slough pups survived beyond 12 months of age.

The Slough pair produced at least four pups at this den in BY '06 and continued to base there at least through August 2006. The two adults and four pups were traveling together (no longer using a homesite) by at least October 2. There were only three pups – five wolves total - traveling together as of October 7, and still only five total on October 27. There were six again by December 9; all appeared to be in good condition. My last good counts were of five total on both February 3 and 18. At least 2-3 were still together on March 14 and at least two on April 16.

12. Starr Lake

A group of six uncollared wolves that I observed sporadically in this area beginning in early 2001 may have been the group that NPS radio collared and named Starr Lake in late February 2006. I began observing the newly collared Starr Lake wolves on March 3, 2006 and located them 11 times through April 20. However, they were almost always in brush, preventing me from obtaining good counts. I saw at least three together on March 3 but never more than two in the subsequent observations. A female whose radio collar I last heard on March 29 apparently drowned after falling through creek ice in April (T. Meier, pers. commun.). There were still at least two wolves in the group as of my April 20, 2006 observation.

I did not obtain any evidence one way or the other about possible reproductive activity or use of a den in BY '06. On November 24, I saw one collared wolf, probably a female, and tracks of at least 3-4 others nearby, but the same wolf was alone the next day. This wolf was together with at least one wolf on December 9, was alone on December 12, then was together with only one wolf on February 3 and 17, apparently the same wolf in both observations. I could determine only that at least one wolf was present in the subsequent observations. There were indications of active traplines in two areas used by Starr Lake wolves during winter 2006-07, north and southeast of Lake Minchumina.

13. Castle Rocks III

A group that I began following in 1995 in this area and areas somewhat eastward and southward, West Flats (Foraker), apparently originated in 1988 and lasted until late 2001 or early 2002. A series of declines beginning in 1997 can be explained in part by natural causes, but as usual there was much trapping activity in the area and not necessarily full reporting of trapped wolves without radio collars. There was also much dog mushing, originating from Minchumina and local base camps, for commercial tours as well as trapping, raising the additional possibility of impacts on early pup survival from canine parvovirus. West Flats consisted of 15-16 wolves at the end of BY '96 (April 1997), seven at the end of BY '97, 8-9 at the end of BY '98, six at the end of BY '99, and probably 3-5 at the end of BY '00. At least two adults died naturally in summer 2001, and only a single wolf, a male, remained as of fall 2001. I last observed him alive on November 26. When I tracked him next, on January 24, 2002, he was dead within the established territory, apparently from natural causes.

In 2003-2005, I tracked a single adult of undetermined origin, probably a male, Castle II, within portions of the West Flats territory. On June 2, 2005, the Castle II wolf was 5-10 miles north of the usual territory, and on July 23 and August 1 was 60 miles southeastward in central areas of the Eagle territory. He was alive on my July 23 observation but dead, five miles away, on August 1. From the air, it appeared likely that death was from a natural cause.

I began following two Castle III wolves – a male and a female – shortly after NPS radio collared them

in March 2006. My BY '06 observations were derived at three summer (May-Sept.) and 11 winter locations. The pair produced at least four pups. On August 9, I observed four relatively large pups at a den or rendezvous site. The four pups were with the adult male 15 miles northward on August 27. The pups were climbing all over an active beaver lodge, and he was at the edge of the pond a hundred yards away, studying a cow and calf moose who were standing 30 feet out in the water, watching him. On January 12, five of the Castle III wolves were together; one of the pups was missing. In two of my previous three observations, November 25 and December 9, I saw at least 3-4 together in brushy, forested areas on or near fresh snowmachine trails that probably represented a trapline. At least four were still together – the two adults and two pups – on April 16, my last observation of BY '06.

14-15. Swift and Swift West (Hawke and 100-Mile)

For much of the past eight years and probably longer, two groups of wolves have ranged across areas 14-15 with considerable overlap in their movements, significant intermixing of individuals, and use of the same established natal dens separately and together. Most likely one group is a derivative of the other, though not necessarily Swift West from Swift; it might be more accurate to refer to them as Swift and Swift East. The recent history of wolves in the two areas indicates the relationship, whatever its details, is probably quite complex and variable.

