

# **Toklat, Margaret, and Sanctuary: The Wolves of Eastern Denali**

## **Biological Year 2001-02 Responses To Disruption**

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## Background and Summary

The eastern wolf family lineages of Denali National Park, specifically Toklat (East Fork) and a succession of neighboring families to the east, long have provided world class research insights and viewing opportunities (“family” is the proper scientific term, not “pack” – see Appendix I). Toklat, in particular, is of immeasurable biological and other value as the oldest known family lineage of any non-human species in the wild anywhere. Nonetheless, these and most other Denali wolves remain vulnerable to hunting, trapping, and other serious human impacts. Near the end of biological year (May-April) 2000-01, the Toklat alpha male and the alpha female of the neighboring Sanctuary family died during questionable radio collaring activities (Haber 2002). Sanctuary also sustained earlier trapping losses and the moose-caused death of its alpha male.

These disruptions led to major changes in both cases – a reformulation of Toklat’s social organization and the complete loss of Sanctuary. My research in Denali, now in its 37<sup>th</sup> year, explores major aspects of the behavior, ecology, and management of wolves and the dynamics of wolf-ungulate systems. I study wolves throughout the north-side park/preserve via aerial radio tracking year-round (14 “groups” in 2001-02) and with additional ground observation of Toklat and the neighboring family to the east from late May-September. However, given the high importance of the eastern families, in this report I focus only on behavioral and colonization responses to the recent Toklat and Sanctuary losses.

I thank 200,000-member Friends of Animals for its generous support of this research and similar wolf research I am doing in other areas of Alaska.

Toklat has survived for the 37 years I have been in Denali and, according to Adolph Murie (pers. commun. 1966), is the same family lineage that was already well established when he began his research in 1939 (Murie 1944). Toklat’s late winter size has generally fluctuated within narrow limits, but not without some dramatic exceptions. In 1998 it decreased to only two wolves, the smallest late winter size of its known history, leaving only a young adult male and female.

This decline began in 1997, due to interacting human and natural causes. The established alpha female failed to produce a surviving litter in May 1997 even though she denned in what seemed a normal way. Canine parvovirus, vectored by heavy sled dog activity in and adjacent to Denali, is a leading candidate as to what happened. The second-ranking adult male and female closely bonded and denned at least once prior to 1997, although no pups emerged. They provided the potential for a second Toklat litter in 1997 (Toklat pro-

duced multiple [2-4] simultaneous litters in 11 of the 31 years I could make this determination through 2001, including in 1996). However, the male was snared in February 1997, shortly before the courtship and mating period, and within approximately a month the female left Toklat for good. Producing young is what wolf and other social organization is about. This amounts to an important social glue during the summer months, in the absence of which some of the adults and subadults are more likely to disperse. The 1997 reproductive failure was followed by a series of known and likely dispersals and at least one suspicious death, until in April 1998 only two of the 11-12 adults and subadults that were present in early June 1997 remained. A dominant adult male appeared with the two in apparent harmony in September 1998 but only briefly, perhaps as a temporary returnee from an earlier dispersal.

This “re-founding” Toklat pair produced litters of four, four, five, and four pups in 1998, 1999, 2000, and 2001, respectively. Eight of the 13 offspring they produced from 1998-2000 were still with the group as of late March 2001, seven as of early summer 2001, and four as of late summer 2001. The same four – now a two-year-old female, a 3-4-year-old female, and two 3-4-year-old males - were still present at the end of April 2002, and at least three in late June 2002. Three of the five 2000 pups apparently died accidental or predation deaths while they were in good condition during 2-3 intervals between early August and late September 2000, and a human cause cannot be excluded in the “dispersal” of a 2001 yearling. Thus, 10 of the 13 pups of 1998-2000 lived long enough to be potential dispersers, but only 5-6 of these have dispersed naturally so far. The four pups of 2001 disappeared suddenly in late September-early October 2001, most likely due to a human cause (Haber 2002).

Two dominant, closely bonded adult males appeared together from almost two hundred miles away within 5-6 weeks of the Toklat alpha male’s March 2001 radio collaring death, soon integrated with his four older offspring, and began attending his four 2001 pups as if they were their own. The mother, i.e., the mate-less alpha female, also seemed to accept the newcomers, albeit more gradually and less completely. She, her four older offspring, and the newcomers were still together in apparent harmony after the 2001 pups disappeared, and they remained together through late March 2002.

The highest ranking (alpha) newcomer mated with both the alpha female and her older daughter in March 2002, with the three interacting cooperatively during these sexual activities. He seemed to bond most closely with the 3-4-year-old daughter, who was probably a little younger than him. Her 5-7-year-old mother was probably a little older than him.

By early-mid April 2002, the mother separated and remained mostly on her own in the western portion of the established Toklat territory. In late May, she seemed to be using

an established Toklat den within the same complex of dens where she and her mate produced their first litter in 1998. However there was little indication of any surviving pups as she continued to range mostly alone in that general area. Simultaneously, nine miles to the east, her daughter produced five pups – her first litter - at the natal den mother used from 1999-2001. The two “newcomers” and her sibs assisted, and the five pups were still doing well as of at least late June 2002. In early July, my last fieldwork before completing this report, she appeared at her daughter’s den, the first time I found her there or anywhere nearby in three and a half months. The details of whatever this means remain to be determined, given that it was based only on telemetry signals.

Three major family lineages have occupied the adjacent easternmost wolf area of Denali since I began my research in 1966. Savage was already well established in 1966 and lasted for an additional 17 years until it was eliminated by hunting in winter 1982-83, based on strong circumstantial evidence and earlier hunting inroads. Headquarters began recolonizing the Savage vacancy within 8-10 months and lasted 11-12 years in the eastern two thirds until it was eliminated by hunting and trapping, primarily from 1993-1995; the established Headquarters alpha male was also killed during radio collaring in 1993. Sanctuary began recolonizing the Headquarters vacancy within a month or two and survived there for six years, until it was eliminated in 2001, largely by 1998-2001 trapping losses, the natural death of the alpha male, and 2001 radio collaring death of the alpha female. Margaret (named after Mt. Margaret) began recolonizing the Sanctuary vacancy within about a month and is still present as of 15 months later. Headquarters appeared to move into the Savage vacancy from just to the east. The founding Sanctuary and Margaret pairs moved into the subsequent vacancies from the west side, where each had already begun “wedging” between Toklat and the eastern group up to a year and a half beforehand.

As with the previous (Headquarters) recolonizers, the Sanctuary pair enjoyed good reproduction and by May 1997 the group consisted of 8-10 adults and subadults. There were 5-6 more surviving pups in 1997, and as of mid BY 1997-98 (October-November 1997) Sanctuary consisted of 15 wolves. All 15 were still together as of late January 1998, spending much of their time outside the east park boundary where there were concentrations of wintering caribou. They were eating well in this area. Within one five-day interval in January, for example, they killed three caribou and found an intact winter killed calf moose. There was also heavy wolf snaring in the area and Sanctuary wolves soon began disappearing, until there were only eight left in March and possibly five in late April.

The missing wolves apparently included key individuals, as there was no indication of any denning or reproduction in summer 1998. Several more disappeared during the summer, most likely because of dispersals related to the reproductive failure, in a manner similar to what I suggested for Toklat in summer 1997, above. Only 1-2 Sanctuary adults remained in early fall 1998, including a female. A middle-aged or older male newcomer – Sanctuary's first black wolf – appeared from an unknown origin in fall 1998 and paired with the female. A third, younger-looking wolf traveled with them throughout winter 1998-99 but was absent occasionally.

The pair, assisted by the "occasional" wolf, produced four new pups in 1999. The pair and four pups were still together in November, but in late November-early December 1999 three of the four pups were trapped along the east park boundary, leaving only the pair and one pup, all three of which survived through the end of the winter. The pair produced 6-7 more pups in 2000, and as of December 23, 2000 there were still nine wolves total, possibly including the surviving 1999 pup.

In late December 2000 or early January 2001 the aging adult (alpha) male was killed in a moose encounter a short distance outside the east park boundary, not far from the Parks Highway and a major hotel construction site. The others lingered in the area where he died, returned at least twice, and were observed by some of the hotel construction workers (S. Castle, pers. commun.), among others. I observed at least five of the Sanctuary wolves in the same area in early December 2000 as well, as did some of the construction workers. I was told, though did not observe myself, that someone set wolf snares in this area in December, primarily along creek beds that were easily accessible from the highway. By January 4, 2001, only the adult female and three of her young remained. She died during radio collaring on March 16, 2001, thus leaving the three pups on their own, two of which disappeared over the next 3-4 days.

Absent the trapping loss of the three 1999 pups, there would have been good odds of at least one subadult surviving with the three 10-month-old-pups on March 16, 2000. At that age (22 months), eastern Denali wolves possess much more knowledge of the established territory and are much better hunters (Haber 1977). The natural and human-caused deaths of the adult male and female 13-16 months later by themselves complicated Sanctuary's outlook for survival as a family lineage. But without any subadults for guidance, there was much less chance that the 10-month-olds would know the family's territory, let alone use it well enough to preclude recolonization by other wolves.

The Margaret pair and a third wolf began recolonizing the Sanctuary vacancy within a month, and less than three months later the surviving Sanctuary wolf shifted to another area 12-30 miles northward. She showed little expertise as a hunter but remained in good condition on her own by scavenging naturally dead moose and caribou. She was often near settled areas, where the primary attraction seemed to be sled dogs rather than food. Eight months later – now a 22-month-old at sexual maturity - she returned to her original area, where Margaret was now active. A few days later she found the Margaret wolves (3 adults and a 10-month-old pup) and began following them, probably with the hope of joining. She did not succeed on this attempt and a few days later was trapped along the east park boundary.

