Temporal use of the Nushagak Peninsula by wolves, Togiak National Wildlife Refuge, southwestern Alaska

Progress Report, 2007 through 2011

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Abstract

We investigated the time budgets of wolves in the vicinity of the Nushagak Peninsula in order to understand their role as a population control of the Nushagak Peninsula Caribou Herd. Using a combination of conventional and GPS radio telemetry; we followed three wolf packs located near the Nushagak Peninsula from 2007 through 2011. We found that only one pack regularly used the Peninsula, while the other two did not. The pack using the Peninsula averaged 32% of its time there, and 68% elsewhere. Its seasonal use of the Peninsula was disproportionately high in summer and fall, and disproportionately low in winter. Wolf use of the Peninsula increased during the course of this study, primarily in late summer and fall. Concurrently, the Nushagak Peninsula Caribou Herd increased. We conclude that wolves capitalized on increasing caribou abundance by focusing more time on caribou predation, but were not a primary population control of the Nushagak Peninsula Caribou Herd.

Introduction

The Nushagak Peninsula caribou (Rangifer tarandus) population was established by relocating caribou from the Alaska Peninsula in 1988 after an absence of >100 years (Hinkes and Van Daele 1996). The population increased from an initial stocking of 146 to a peak of ~1,400 in 1997, then declined to a 2006 level of ~500. Potential causal or contributing factors to the population decline were habitat quality decline, age structure changes, and increased predation by wolves (Canis lupus) and brown bears (Ursus arctos). This project investigated the seasonality and duration of wolf use of the Nushagak Peninsula. Understanding the degree to which wolves used the Nushagak Peninsula allowed an assessment of whether predation was a likely factor in driving population dynamics of Nushagak Peninsula caribou.

Wolf predation on caribou has been described by many investigators as the leading source of mortality, and it is commonly related to population declines. McLoughlin et al. (2003) found that predation by wolves was the most common cause of death in caribou in six populations in northcentral Alberta, Canada. Jenkins and Barten (2005) described a population decline of caribou in the Wrangell Mountains of Alaska, and found the decline to be related to increases in predation rates among wolves primarily and other predators secondarily. Farnell and McDonald (1988) found wolf predation to be the principal cause of mortality in the Finlayson caribou herd in the Yukon, and both calf and adult survival were correlated to wolf population density. Gunn et al. (2006) described a 98% decline of caribou on three islands in the south-central Canadian

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Arctic over a 15-year period. They suspected the causes of the decline were a decrease in adult and juvenile survival associated with human harvest rates and increasing wolf predation. Kojola et. al (2004) found that wolf predation in Finland was an important factor limiting European wild forest reindeer (R. t. fennicus) population growth. Hayes et al. (2003) described an increase in a woodland caribou population in southwestern Yukon following wolf population reduction. The increase was attributed primarily to increased calf recruitment.

It is reasonable to hypothesize that wolves are an important modifier of the Nushagak Peninsula caribou herd, and this concern was regularly voiced during public meetings by the Bristol Bay Federal Subsistence Regional Advisory Council, the state Nushagak Fish and Game Advisory Committee, and the Nushagak Peninsula Caribou Herd Advisory Committee. These concerns often resulted in requests for predator control.

However, there are other possible explanations for the decline in Nushagak Peninsula caribou numbers. Collins et al. (2003) hypothesized that unreported human harvest played a large, but poorly understood role in modifying Nushagak Peninsula caribou population size. Secondly, it is possible that a decline in habitat quality is related to the population decline. Aderman (2006) documented an increase in caribou utilization of lichens during the period 1993-2002, and found that the greatest impact to lichen communities took place on the south half of the Peninsula, which is consistent with a higher population density of caribou in winter, when lichens dominate their diet. Age structure changes have also been hypothesized to be related to the population decline (personal communication, Bruce Dale, Alaska Department of Fish and Game). Under this scenario, the rapid initial growth of the caribou population prior to 1997 resulted in disproportionately high numbers of old, less productive cohorts of females during the subsequent decade, and this, combined with some additional population-lowering factor(s), such as severe winters or high human harvest, could explain the rapid population decline.

Until this study, there have been no investigations of predation impacts on Nushagak Peninsula caribou. This project assessed whether wolf predation is a likely driver of Nushagak Peninsula caribou population dynamics based on wolf time budgets on and off the Peninsula. This progress report covers the time period March 2007 through September 2011.

**Objectives:**
1. Determine the number and pack size of wolf packs located on and adjacent to the Nushagak Peninsula.
2. Determine the seasonality and proportion of time throughout the year that wolves in packs adjacent to the Nushagak Peninsula spend on the Nushagak Peninsula.
3. Relate wolf use of the Nushagak Peninsula to caribou demographics.