Seven wolves that were ranging across most of the upper Foraker-upper Swift Fork area produced at least 3-5 pups in May 1999. There were still 11-12 wolves total in this group, Swift, as of April 29, 2000. In May, they produced at least 7-8 and perhaps as many as 12-13 pups in multiple litters at an old natal den in the upper Swift Fork area. By October 2000, 23-25 wolves were ranging in two groups within the Foraker-Swift Fork area and westward – usually 17-18 and at least once 19, including at least 7-8 pups, in Swift, and usually six, including 2-3 pups, in Swift West. By December 2000, 17 wolves (including 7-8 pups) consistently traveled together in Swift and six (including 2-3 pups) in Swift West. The six included a high ranking, radio-collared adult who had associated primarily with the larger group at the 2000 natal den and through at least November 8. The high ranking adult and apparently one other of the six was/were temporarily back with the larger group in February 2001, at which point that total was 18 (one of the 17 died in December or early January).

On April 28-30, 2001, the 16 Swift wolves headed north down Birch Creek on an extraterritorial foray. While passing through the West Flats territory they encountered two radio-collared West Flats wolves, a male and a female, and may have injured the female. Afterward the male aggressively followed the sixteen a hundred feet behind as they continued single-file down Birch Creek, until two Swift leaders finally saw him and chased him for about a quarter mile back upriver. The 16 resumed their northward trip and he returned to the female's location, out of view in heavy forest cover. I was not able to monitor the Swift wolves' foray after April 30, but when I left them on that date they were confronting a large grizzly bear guarding a cached moose carcass five miles southeast of Lake Minchumina, just off a snowmachine trapline trail from Minchumina. Meanwhile, the six Swift West wolves were ranging within established areas east and northeast of the upper Swift Fork.

Apparently nine of the 16 Swift wolves and four of the six Swift West wolves present at the end of BY '00 raised about a half dozen pups in BY '01. The major den used in 2000 was not occupied in 2001, but the Swift West adults and subadults appeared to be based at another established den a few miles away. On August 1, I observed at least eight of the Swift wolves within 3-5 miles of the 2001 den, heading toward it from two locations while the Swift West female was present. At least one of the Swift wolves (radio-collared) was carrying a large chunk of red meat, as if to provision pups, although no pups were visible during my checks of the den on this and two other summer 2001 flights. I did not find any other active natal dens. Thus it is possible that in 2001 Swift and Swift West wolves again provisioned multiple litters at a single den.

By November 2001, two groups were ranging across widely separated areas again – 12 Swift wolves, including at least three pups, and up to seven Swift West wolves, including 2-3 pups. Swift West remained within the upper Swift Fork area and somewhat westward during my remaining BY '01 observations. Swift's movements increasingly extended to caribou wintering areas well beyond areas 14-15, for example 5-10 miles eastward to Slippery Creek and north of Birch Hills in late November, 20-25 miles northwestward to Spectacle Lakes in late January, and 30 miles northeastward to upper Bear Creek in February.

Swift's February 2002 foray to the Bear Creek area resulted in a strange interaction with the Eagle male (#4), while he was 10-15 miles northwestward of his territory. Two Swift wolves followed the Eagle male's trail through deep snow to where he was resting next to a wolf of undetermined identity that he had pursued and killed minutes earlier; the Eagle female had become separated and was now well to the southeast. The two Swifts arrived and almost immediately began eating the dead wolf as the Eagle male continued resting five feet away, with his back to them. The Swift wolves showed no hesitation in approaching. He and they seemed to be "ignoring" each other in a ritualistic way, perhaps after a confrontation further back on the trail. Several minutes later he stood, snarling, with his back humped up like a cat. One of the Swifts retreated into nearby trees, but the other – the largest of the two and larger than the Eagle male - remained at one side the carcass eating, as the Eagle male, still snarling and moving in slow motion with his back humped like a cat, ate from the other side. They continued eating for 10 minutes while glaring at each other across the carcass. The Swift wolf then joined the other Swift wolf in the trees. When I returned the next day, the two Swifts were resting at the eaten carcass and the Eagle male was out of view in heavy brush a hundred yards away. Shortly afterward the two began searching for him aggressively. They had not yet found him in the nearby brush (his radio collar indicated he was still there) when fuel limitations forced us to leave. Two days later, the two Swifts were in the same area but the Eagle male was alone 20 miles southeastward, uninjured, apparently looking for his mate.