By this time, Margaret was occupying approximately the northern half of the Sanctuary vacancy. Toklat also made several major winter 2001-02 forays deep into the vacancy, especially southern and central areas, but has not yet occupied any of it. 3-4 Margaret wolves are currently raising six pups at an old den within the central portion of the area thus far occupied.

### **Fieldwork**

Field routines in BY 2001-02 were similar to previous years.

I derived the May-September information for Toklat from 90 hours of close observation at the natal den during 15 ground sessions (15 different days), June 3-August 8, four ground telemetry checks of the den during the same period without observation, 13 ground telemetry checks and related observations in the Sable-Toklat area of the road corridor, August 19-September 17 - while Toklat wolves used a rendezvous site in that area, and 10 aerial radiolocations during 10 flights (on 10 different days) from May 29-September 26. All of my October-April (10/20-4/30) observations were from the air. I radio tracked Toklat wolves during each of these seven months, 53 times on 38 flights (38 different days).

I did not begin observing Margaret wolves until August 1. I derived the August-September information primarily from 48 ground telemetry checks and related observations on 34 different days while Margaret used two rendezvous sites in the Jenny Creek-Savage area of the road corridor, and from seven aerial radiolocations (6 flights, on 6 different days) at and away from these sites. All of my October-April (10/20-4/30) observations were from the air. I radio tracked Margaret wolves during each of these seven months, 34 times on 32 flights (32 days).

I listened for the surviving Sanctuary wolf's radio collar in the east park boundary-Savage area at least 70 times (60 from the ground) on 57 different days from May-September, from which I located her six times on six different days. All of my subsequent observa-

tions, until she was trapped along the east park boundary on March 15-17, 2002, were from the air. I radio tracked her 17 times on 14 different days during each of these six months.

Bus drivers, photographers, National Park Service (NPS) employees, and others regularly provided valuable tips and other information from their May-September road corridor observations of Toklat and Margaret wolves.

## **Toklat**

### Appearance and integration of the newcomers

The major Toklat event in BY 2001-02 was the appearance of two newcomer males less than two months after the March 21, 2001 radio collaring death of the established Toklat alpha male. Both newcomers wore ear tags suggesting they had originated from a state wolf control program in the Fortymile region of eastcentral Alaska, where I have been studying wolves concurrently with the Denali research since 1993. Both are black, which easily distinguished them from the Toklat alpha female and offspring, all of which are variations of tan-gray (black was a common coat color for Toklat and predominated in the neighboring Savage family until the mid 1970s but since then has been absent from Toklat and largely absent from Savage and its successors). NPS radio collared the dominant newcomer on September 29, 2001 and obtained his ear tag number. This indicated he was captured by state biologists together with two other black wolves in upper Chena River (east of Fairbanks) on April 5, 2001 (C. Gardner, ADF&G, pers. commun.). The three wolves were flown about 250 miles westward and released on the Melozitna River the same day (4/5/01).

One of the three, a female, was shot 350-400 miles east-southeastward, in the Tok area, by late summer or fall. Another – the dominant Toklat newcomer-to-be, found his way to the Teklanika-Igloo area of Denali, about 180 miles to the southeast, by early May. The ear tag number of the black male with him is not known. However the tag looks the same, indicating that he most likely accompanied the dominant newcomer from the Melozitna River as another relocated “Fortymile” wolf. They seem closely bonded, much like older-younger brothers.

Eight of the 10 Toklat family members that were together when three of them were radio collared on March 19-21, 2001 were still together at the beginning of BY 2001-02 (I observed them on the last day of BY 2000-01, i.e., 4/30/01). The alpha male died during collaring on March 21, 2001 and since then I have not seen a young female who was also collared on that date. As I began the BY 2001-02 fieldwork in late May, there were reports from various observers of two black wolves frequenting the Igloo-Teklanika area, within the heart of

the Toklat territory, only 2-3 miles from the active natal den. The newcomers were observed alone in some cases, and with up to several tan-gray wolves in others. These observations indicated they probably arrived in early May and shortly thereafter began associating with at least some of the Toklat wolves. This may not have included the alpha female, given that her 2001 pups were born in mid-late May and she was heavily occupied with them inside the natal den until their first emergence on June 6-7.

My first observation of the newcomers at the natal den - though probably not their first appearance there - was on June 10. They were not present during my first three ground sessions, on June 3, 5, 8, although several of the female's 2-3 year-olds were there during the second and third sessions. On June 10 they showed the same eagerness to approach the four newly emerged pups as did the 4-5 older offspring, who were also present. Parents and non-parents alike typically enjoy interacting closely with pups at this early age, just after first emergence, and show much affection for them. There was no doubt from what I saw that the newcomers felt the same way. As usual, the alpha female allowed her older offspring full access to the new pups, inside and outside the burrows, including while she nursed them. But she would not allow the newcomers to approach closer than 25-30 feet.

The first time I saw her do this the newcomers and several of her older offspring approached together from nearby brush where they had been sleeping, shortly after she began nursing the pups on an open slope, stretched out on her side. The older offspring continued excitedly right to the pups but the newcomers stopped abruptly in their tracks, showing bewilderment but no hint of a challenge (or submission), as the female began growling. She did this as she continued to nurse, without raising her head and while barely even looking toward the newcomers. This had no effect on her offspring but within a minute or two the newcomers returned to their resting site 50-100 feet further away. She made no attempt to get up or in any other way drive them off, suggesting that she had already met them.

The next time I saw the newcomers at the natal den was on June 18. The alpha female (mother) and four of her older offspring were also present. She no longer showed any reservations about the newcomer males being near her pups. Both now mixed freely with the pups whether she was nearby or resting several hundred yards away. Throughout this session and during all subsequent observations the interactions between the newcomers and pups seemed normal. I could not see any major differences between the way they interacted with and hunted for the pups and the way the pups' mother and older sibs did this or their father (the dead alpha male) had done with his previous litters. If anything, the newcomers seemed *more* attentive.

Only rarely have I observed scent marking by family members at their own den site. However, during three sessions after the newcomers gained full access to the pups, the dominant male urinated and scratched assertively all over the site, at times profusely, even directly across the entrance to the main burrow.

From the outset, he showed clear dominance over the other newcomer and all of the Toklat offspring, including a 2-3-year-old male who was about his size or a little larger. His assertiveness was usually firm but without violence. Four or five times in June and July I saw him express this dominance in sexual ways toward the two young females – twice with mounting and thrusting, even though one of the females was probably only a yearling and mature females do not come into estrus at this latitude until late February-mid March. The females responded submissively in all cases but were not sexually receptive and seemed uncomfortable.

The alpha female was dominant over all of her offspring, males as well as females, even though all but one is larger than her. I have not seen any dominance – in either direction – between her and the male newcomers, both of which are larger. The only directed assertiveness I saw was from her, during the short period after first emergence of the pups when she kept the newcomers from fully mixing with them (per above). Throughout most of the biological year her relationship with the highest-ranking newcomer in particular was cooperative but somewhat “standoffish.”

There was much cooperation and sometimes bouts of friendly, even affectionate socializing. But overall the newcomers’ relationship with her was noticeably more restrained than with her offspring. She was likely 5-7 years old when the newcomers arrived in May 2001. My impression is that she is probably a little older than the dominant newcomer and that he is about the same age or a little older than her oldest offspring. He was estimated to be a “young adult” when captured east of Fairbanks on April 5, 2001 (J. Selinger, ADF&G, pers. commun.).

As indicated, the newcomers seem closely bonded and act like sibs, though I have no conclusive evidence of their relationship. They were together in all but one of my observations in BY 2001-02, summer and winter, whenever I could determine presence or absence. The one exception was on July 1, when the dominant newcomer departed the natal den alone on a night hunt as the other remained behind with three older Toklat offspring and the pups.

At the beginning of the biological year, seven of the alpha female’s older offspring were still present. However, as of June 25, there appeared to be only four older offspring – two males and two females. The three others most likely dispersed. Of the four that re-

mained, one of the males was somewhat larger than the other, and one of the females was noticeably larger than the other (the smaller was a yearling). The four were still present during my last observations of the biological year, April 28-30, 2002, and at least three in late June 2002.

Based on aerial and ground observations, and her collar signal as well as direct observation, the alpha female (the only collared Toklat wolf I tracked during BY 2001-02 until October) was present at the natal den on 10 of my 25 checks while this den was still occupied. She was present during five of my 15 ground sessions and departed shortly before another. The two newcomers likewise were present during five sessions and departed or were about to arrive shortly before/after two others. The newcomers were with the alpha female at the den two of the five sample times she was present, in both cases with most of her older offspring also present – 4-5 in one case, four in the other. The newcomers were also with her (and offspring) on a departure just before one of these sessions. They were at the natal den during three other of my 15 sessions, in all three cases with at least one of her older offspring but not her. The four pups were alone at the natal den during 2-3 of the 15 sessions, although following one of these 2-3 sessions an older sib was on its way back to the den and would have arrived shortly thereafter.

#### Late-summer division of pup care

The older wolves attended the four pups at the natal den through about the first week of August. I last observed the pups there on August 4 but also heard the female's collar in the area on August 7-8. At least twice on August 11-13 other observers saw this (collared) female and four pups together on or near the park road in the Teklanika-Igloo area, 1-2 miles from the natal den, indicating that a move to other sites was likely underway.

By at least August 25 two of the four pups had been moved 9-10 miles southwestward to and somewhat beyond the East Fork bridge area. This closely followed a noticeable early-mid August increase in caribou activity in the Sable-East Fork-Polychrome area, primarily of mature bulls. These two pups were then moved - probably by August 26 - to a rendezvous site near the headwaters of one of the branches of the East Fork River, six miles upstream from the bridge, where they were attended through September 22-25. The alpha female seemed to focus her activities at this site. I heard her collar (and/or saw her) in the East Fork-Polychrome area on 13 of my 17 searches of that area (13 ground, 4 aerial) from August 19-September 26. In 8-9 of these 13 locations she was either at, going to, or coming from the upriver rendezvous site. On the way to and/or from all of the 17 East Fork-Polychrome searches and two others (ground) during the same period, I also listened for but never heard

her collar to the east, in the Igloo-Teklanika-Sanctuary area, though in one case she was just leaving the Igloo area, at the head of Tatler Creek.

There was strong circumstantial evidence that the other two Toklat pups were attended at 1-2 rendezvous sites within two miles of the natal den after it was vacated. Twice – on August 27 and September 7 – 1-2 pups howled in response to my howls in this area, the first time at a location about two miles northwest of the den and the second about 1-2 miles northeast. On September 13, two adults responded from the second location or nearby. On September 18, several buses watched one of the newcomers and two uncollared tan-gray adults lead two pups through the Teklanika Rest Stop, about a mile from the latter howling location. These and other observers later watched the three adults and two pups head downstream on the open Teklanika River bar.

My last observation of the (collared) alpha female at the upper East Fork rendezvous site was on September 22. Only two of her four pups were with her. My next observation was on September 26. The alpha female, four of her older offspring, and two pups were traveling together in Polychrome Flats, six miles west of the upper East Fork rendezvous site. On September 28-29, NPS observers (L. Adams, pers. commun.) saw all 11 Toklat wolves (including four pups and the newcomers) traveling together some 12-15 miles east of my September 26 observation, just prior to the September 29 capture of the newcomer alpha male for radio collaring.

Thus it is likely that the Toklat litter was divided into two pairs at rendezvous sites 10-12 miles apart during all or most of the period following abandonment of the natal den in early-mid August. It is also likely that the pups' mother, the alpha female, spent much more time attending one of these pairs than the other. The newcomers and older offspring were observed fairly regularly in both areas (Teklanika-Igloo and East Fork-Polychrome), so it remains an open question as to whether any of them similarly focused on the other pair.

#### Sudden disappearance of the pups

NPS radio-collared the dominant newcomer male on September 29, which meant there were once again two active collars in the group. The four pups were together with the seven adults at that time. NPS returned the next day but did not obtain a visual, and bad weather precluded subsequent observations (L. Adams, pers. commun.). The next observations of Toklat wolves were by me on October 20-29, via air. The seven adults were still together but the four pups were missing and none has been seen by NPS or me in our many observations since then.

It would be highly unusual for an entire litter to disappear under natural circumstances over such a short period at this time of the year, especially given that there had been no obvious physical or developmental problems. The pups looked healthy and behaved normally. They seemed somewhat small as of late September but not beyond a range of variation commonly seen in this area between litters and between summers. They lagged somewhat during their early travels together with the older wolves in late September. However, they were able to catch up each time in my observations and never seemed in danger of becoming completely separated.

It is not unusual for adult wolves in Denali to allow their pups to begin traveling with them away from dens and rendezvous sites in late September, then to provision them at additional rendezvous sites in October and November when they cannot keep up because of small size or for other reasons (Haber 1977 and unpublished data). Toklat attended pups (4) at a rendezvous site well into November as recently as 1998, as did Sanctuary (4 pups) in 1999. All of the 1998 Toklat pups survived at least to yearling age, and all of the 1999 Sanctuary pups were doing well until three of the four were trapped along the east park boundary in late November-early December 1999. In some years it is necessary for the wolves to work their pups into the continuous winter travel routine more gradually than in others, and 2001 was probably destined to be another such year.

A simpler and more likely explanation cannot be excluded, as to what happened to the 2001 Toklat pups (Haber 2002): They scattered in panic and became lost when the NPS helicopter approached the group on September 29 to separate out the dominant newcomer for capture and radio collaring. Pups of that age could not survive on their own for long. The bottom line is that approaching 4-5-month-old wolf pups closely with a helicopter is a virtual invitation for if not a guarantee of a problem and never should have been attempted. The capture effort could have waited 2-3 months, when the risks of separation would have been much lower.

#### Winter associations

##### 1. October-late March

I radio tracked Toklat wolves 34 times on 28 different days from October 20 through March 21, during all six months of this period. On 20 of these days I was able to count all wolves that were present. The seven adults were together in 19 of these 20 counts, acting harmoniously and typically with the two newcomer males - especially the dominant (newly collared) one - leading during travel and taking the initiative in most other activities. In the other count, the newcomers were together at a mostly-eaten moose carcass on October 25

while the five others were together 12 miles away, near the upper East Fork late summer rendezvous site (looking for the missing pups?). All seven were back together at the moose carcass on my next observation, October 27, where they had also been together from October 20-22. On five other of the 28 observation dates I could not obtain complete counts (usually because the wolves were in forested areas) but could at least determine that both newcomers, the alpha female, and some of her older offspring were together – i.e., that if any wolves were temporarily separated they were offspring.

## 2. Courtship and mating

This cohesion and apparent harmony were also apparent during the annual courtship and mating activities, which were underway by March 4-8, peaked on or about March 13, and ended by March 15-18. Wolves seem to associate courtship and mating with denning and the production of young, as evidenced by the way they often go to established natal dens for these activities and/or clean them out immediately before or after (Haber 1977), even though parturition is still two months away. Toklat did this in 2002. Led by the two newcomer males, the seven wolves went more-or-less directly to the 1999-2001 natal den from at least five miles away and cleaned it out on March 4 or 5.

My next observation was on March 7, at which time at least six of the seven rested seven miles west of the den. There was no obvious sexual activity but the alpha male was snuggled head-to-tail with the alpha female, indicative of courtship activity (Haber 1977). On March 8 the seven rested and socialized at a location almost five miles away. For much of the time the alpha male, alpha female, and one of her older offspring rested within 10-15 feet of each other, 20-30 feet or more from the others. At one point as they lay together the male spent several minutes licking the alpha female's genitals while she held her tail aside receptively. Later these two stood together, noses-to-tails, licking each other simultaneously. At another point the second newcomer male joined them and the two males walked together with her, heads and shoulders pressed tightly against her head and shoulders on either side, again indicative of courtship (Haber 1977). I saw no hint of any aggression or other assertiveness between the males, nor did the nearby wolf or any others show or receive interest.

It was too windy for close, extended observations on March 9-10. However the wolves were still together at the same location and nearby, without a kill or winter kill. This likewise is typical of courtship and mating, i.e., long diversions from hunting and other normal activities. There was some hunting activity (without success) during my next observations on March 12, nine miles away. Afterward, while the seven wolves rested together, the alpha female appeared to be soliciting sexual attention from the second newcomer, and while she did

this her daughter also showed interest in this male, almost to the point of interfering with her mother's attempts - though I did not see any clear-cut aggression.

At noon the next day, March 13, the wolves arrived back at the 1999-2001 natal den, 11 miles away. For about the next four hours the two newcomers, the alpha female, and her older daughter engaged in intense sexual activity on an open river bar within 200 yards of the den, while the others rested mostly out of view at nearby locations. The alpha female solicited from the second newcomer but could get him only to mount her briefly, without a copulatory tie. For most of the rest of the time he slept or chewed on an old bone, showing no interest in her or any other sexual activity. She snuggled against him for long periods, stood in front of him holding her tail aside, and even stood over him and squatted over his head. However, after the first few, half-hearted mounts he showed no interest in her or her daughter, both of whom were obviously now in full estrus.

Meanwhile the alpha female's daughter was together with the alpha male 200 feet away. She approached him excitedly a few times, then went just ahead and stood with her tail aside, looking back at him. He mounted her several times as they moved around the area a little, then tied with her for 12-13 minutes in various prone and standing positions. Afterward they rested together for about two hours. He then went to the alpha female, who was now resting about 50 feet from the second newcomer as he continued resting and chewing on the old bone, still not showing any interest. Her daughter followed, and soon the alpha male mounted and tied with the receptive alpha female. They remained tied for about 10 minutes. For much of the tie her daughter stimulated him orally in the scrotal-anal area, showing heightened excitement herself, with her tail wagging rapidly. Afterward the three rested together, ignoring the other male and he them. At no time was there any indication of aggressive behavior between any of these wolves. Virtually everything I saw (other than the second male's lack of sexual interest) was to the contrary – receptive and cooperative.

My next observations were on March 15, as the seven wolves rested at some old, eaten moose remains seven miles away. The alpha male, alpha female, and (probably) her daughter rested together separate from the others, suggesting there might still be some residual sexual activity. I could determine that the two collars were in the same general area the next day but high winds prevented me from flying close enough to determine anything else. By March 18 they were seven miles away, about four miles outside the group's normal territory to the east, in a standoff with an adult moose. There were no indications of any further sexual activity on this date or March 19-21 while the seven were still together at this location.

### 3. Separation of the alpha female

On March 22, the two newcomers led 2-3 of the alpha female's offspring from the March 18-21 location and headed directly back westward to the established territory. The alpha female and 1-2 of her offspring remained behind with the "standoff" moose, which ended up dead between March 24 and 31 and was completely eaten by the female and two others as of April 4. Earlier the seven wolves had also dug out some old moose remains from 3-5 feet of hardened snow, 200 yards from the live moose.