Meanwhile, a radio-collared Swift male and (based on tracks) 9-10 other wolves, probably from Swift, were in separate areas a few miles to the east. The 9-10 did not include any radio-collared wolves, so I did not determine where they ended up after mid February 2002. The collared male was soon ranging alone widely, in the Kantishna-Eagle Gorge-lower Moose Creek-Bearpaw areas, still well northeast of the Swift territory. By mid March he was with two other wolves in the lower McKinley River area, a triplet that I began referring to as Swift Northeast (#6). I do not know the origin of the two wolves he joined in that area; perhaps they were other Swift wolves, from the 9-10 that I last tracked a few weeks earlier just to the east. By March 7, the only other radio-collared Swift wolf – one of the two Swifts that interacted with the Eagle male in February - was well to the north with its radio collar on mortality mode.

In BY '02, the two collared Swift West wolves and at least four others raised seven pups at an established den and two rendezvous sites within a few miles of the den used in BY '01, and 13 wolves were still together as of at least April 11, 2003. For the most part they ranged eastward to the same areas (upper Highpower Creek, etc.) that Swift West used in BY '01 but now seemed to be expanding further westward (Red Paint Creek, Pingston Creek) and northwestward (Shisona River). I was not able to determine anything specific about Swift in BY '02. However, my observation of 14-16 wolves, including the two Swift West collars, together on February 15 but no more than 13 in the earlier and later observations leaves the possibility that a few Swift wolves joined temporarily.

In BY '03, by July, Swift West appeared to be using a den and/or rendezvous sites 10-11 miles westward of the established upper Swift Fork dens used the previous three years, and in general continued ranging further westward and northwestward – for example, 20 miles northwestward to the Slow Fork Hills in July (1+ wolf), 80 miles northward to the Haystack Mountain area (upper North

Fork of the Kuskowim River) in January (5-7+ wolves), and 15-20 miles southwestward to the upper Tonzona River/Red Paint Creek/Pingston Creek areas at least three times in December-February (up to 6-8 wolves). I was not able to determine the number of pups produced, but at least six wolves were still present during my last good visual observation of the biological year, at the end of February 2004.

In December 2003, I established contact with a neighboring group of eight wolves – most likely Swift - that ranged from the upper Foraker River to somewhat west of the upper Swift Fork. There were still eight wolves in this group at the end of February 2004 and 6-8 in late April. A collared wolf that I located only to the west in all subsequent observations, within the area used by Swift West, was with another wolf a half mile or less from the eight Swift wolves on January 25, 2004.

In BY '04, I maintained contact with Swift West only from June-December and with (putative) Swift from June-November. Swift West consisted of at least three wolves and ranged from 6-7 miles southwest of the upper Swift Fork to 20-25 miles further southwestward in the upper Little Tonzona River area. Swift consisted of at least four wolves and ranged from the upper Foraker westward to the upper Swift Fork. Swift used an established natal den 5-6 miles northeast of the upper Swift Fork dens that both groups had used at intervals over the previous 4-5 years. I did not determine where Swift West denned (if at all) or how many pups either group produced.

Due to the loss of radio collars, I had little contact with wolves in areas 14-15 during BY '05 (only in June and March). The last Swift West collar I tracked in BY '04, in late December 2004, was on mortality mode in the Slow Fork Hills by early June 2005. In March 2006, NPS collared two wolves in a group of three that ranged west of the upper Herron River and near the upper Swift Fork dens during my five subsequent BY '05 observations (3/12-27). In BY '06, these two collared wolves (both females) and apparently the third wolf denned just east of the upper Swift Fork dens, on the western side of the upper Highpower drainage. I did not see pups at the den, but the total of seven wolves traveling together as of my early winter observations indicates that the three produced at least four pups.

One of the collared females left the group sometime between January 12 and February 3. The next time I found her, on March 14, she was with another wolf, probably a male, about 20 miles southwest of my westernmost BY '06 observations of the group. Six remained together in the group through at least late February, but I could account for only 3-4 in my last three observations of the biological year, from April 14-21. What role, if any, trapping played is unknown. In late November, there were fresh Super Cub ski-landing tracks along the fresh snow trail of the seven just west of the upper Swift Fork River, 4-5 miles outside the park/preserve. The pilot's tracks led 100-200 yards from the Cub tracks to the wolf trail at the kind of brushy locations where a trapper would typically set wolf snares. It should also be noted that this area is only 40 miles east of the current Game Management Unit 19D east (McGrath) state aerial wolf control area. State wildlife troopers have already caught GMU 19D east aerial-hunting permittees hunting wolves illegally at locations more than 40 miles outside the control area to the south.