This separation seemed uneventful and may have been accidental. The three may have been inside the moose excavation site at the time, unaware that the others were leaving. However, in all of my ensuing BY 2001-02 observations, 19 locations on 10 different dates, and four more from May 25-30 (all aerial), the alpha female remained separated from the two newcomers. Three times two of her four offspring were with her, once each 2-3 and one, and 7-9 times she was alone (4 times in late May). She was alone in all of my ground and aerial observations during June (details in next annual report).

However, in early July 2002, my last fieldwork before completing this report, she was stationary for at least two hours at a location about 1-2 miles from her daughter's active natal den along a major travel route to/from it while the alpha male was present at the den (7/4), then was at the den when he was absent (7/5). Both observations were based only on ground telemetry triangulations, thus the details of whatever they mean remain to be determined. This was the first time in three and a half months that I found her at or anywhere near this den, even though she mated there with the alpha male in March 2002 and produced litters there in each of the three previous years.

I could not determine if her three-month separation (perhaps with more to come) was her choice or was triggered by the newcomers or certain of her offspring. The two offspring that were with her from March 22-April 4 rejoined the others by April 12, shortly after the three returned to their territory from the moose standoff/meal. This suggests that she was at least able to find or was found by the others. On April 13-14 she followed a several-day-old trail seven miles to a winter kill the others had cleaned up, well outside the Toklat territory. But there was no clear indication she was trying to rejoin them at that time or any other. She seemed relaxed and remained in good physical condition in all of my observations.

On April 28 she was at a fresh sheep kill inside the Toklat territory with one of her offspring and a radio collared male who normally ranges in an area about 30 miles to the west, south of Wonder Lake. I do not know when he first joined her but it was after April 16

and likely included an April 25 sheep kill eight miles to the north, also within the Toklat territory. On February 17 this male and his mate became separated in a confrontation with 1-2 other groups of wolves 15-20 miles north of their usual territory. He traveled widely for the next two months, including at least twice to the Teklanika-Sushana area north of the Outer Range, 40-45 miles to the northeast. On one of his returns to his territory south of Wonder Lake, March 9, he was within three miles of his mate, who had returned shortly before, but apparently did not find her and departed on another eastern trip. When I observed him with the Toklat female inside the Toklat territory on April 28, they (and one of her offspring) were resting in apparent harmony at the cleaned-up sheep kill. He was still with her on April 30, a few miles to the north. When I next checked, on May 25-30, he was back with his previous mate in their usual territory 30 miles to the west.

Simultaneously (April 28-30) the Toklat newcomers and alpha female's three other offspring were together within the Toklat territory at and near the 1999-2001 natal den, 15 miles eastward from the alpha female's locations. While I observed them at this den on April 28, one of the offspring- probably the alpha female's daughter, who also had tied with the alpha male in March - emerged from the main burrow. Fresh dirt outside the entrance indicated she had just cleaned the den out. My next observations were on May 25-30. The daughter was now using this den, and five pups (4 black, one gray) emerged in early June. Her mother seemed to be using another established Toklat den nine miles away, within the same denning complex where she and her original mate produced their first litter in 1998. But subsequently I saw no indication she was attending any pups, and in early July she appeared at her daughter's den, the first time I found her there or anywhere nearby in three and a half months.

Prior to his radio-collaring death in March 2001, the alpha female and her mate were the core of the Toklat family's social structure. Their bond was one of the closest and most efficient I have seen in 37 years of research. My impression of her situation now is that she is the "odd female out," if only because she is likely the oldest wolf in the group and her daughter has become closely bonded with the new alpha male. It remains to be seen how she will continue to relate to the group.

#### Territory and extraterritorial forays

Historically, Toklat's territory extended from the Alaska Range into the Outer Range across central and eastcentral areas of the park but over the last several decades has shifted and contracted substantially eastward. This followed the budding of a new group from Toklat on its west side in 1971 and the loss of Savage on its east side in 1982-83 (Murie 1944; Haber 1977 and unpublished data; Mech et al 1998). For most of the last 15 years, Toklat

has ranged within the traditional north-south area and east from somewhat east of the Sanctuary River to somewhat west of the Toklat River, with occasional, unpredictable winter forays well outside this area.

Figure 1 shows the 63 Toklat aerial radiolocations I obtained from May 2001-April 2002. For comparison, Figure 2 shows my 171 Toklat *winter*, i.e., October-April, aerial radiolocations for the previous six biological years, dating back to 1995. I have not included any summer ground locations in Figure 1 or summer ground or aerial locations in Figure 2 to avoid pinpointing sensitive natal sites and for easier interpretation of the maps (the same applies to Figs. 3-4). Most of these sites were within the core areas of the locations shown. I included locations from the same dates only if they were at least a mile apart. Only one location is shown even if two or more collars were present together. Two or more locations are plotted together only if I found the wolves there on separate dates, successive or otherwise. In some cases during winter, I tracked the wolves represented by these locations over extended routes for up to several days or more; this information is not shown. All of the outlying locations represent winter forays from which the wolves returned, usually within days. No dispersals (one-way movements) are included.

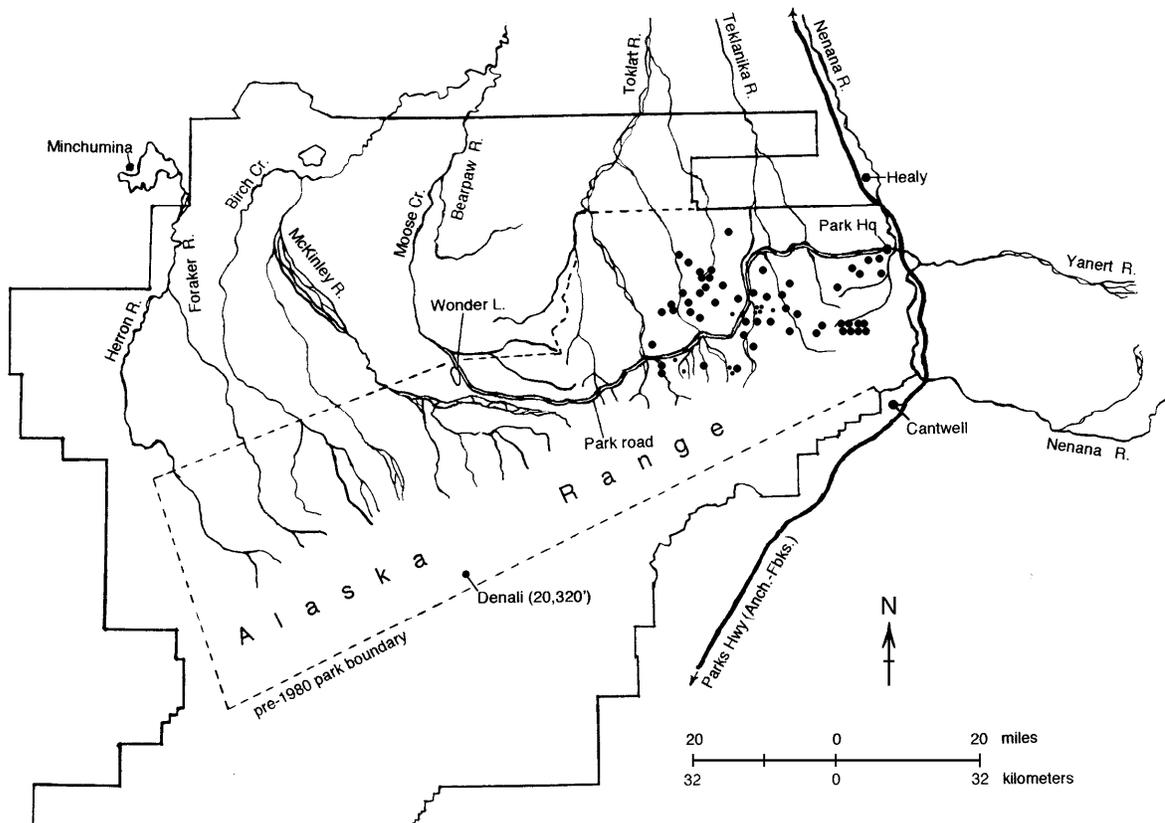


Figure 1. Toklat locations, May 2001-April 2002. Small dots=May-September aerial (10), large dots=October-April aerial (53).

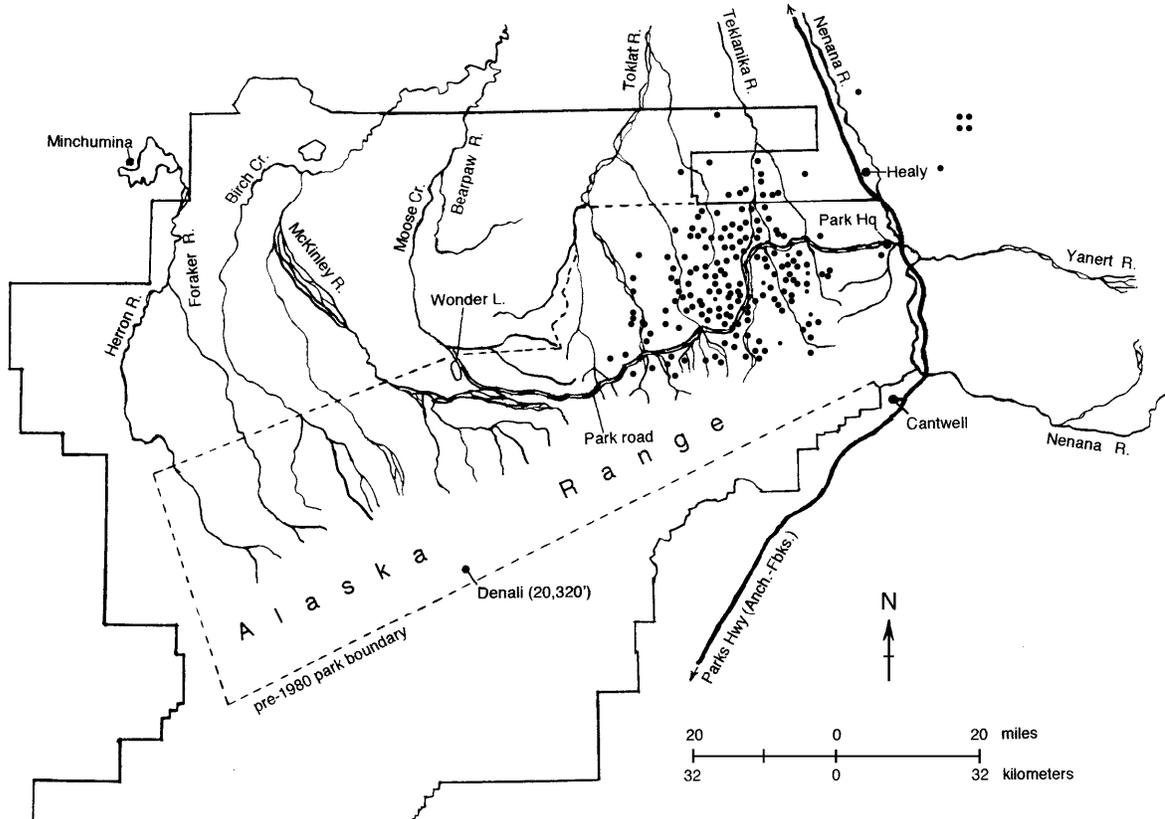


Figure 2. Toklat winter locations, October 1995-April 2001 (171).

37-39 of the 53 winter 2001-02 aerial radiolocations were within the Alaska Range-Outer Range/Sanctuary-Toklat area. The other 14-16 were to the east, representing (a), a 2-3-day foray to an area near park headquarters in late November by the seven Toklat wolves, possibly beginning as a pursuit of the four Margaret wolves from further west, (b), a foray of at least 18 days into upper Riley Creek during mid March-early April (the cluster of 8 locations in Fig. 1), for the first five days by all seven Toklat wolves, then three, with the seven scavenging a partially buried moose carcass and later the three eating a freshly killed moose 200 yards away, (c), a 2-3-day foray down the northern branch of Riley Creek in mid April by six Toklat wolves during which they scavenged a dead caribou or moose, and (d), a foray of at least five days into the same area and northward just afterward by the alpha female traveling alone, during which she apparently backtracked the six to the above (completely eaten) carcass remains.

Wolves commonly kill and scavenge while on extraterritorial forays. However their inherent exploratory nature, interactions with neighboring wolves, and an uncanny ability to quickly detect nearby vacancies in good hunting areas, in some cases enabling an established group to improve its territory, also explain many forays (Haber 1977; Mech et al 1998).

Toklat's prominent eastward forays in winter 2001-02 were probably motivated in large measure by the vacancy resulting from Sanctuary's demise in March 2001. Toklat similarly began probing a large vacancy east of the East Fork-Teklanika divide soon after the well established Savage family's demise in winter 1982-83 and within a year had shifted much of its activity eastward into the Teklanika-Sanctuary area, i.e., the western third of the Savage vacancy. This shift was not surprising, given the good moose and sheep hunting of this and other eastern areas and the history of hostilities and reciprocal probing between Toklat and Savage (Haber 1977). Toklat's latest eastward winter forays were largely into southern and central areas of the Sanctuary vacancy. They may have been influenced by Margaret's rapid recolonization of the northern half (Figs. 3-4). Likewise, Toklat's less frequent travels into northern areas of its traditional territory and beyond (Figs. 1-2) are probably related in part to increasing use of the north park boundary area by a larger family of wolves (13-15 wolves in this group at the end of the biological year, up to 17 the year before).

#### Kills and scavenging

I recorded information on two kills by Toklat wolves in summer 2001. From August 25-27, at least 5-6 of the adults, including the alpha female and both newcomers, were involved at intervals in a standoff with and kill of a mature bull caribou near the East Fork bridge. On September 21, the alpha female killed a calf caribou or moose (probably a caribou) near the head of East Fork River, then brought a hindquarter back to two of her pups at a nearby rendezvous site - carrying it for much of the distance, then eating most of it, caching the rest, and continuing to the pups to regurgitate for them. The next day, the pups were asleep with her at the rendezvous site, with bulging stomachs.

Toklat wolves were at a total of 10 meals the 53 times I located them on 38 different days from October-April. The 10 meals consisted of five kills (2 adult moose, 3 sheep), four scavenged (already-dead) moose, and a caribou or moose that they probably scavenged. Winter scavenging provides Denali wolves with half or more of their total diet by weight in some winters (Haber 1977).

Denali wolves usually test an adult moose in less than 5-10 minutes, then leave without attempting to kill the moose in more than 90 percent of these tests (Haber 1977). They usually succeed when they do decide to try for a kill, generally within 1-2 hours, sometimes 2-3 days. One of Toklat's winter 2002 moose kills - on the mid March-early April extra-territorial foray into upper Riley Creek (the cluster of 8 locations in Fig. 1) - much exceeded these normal limits. The Toklat wolves kept an old cow moose standing in the same spot, with little or no chance for her to eat or even lay down, for at least 7-10 days beginning on

March 17-18. Four or five of the wolves left on March 22 and went back home, with no indication that any blood had been drawn yet. The alpha female and 1-2 of her older offspring remained and were still in a (bloodless) standoff with this moose on March 24.

When next checked, on March 31, the three wolves were resting nearby and the moose was largely eaten, within the same 10-20-foot circle where the standoff had continued since March 17-18. Most likely she collapsed after 7-10 days of standing in one spot and eating little or nothing. Killing her over the final few minutes was probably academic. The three wolves ate her almost completely by April 4 and returned to their territory by April 12. They and the other four wolves had also partially excavated a moose carcass two hundred yards from the first moose, mainly during the standoff. However this did not appear to provide much more than superficial gnawing for any of them.

### **Margaret**

Margaret is a new family lineage. Much is already known about the social organization and other behavior of wolves in young, short-lived family lineages; widespread human exploitation unfortunately assures many opportunities to observe these. It is the much older, persistent lineages such as Toklat for which behavioral details are most needed (Haber 1996), and I emphasize the Toklat work accordingly. For now, apart from a few other basics, my emphasis with Margaret is on details of its recolonization of the Sanctuary vacancy, including homesite patterns, overall territory, and extraterritorial forays.

#### Homesite patterns

I did not begin Margaret observations until August 1. At that time, Margaret consisted of three older wolves (adult male, adult female, and an adult or subadult of undetermined sex and origin) and three pups of 2001. The six apparently had already vacated a natal den and were using a rendezvous site about a mile from a den that had been used for natal purposes by at least two earlier family lineages (Savage in the late 1960s and Headquarters in the late 1980s-early 1990s – Haber 1977 and unpublished data; Mech et al 1998). The previous family, Sanctuary, used this den and a nearby rendezvous site in late summer-fall 1999 and 2000, but not for natal purposes.

One of the Margaret pups disappeared between August 10 and 24, while all three seemed to be in good condition. The two survivors were moved about two miles westward during the first week of September and were attended there until September 25. On September 26, they were five miles further west, traveling westward with the three adults. My next

observations began on October 20, by which time another pup had disappeared, leaving four wolves in the group - one pup and the three older wolves. No more homesites were used.

I am aware of one good pup observation, likely of the Margaret wolves, prior to August 1. On July 16, an NPS volunteer worker had a close, unobstructed observation for about 10 minutes of three pups together with two adults on an open river bar. This was about four miles westward from where I began observing them on August 1.

It was easy to listen for the adult female's radio collar from the park road while Margaret was using the August-September rendezvous sites (NPS did not collar a second Margaret wolf – an adult male – until September 29). I listened for her collar at these sites 52 times – 48 times from the ground and four from the air. Among other things these telemetry “checks” indicated that she spent significantly more time away, hunting, than at the sites, and that she was more likely to depart on than arrive from a hunt in the evening. Neither result is surprising or unusual for wolves in eastern Denali (previous section and Haber 1977).

More specifically, she was present at the current rendezvous site in 13 of the 52 checks, on 11 of the 38 days I did these checks. On 25 of the 38 days I checked only once. She was present in five of the 19 single-checks that I did before 7 p.m., in one of the three I did after 7 p.m., and in one of the three (prolonged checks) that lasted from before until after. On 13 of the 38 days, I checked twice, at intervals ranging from 3.5 to 10 hours (mean=5.7). Twice she was present during both checks, three times during the first but not the second, and 0 times during the second but not the first. She was absent during both checks in eight of these 13 double-checks. Nine of the 13 included checks before and after 7 p.m., with about the same results: In two of the nine she was present during both checks, in two she was present for the pre- but not post-7 p.m. check, in 0 of the nine she was present for the post- but not pre-7 p.m. check, and in five of the nine she was absent during both.