Use of the upper Swift Fork-upper Highpower denning area in BY '06 by itself does not establish the identity of the newly collared wolves as Swift versus Swift West, given that both groups have used the dens of this area over recent years. However, eight of my 22 winter locations of these wolves since they were collared in late BY '05 were west of the Swift Fork River and near the mouth of Highpower Creek (40 miles northwest of the denning area), and only one location was as far east as the upper Herron River. Use of these westward and northwestward areas would be more characteristic of Swift West. In March 2007, NPS collared another group of three wolves to the east. The six locations I obtained for these three through the end of BY '06 were scattered from somewhat

east of the upper Foraker River westward to the Herron River, within the area used most heavily in the past by Swift.

Subsequent observations should help to sort out these latest uncertainties about group identities and interactions in areas 14-15.

16. Chilchup (Kantishna River)

I began observing the “Chilchu” wolves, a group with a territory surrounding Chilchukabena Lake (a large lake 17 miles east of Lake Minchumina), in early 2000. Chilchu typically maintained a late winter size of 5-7. In BY '05, the two established adults produced five pups and all seven were still together on March 27, 2006. When I tracked them again two days later, everything still seemed normal. Chilchu was doing well, in no small measure from eating at least two winter killed adult moose in February and March alone; especially impressive was the large size of the pups.

When I returned next, on April 15, I was unable to track them all the way but could hear both of the adults' radio collars on mortality mode several miles southwest of Chilchukabena Lake, near the interface of the Chilchu and Starr Lake (#12) territories. Both of the Chilchu adults had been killed in a confrontation with the Starr Lake wolves earlier in April (T. Meier, pers. commun.). Shortly afterward, NPS radio collared two of the Chilchu pups, one of which then dispersed northward (T. Meier, pers. commun.). The uncollared pups were not seen again.

Once before, on February 19, 2001, I watched the aftermath of a confrontation between seven Chilchu wolves and an uncollared group of six wolves in the Starr Lake territory, four miles east of Lake Minchumina. Most of the wolves were ruffled up and acting aggressively. The collared Chilchu adult male was within 200 yards of the uncollared six and retreating, but there did not appear to be any injuries.

I began tracking the remaining (radio-collared) Chilchu wolf, a male pup, on April 18 and 20, 2006. He was still inside the Chilchu territory on April 18. However, most of his subsequent BY '05 and BY '06 locations were well southeastward, in and between the Bearpaw, Swift Northeast, and Slough territories (Figs. 1-2). Correspondingly, by winter 2006-07 much of Starr Lake's activities were shifting eastward into the vacated Chilchu territory.

Given his disassociation from the Chilchu territory and Starr Lake's apparent appropriation of the vacancy, a name change seems in order – for now, “Chilchup,” although if he settles somewhere in the current area “Chilchu South” (or “Southeast” or “Southwest”) will be more logical and consistent.

He was in forested areas most of the 23 times that I located him in BY '06, which made it difficult to determine if he was with any other wolves. Tracks suggested that he was generally alone; I could determine this for certain on October 2 and March 6. A somewhat smaller wolf was with him on October 7 in the southern portion of the Bearpaw territory and again on October 28 about five miles further south, in a western area of the Swift Northeast territory. Tracks indicated another wolf might have been with him on February 3 as well, when he was temporarily back inside a northern area of the former Chilchu territory. Whenever I could see him, in the open or via glimpses in trees and brush, he seemed to be in normal, good condition.

He spent much his time along and near sections of lower Moose Creek, summer and fall/early winter, perhaps drawn in part by the salmon fishing of this area (hot springs result in open leads during the winter). Apparently he was able to avoid the resident Bearpaw wolves who appeared to be doing the same during fall/early winter (#10). I located him in this area on October 2, 7, November 25, 28, and December 9, 12, and Bearpaw on October 27, 28, November 5, 24, 25, December 12, and January 12.

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