#### Winter associations

A large adult male – the collared female's likely mate – was collared by NPS on September 29, 2001, which meant there were now two collared Margaret wolves. Five wolves, including two pups (undoubtedly the same five I observed on 9/26), were present when the male was helicopter-darted and collared and the five were observed together a short time afterward (L. Adams, pers. commun.). The next known observations were by me when I began my winter aerial work on October 20. Four wolves, including only one pup, were traveling together at that time, and no more than four (one pup) were seen in subsequent observations. I do not know what happened to the second pup. As was the case with

the first missing pup (in August) and the survivor, it seemed in good condition and looked and behaved the same as the others shortly before disappearing.

The three adults and surviving pup that were present when I began the winter observations on October 20 were still alive through at least April 16, although I have not seen more than three since then. I radio tracked Margaret wolves 34 times on 32 different days from October 20 through April 30, during all seven months of this period. On 15 of the 32 days I obtained complete counts of all wolves that were present. Four wolves were together in 13 of these 15 counts. In the two other complete counts, three wolves were present (together), including both collars in at least one case. On five other of the 32 observation dates, I could determine that at least three wolves were present, including both collars. On 11 of the remaining 12 observation dates I could determine that at least the two collared adults were present and, on the other, that at least one of the collared adults was present.

#### Preparation of the 2002 natal den

I did not observe Margaret's courtship and mating activities in March, due to my emphasis on Toklat's sexual activities at that time. Nonetheless I expected that a new litter would be produced in mid-late May and on April 14, 2002 saw the first strong indication that this would happen. I radio tracked the collared adult male and female to the aforementioned old natal den near which Margaret used a rendezvous site in August 2001. As indicated, this den had been used as a natal site by the predecessor Savage and Headquarters wolves but to my knowledge not Sanctuary (1995-2001). It was clear that Margaret had found it by April 14 and wanted to use it. Both collared adults were inside the main burrow together, out of sight, when I radio tracked them on April 14. There was a large pile of fresh dirt just outside the main burrow, indicating they were in the process of re-excavating virtually the same tunnel that had been used years earlier. I tracked them to this den again on April 28 and to at least the immediate area on April 30. When I resumed field observations on May 25-30, at least three Margaret wolves were occupying the den, and as of this writing they are still occupying it and nearby areas with six pups.

#### Territory and extraterritorial forays

Figure 3 shows the 41 Margaret aerial radiolocations I obtained from May 2001-April 2002. Figure 4 shows the 119 *winter*, i.e., October-April, aerial radiolocations I obtained for the predecessor Sanctuary family lineage during its history over the previous six biological years, dating back to 1995. The same details described for Figures 1-2 of the Toklat section as to what constitutes a "location" also apply here. I again emphasize that all of the outlying

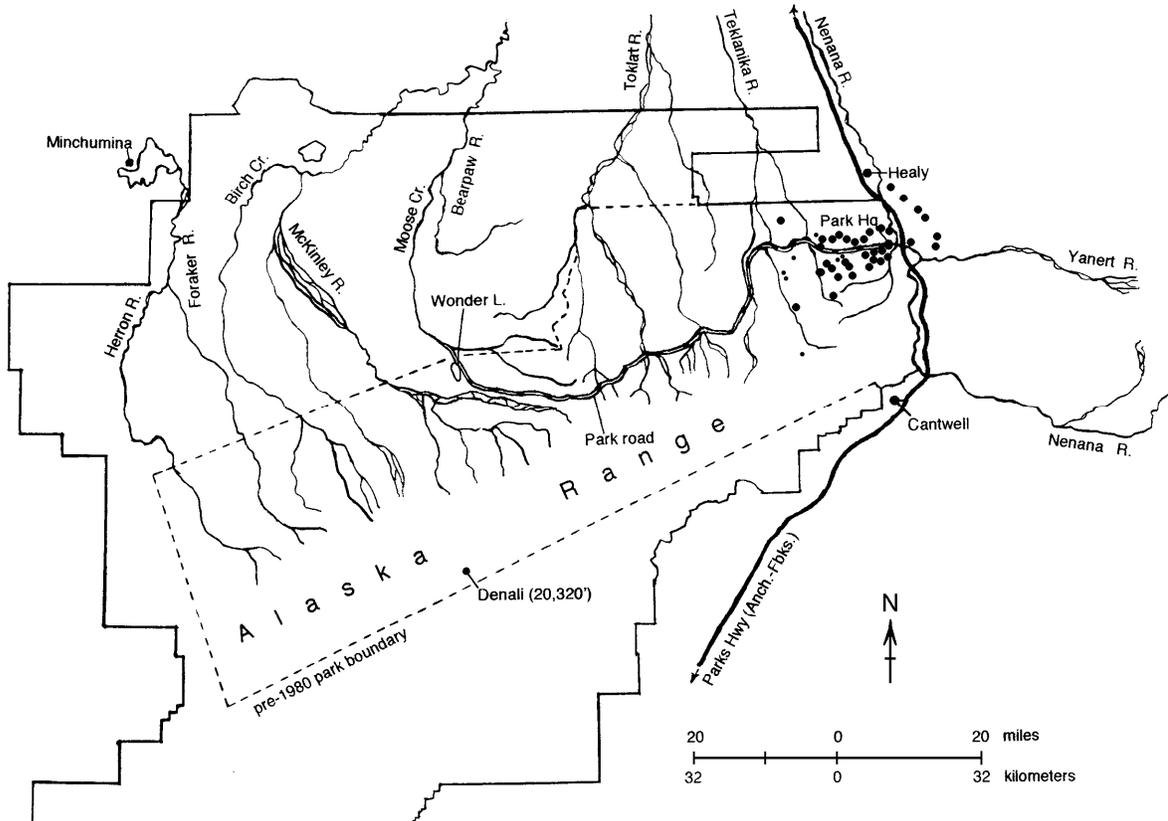


Figure 3. Margaret locations, May 2001-April 2002. Small dots=May-September aerial (7), large dots=October-April aerial (34).

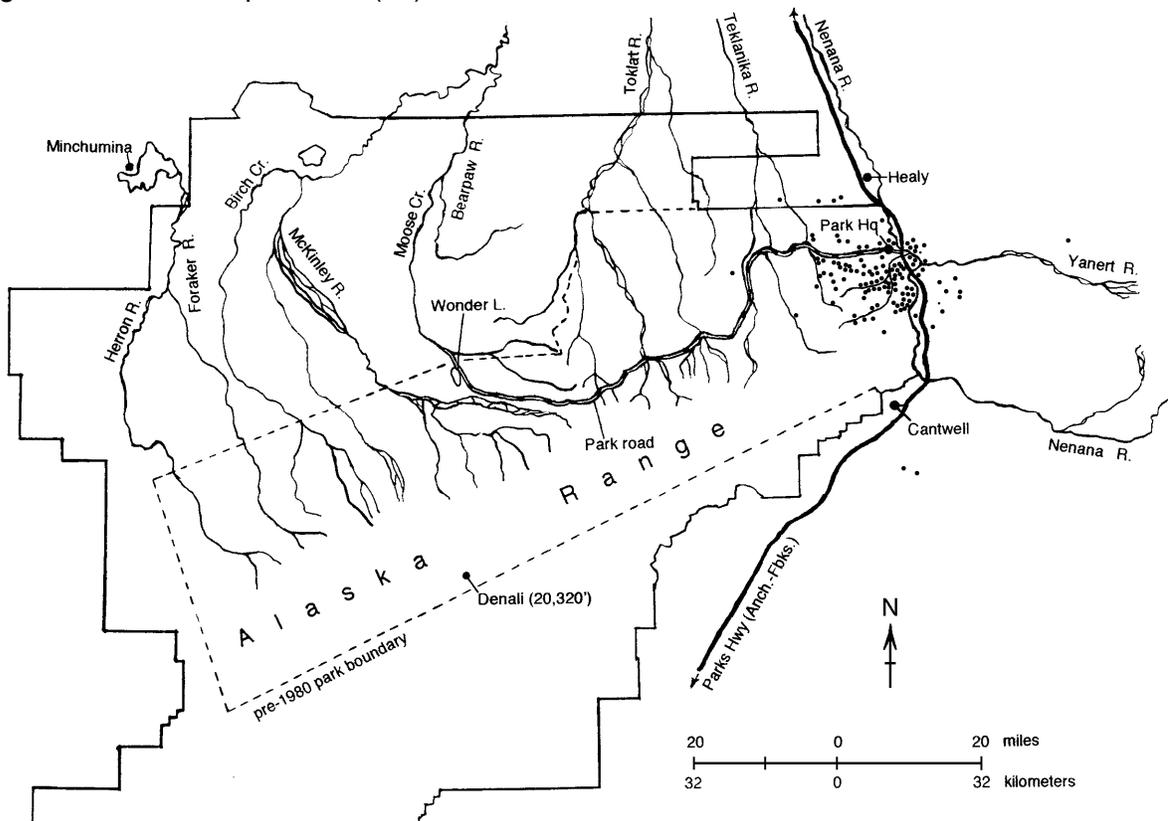


Figure 4. Sanctuary winter locations, October 1995-April 2001 (119).

locations represent winter forays from which the wolves returned, usually within days, not dispersals. (Sanctuary was essentially eliminated in late March 2001, with only one known survivor, a 10-month-old female pup. Her locations through April 2001, i.e., the end of BY 2000-01, are included in Figure 4. Her locations from May 2001 until she was trapped in March 2002 are shown in Figure 5).

These data illustrate Margaret's rapid recolonization of approximately the northern half of the Sanctuary vacancy to date. They also provide another illustration of the significance of extraterritorial forays. Seven of the 34 Margaret winter 2001-02 aerial radiolocations were outside the usual Sanctuary area (and the park) to the northeast and east, representing (a), a 3-5-day foray into the Moody Creek area and within four miles of Healy in early March by all four of the Margaret wolves and, (b), a 3-day foray into the Mt. Fellows-Montana Creek area beginning a day later, again by all four. The outlying westward locations probably qualify at least as much as artifacts of the previous territory as they do forays, given that this is more-or-less where Margaret originated in 1999-2000, as the founding pair attempted to wedge between Toklat and Sanctuary.

#### Kills and scavenging

Margaret wolves were at a total of six meals the 34 times I located them on 32 different days from October-April. The six meals consisted of two kills (2 sheep), two scavenged (already-dead) adult moose, a yearling or small adult moose that they probably scavenged (vs. killed), and a calf moose or caribou that they probably scavenged. I did not obtain any information on summer kills or scavenging.

#### **Sanctuary Survivor**

The 25 locations I obtained for the surviving Sanctuary female from March 16, 2001 when she was orphaned as a 10-month-old pup through the remainder of BY 2000-01 (4/30/01) were primarily along the middle 8-10 miles of the east park boundary. Figure 5 shows her subsequent locations. She was still ranging primarily within the same east boundary area through about mid July 2001. By July 22, 2001 she had moved about 10 miles northward to the Healy area. My next 10 locations, from October 29, 2001-March 4, 2002 (during each of these 6 months), were in the Healy-Ferry-Jumbo Dome areas, 12-30 miles north of her original range. On March 4 she was traveling east on the Ferry Trail. On March 8, my next location, she was 26 miles south, back within her original range, apparently for the first time in eight months. All seven of my March 8-15 locations were in this area (one 6-7 miles east of the others). She was trapped or snared just outside the east park boundary

shortly after I located her near the trapper's residence and trapline on March 15. He returned her radio collar to park headquarters by March 20.

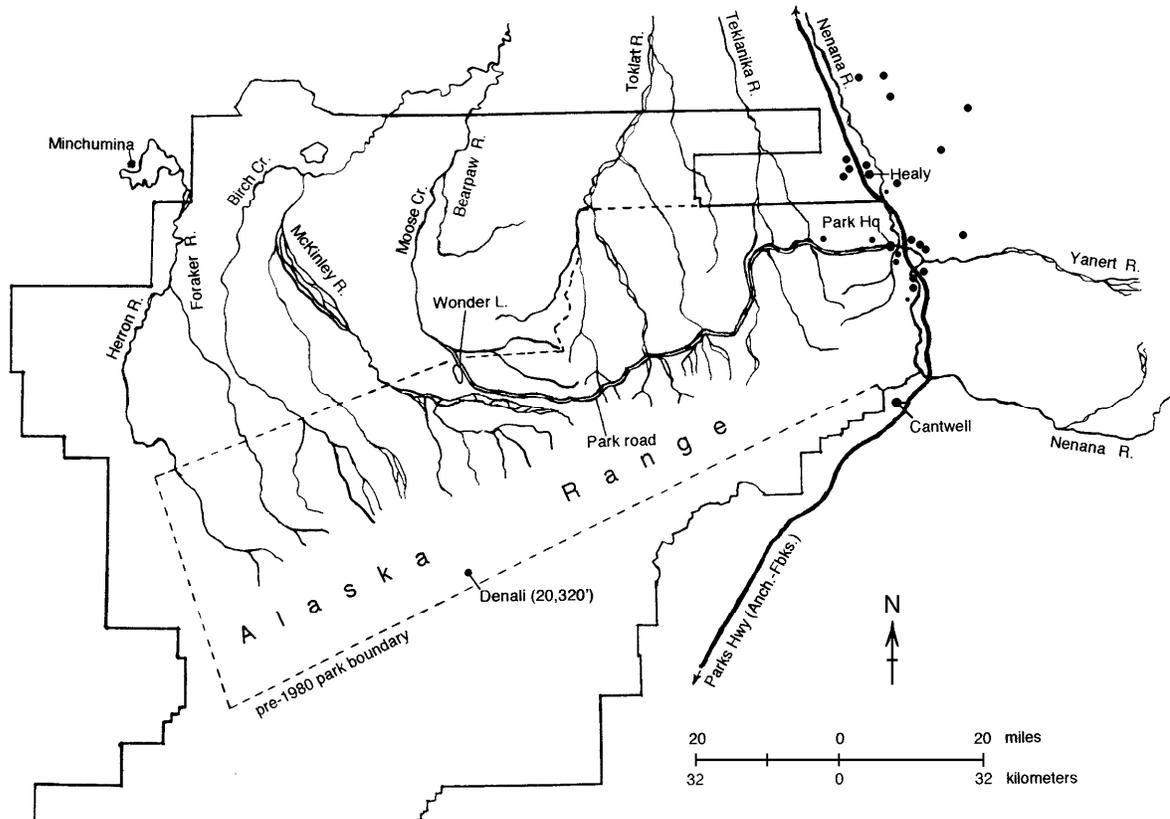


Figure 5. Sanctuary survivor locations, May 2001-March 2002. Small dots=May-September aerial (2), medium dots=May-September from ground (4), large dots=Oct.-March aerial (17).

Why she used so little of the established Sanctuary territory (Fig. 4) and departed northward for almost eight of the 12 additional months that she lived is probably best explained by two factors apart from her status as a loner: (a) In eastern Denali, 10-month-olds are still heavily dependent on older wolves for territory knowledge, hunting expertise, and much else (Haber 1977), hence there had been little chance for her to develop a normal fidelity to the area; (b) The three Margaret wolves began occupying major portions of the Sanctuary territory within about a month of Sanctuary's demise and thus probably deterred her from the area. On one occasion the three ate much of a winter-killed caribou she had found 2-3 days earlier and possibly chased her from it.

The trapper who trapped or snared her felt she was starving, based on what he described as an absence of body fat (M. Weiner, pers. commun.). However, all of my close aerial observations, including the last good visuals on March 9 and 12, indicated she was alert, energetic, and seemingly otherwise normal. There were no hints of any lethargic behavior. Throughout the winter my pilots and I were generally impressed with her excellent

overall appearance and the sprightly way she moved, even in deep snow. A week before she was trapped she returned to her original range by traversing at least 26 miles of rugged mountain terrain in 3-4 days or less.

I watched her attempt to stalk and chase caribou and moose four times, and in each case she seemed inept. However, almost from the beginning she enjoyed a combination of skill and luck in finding winter killed caribou and moose. Ten days after she was orphaned she found an intact adult caribou carcass, for example. She was at three meals the 17 times I located her on 16 different days from October 29, 2001-March 15, 2002. The three meals consisted of two scavenged adult moose and one scavenged moose that was probably an adult. This suggests a comparable if not better winter food consumption rate than I observed for the Toklat and Margaret wolves.

Every time I saw her she was alone. Nonetheless these visuals and her other locations indicated she was trying to find other wolves. For the first several days after she was orphaned on March 16, 2001 she remained in the same area, repeatedly scenting trails and call-howling. Several times over the next few weeks I found her seven miles northward at or near the Denali National Park headquarters sled dog kennels. Given her observed food consumption outside these areas, finding canid companionship was probably also the primary motivation for her ventures into residential subdivisions in the Denali Park, Healy, and Ferry areas, where sled dogs are common.

On March 10 or 11, 2002, she apparently found the trail of the four Margaret wolves and followed them into the Mt. Fellows-Montana Creek area. On March 12 she was resting on a high ridgetop looking intently in the direction of the Margaret four as they rested just below a ridgetop two miles to the west. Four hours later the Margaret wolves had moved six miles westward and she was less than a mile behind them (heavy forest cover precluded visuals). On March 13 they were in the same general area but now three miles apart. When I next checked, on March 15, the Margaret wolves were five miles further west and she was five miles to the south, where she was trapped shortly thereafter. Had she lived, there were probably good odds – as a female just reaching sexual maturity - of eventually being accepted by the relatively small, new Margaret family.

### **Discussion**

The eastern areas of Denali generally provide good year-round moose and sheep and seasonal caribou hunting for wolves, thus it is to be expected that they would also support persistent wolf family lineages. Toklat has survived for 62+ years. Savage survived for

more than 17 years before it was eliminated, Headquarters for 11-12, and Sanctuary six. Now Margaret is occupying much of this area and, like its predecessors, is foraging significantly into unprotected areas further to the east, where it faces the same high risks of being eliminated by hunting and trapping. Each of the previous groups, especially Savage, likely would have persisted for decades longer in the absence of hunting, trapping, and related human impacts. Toklat's 62+ years would not be so unusual were the wolves of this adjacent eastern area (and other areas) afforded better protection.

Not surprisingly, the persistent, relatively stable Toklat and Savage families each also had durable social relations over much of their known histories. For example, there were only two successive Toklat alpha females over a 21-22-year period, and one of them held the position for 13-14 years until dying a natural death. Most likely the Toklat alpha males would have enjoyed comparable longevity under natural conditions. However, at least two and probably three have died human-caused deaths since 1987 alone. I observed similarly durable social relations in Savage, but in reverse: The same top two males (who were probably sibs) maintained their clear-cut roles leading Savage for at least 7-8 years until they dropped out at old age, and both were well established in these positions when I began observing them. However, the alpha female was shot in 1968 and the alpha male ended up breeding (successfully) with two of his daughters in succession, the second after the first probably died a natural death (Haber 1977).

From this historical perspective, Toklat's recent, largely human-caused, disruptions (including reduction to a pair in early 1998), its current reformulation, and the three complete turnovers in the adjacent eastern area since 1983 cannot be brushed off as only minor departures from what happens naturally. I have heard comments to the effect that natural causes could have produced these results. Trying like this to minimize the significance of what *did* happen - to Toklat, for example - is comparable in worth to pointing out that a heart attack could have produced the results facing a family that has just lost its father/husband to a drunk driver. The recent Toklat and other eastern wolf disruptions amount to unfortunate human-caused experiments that are yielding interesting insights at the expense of more interesting and biologically more valuable insights and streams of information (Haber 2002). They also raise legitimate ethical, esthetic, and viewing concerns.

Toklat's reformulation may still be in progress, with the recent separation of the original alpha female. Whether this leads to the budding of an offshoot group (the female and a new mate, her and 1-2 of her older offspring, or some other combination) remains to be seen. At least once before Toklat budded a small group within the western portion of the es-

established territory, in 1971 when a “co-alpha” male separated naturally (Haber 1977). The parent group ended up with a reduced territory. There is already a hint of a similar territory split in the current reformulation, although so far the female has remained primarily alone.

Wherever the Toklat changes end, it is again obvious that in a social group such as this there are complex, widely varying interactions and bonds among the members. Losses of some individuals and disruption of certain bonds lead to much greater responses than do other losses and disruptions. For example, the Toklat alpha female’s close bond with her original mate apparently could not be replaced merely with the appearance of another capable, non-offspring male (who her mate almost certainly would have evicted from the area).

The Toklat alpha male died during radio collaring somewhat less than three months after the Sanctuary alpha male died while skirmishing with a moose. Toklat reformulated but Sanctuary terminated. The difference was in what happened before and after. Earlier and subsequent trapping left only the Sanctuary mother and three dependent 10-month-old pups soon after the alpha male died. Two and a half months later she died during radio collaring, leaving the three pups on their own, two of which disappeared within a few days (the third pup’s remaining 12 months are recounted above). Toklat’s response illustrates a certain amount of resiliency, but what happened to Sanctuary indicates that just beyond there can be a sharp threshold to much different results, again with the outcome depending heavily on which specific individuals, bonds, and other relationships are affected. Sometimes it amounts to a throw of the dice. New males were on the scene a month and a half after the Toklat alpha male died. None appeared for the Sanctuary female during the two and a half months she was available, even though necropsy indicated she was in her prime and had come into estrus during this period (J. Blake, pers. commun. 2001).

There was ongoing hostility between the neighboring Toklat and Savage families. This was characterized by highly aggressive and often-reciprocal winter probes across a well-defined territorial divide, even when the data indicated both groups were eating well within their own territories (Haber 1977). Within a year of Savage’s demise, Toklat shifted its territory 10 miles eastward and annexed more than a third of the vacancy, most of which provides good moose and sheep hunting. None of the Savage successors has yet reclaimed the annexed portion from Toklat. Each has used about the same, reduced territory (e.g., compare Figures 3-4 with Figures 2-9 of Haber 1977). In this sense, elimination of the well-established Savage family has resulted in a major long-term change.

Even when one group rapidly replaces another and uses the same territory, it is the details of how it uses the territory – where it dens, its hunting patterns, and related learned

behaviors - that ultimately determine many of the biological and other consequences of the turnover. The post-Savage results have been mixed at this scale, at least with regard to dens and rendezvous sites. Headquarters and Margaret quickly found and used an old Savage den in the eastern portion of the original territory (central area of the reduced territory) as a natal site. Sanctuary used this den and nearby sites as a late summer-fall base ("rendezvous site") for provisioning its pups in the fourth and fifth (last two) years of its occupation of the area but apparently did not use it before this or as a natal site. None of the Savage successors or Toklat has occupied a more heavily used Savage homesite complex consisting of dens and rendezvous sites in the Sanctuary valley and eastward to Savage River, even though the two major dens of this complex have been partially maintained by foxes over the subsequent 20 years and are still identifiable. Within 4-5 years of annexing the western portion of the Savage vacancy, Toklat found a major Savage natal den in the Teklanika area and has used it extensively at intervals since then.

What determines homesite rediscoveries and how long these traditions survive may be fairly simple in many cases: All of the above sites except in the Sanctuary-Savage River complex are on obvious natural travel routes. It could be that wolves rediscovered some or all of the Sanctuary-Savage River sites but are not using them because of the way Toklat's annexation of the western third of the Savage vacancy changed their location relative to territory boundaries. They were in the central area of the Savage territory but now are on or close to the divide between the new territories - the kind of high-risk location with restricted foraging options that intelligent territorial animals usually avoid for natal purposes.

The appearance of the newcomer males and their takeover of the alpha-less Toklat family illustrate an important point about the evolution of cooperation among vertebrate societies in general and cooperative breeders and hunters in particular. Kin selection is often considered to be the primary mechanism by which helping and other sophisticated cooperation arise. In Haber (1977), I attributed the high levels of cooperation among wolves primarily to kin selection, as have other authors. Clutton-Brock (2002) reviewed recent studies of cooperative breeders and concluded that the underlying mechanisms are probably more diverse and more alike the underpinnings of human social systems. He suggested that the indirect fitness benefits to be gained by helping and otherwise cooperating with close relatives are often overestimated while direct fitness benefits, particularly involving reciprocity between non-relatives, have been underestimated.

Some form of generalized reciprocity (Clutton-Brock 2002) probably best explains the intense, almost immediate, major ways the newcomer males – who were unrelated to the

Toklat wolves – provisioned and otherwise cared for the 2001 Toklat pups and the obvious affection they showed for them. An alternative to reciprocity is that the newcomers stood to benefit directly by being deceptive, to gain the confidence of the two mature females (alpha female and daughter) in order to breed with them 9-10 months later. However, the intensity of their affection toward the pups during the summer homesite period by itself (not to mention their attendance of two of the pups largely in the absence of the alpha female for almost two months) makes it difficult to imagine how this could have been an act. There was nothing to suggest that the pups' sudden disappearance in the fall was because the newcomers killed them, such as newcomer African lion males often do. Nor would this line of argument explain why one of the newcomers did not tie with the alpha female during her next estrus cycle despite her solicitations, unless he was not yet sexually mature - which seems unlikely if only because of his other behavior (e.g., dominant over most others) and her solicitations.

The alpha female's separation after breeding with the dominant newcomer further complicates any explanation featuring deception by him to gain her confidence as a route toward replacing the former alpha male's genes (pups). Whether she chose to separate (which seems most likely) or in some way was pushed (or nudged) out, there would be few if any direct fitness benefits from winning her confidence and an auxiliary breeding opportunity only to have the resulting genes end up on their own at a clear survival disadvantage.

Toklat's cooperative polygyny in at least March 2002 and the contrast between this and the former Savage family's competitive sexual behavior (female-female as well as male-male and almost exclusively monogamous; Haber 1977) illustrate the importance of thinking in terms of diverse underpinnings within and between societies, as do other fundamental social differences between these neighboring families. Reciprocity may best explain the Toklat newcomers' integration and is probably at work in other important ways, but much of the other sophisticated cooperation I have observed among relatives in Savage, Toklat, and other groups indicates that kin selection is also a prominent force in shaping these societies.

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### **Appendix I**

#### **“Family” and “family lineage” vs. “pack”**

Wolves typically live in social groups consisting of breeding adults, their offspring from multiple years, and siblings. Simply put, they live in “families,” most commonly extended families, in both biological and common sense interpretations of the term. “Family” is not human-specific. Along with related terms such as “mother,” “father,” “daughter,” “sister,” “brother,” and “uncle,” it has long seen routine use in the world’s leading scientific journals (e.g., *Science*, *Nature*, *Conservation Biology*) in papers about aspects of social organization in non-human species.

Use of “family” with regard to wolves is sometimes belittled in Alaska. However the joke is really on the biologists, reporters, and others who do the belittling. A biologist who chuckles at the use of this term for wolves or other species reveals his or her ignorance of the scientific literature and about one of the most active areas in all of science (sociobiology) – and sometimes also betrays an underlying social or political agenda (Alcock 2001).

“Pack” is unscientific and misleading. Not only does it fail to convey the fascinating essence of what sets wolf social organization apart from the organization of many other species (Haber 1996) but it connotes almost the opposite. It is used by many biologists and others for little reason other than that many use it.

By “family lineage” I refer to the continuity arising from combined learning-based and genetic transfer of information across generations of a family. The genetic portion of this continuity might erode progressively through “dilution” (Mech et al 1998), but learned traditions in hunting methods, use of the same core territory, homesites, travel routes, and in other aspects of behavior are likely to remain strong, as observed for Toklat and Savage (Haber 1977 and unpublished data). Learning and resulting traditions assume particular importance where

there is prolonged dependency of the young, such as in moose-dependent wolves (Haber 1977).

Farm family lineages, e.g., in Nebraska, provide a rough analogy. Many have turned over. Here and there others have persisted for a hundred years or more, especially where soil and water conditions are the best. Family members continue to breed and die on the farm, disperse to distant areas, and start new farms nearby, and newcomers are added now and then through marriage and adoption. But even in an old lineage the early genes still have a recognizable presence. There are also strong family memories and traditions. Most of the original farmstead remains in production, though some inferior acreage has been sold on one side and some productive neighboring acreage has been annexed on another. The original (renovated) house and barn are still home.

Distinct short-lived and persistent farm family lineages can be identified in mosaics across the landscape. And for the oldest of these we recognize important cultural, esthetic, biological, and other values – just as we should recognize the enormous values of an old non-human family lineage such as the Toklat wolves of Denali National Park.