**Study area**

The study area covered the likely ranges of wolves that have the potential to prey on Nushagak Peninsula caribou. This area included the Nushagak Peninsula, plus the headlands of the Peninsula to a distance of approximately 50 km (Fig. 1).
The Nushagak Peninsula, located at approximately 58.6° N latitude, 159.0° W longitude, is a 16 km wide peninsula of treeless lowland tundra extending approximately 32 km into Bristol Bay of the Bering Sea. Plant communities include a mixture of gramminoid-dominated wetlands and dwarf shrub heath communities. Lichens are important components of these dwarf shrub communities. A lichen monitoring project determined that lichen cover averaged 48% in 2002 and 45% in 2007, but given the precision of the estimates, no difference could be determined (Aderman 2011).

The Nushagak Peninsula has provided habitat to barren ground caribou since 1988, at which time a population was established through relocation. This population has remained relatively sedentary (Fig. 2), with few forays from the peninsula, and grew rapidly from the initial stocking of 146 to approximately 1,400 individuals in 1997, then declined to approximately 500 individual in 2006.
The headlands of the Nushagak Peninsula include a greater variety of landforms, including the southern extent of the Ahklun Mountains, which is composed of rolling hills up to mountains of 1,000 m elevation. The mountainous terrain is primarily vegetated with dwarf shrub plant communities above alder (*Alnus*) slopes at the bases.

Glacial valleys between mountains include three large lakes and six major rivers (the Igushik, Tuklung, Weary, Snake, Kanik, and Ongoke Rivers), as well as many smaller lakes and streams. Lake shore and riparian corridors include mixtures of willow (*Salix*)-dominated tall shrub communities and deciduous forests. Approximately 20% of the Nushagak Peninsula headlands is forested with white spruce (*Picea glauca*). These communities provide habitat to moose (*Alces alces*). In March 2006, a total-count population estimate found a minimum of 165 moose in the Nushagak Peninsula headlands (Togiak Refuge unpublished data). Brown bears (*Ursus arctos*) are common throughout all portions of the study area.

The study area climate is sub-arctic maritime. Temperatures range from average daily low and high of -11.9 and -5.8°C in December, the coldest month, to 9.1 and 16.1°C in July, the warmest month (NCDC 1971-2000, Western Regional Climate Center, data for Dillingham). Annual precipitation (which includes rain plus melted snow) averages 64.5 cm and snowfall (unmelted) averages 210.6 cm.
There are no roads or human infrastructure within the study area with the exception of the village of Manokotak, a community of approximately 500 individuals located on the Igushik River north of the Nushagak Peninsula, and a commercial fishing village used during the summer at the outlet of the Igushik River. The majority of human activities in the study area consist of subsistence resource gathering activities (hunting, fishing, berry picking, trapping, and wood cutting) accessed primarily via boat traffic from the Igushik and Weary Rivers and associated lakes during summertime. During winter, snowmachines provide access to the majority of the study area. Individuals from the villages of Togiak and Dillingham (located to the east and west of the study area) access the study area for subsistence and recreational pursuits, although at a lower rate than residents of Manokotak.

Methods

Wolves were captured and instrumented with either conventional VHF radio collars (Lotek™ model LMRT-3 VHF radio collar with mortality sensor) or remote-downloadable GPS collars (Lotek™ model GPS4400S collar with mortality sensor and advanced scheduler options). The GPS collars were programmed to determine the animal location every three hours throughout the year. Data from the GPS collars were used to provide the primary basis for addressing the time budget questions. Conventional collars were used to supplement the number of radioed wolves and maintain contact with packs in the event that GPS collars were lost.

Capture was performed during spring and fall. Capture operations included spotter crews in one or two fixed-wing aircraft in communication with a capture crew in a helicopter. Upon locating a group of wolves, the spotter crew directed the helicopter to the location, then maintained visual contact with wolves after they had been darted. Wolves were captured using doses of 572 mg of Telazol dissolved in 2.6 ml of sterile water and delivered with 3 cc Palmer™ darts with 1.9 cm barbed needles. Darts were fired from a Palmer™ capture rifle charged with Very Low Power (brown) .22 charges. Wolves were sexed, weighed, measured, aged by tooth wear (Gipson et al. 2000) into three age classes: Juvenile (< 1 year), Young adult (1-2 years), Mature adult (>2 years), and fitted with radio collars. VHF collars weighed approximately 500 gm and GPS collars weighed 750 gm. Animal care and handling was consistent with the Animal Welfare Act as Amended, 7 USC, 2131-2156 under an Alaska Department of Fish and Game ACUC Assurance.

Radio tracking surveys were flown approximately monthly. Wolf locations were recorded, as well as activity, habitat, and composition of group when other wolves were present. Additionally, location data stored in GPS collars were remotely downloaded using a Lotek™ Hand Control Unit. Downloaded data were entered into ESRI™ ArcMap v9.0 GIS and used to describe the daily and seasonal use by wolves of the Nushagak Peninsula.

Time budget was determined by calculating the proportion of wolf locations or days by season on and off the Peninsula. The Peninsula was geographically determined by delineating the distribution of 95% of caribou locations (Fig. 2) collected monthly 1988—2007 (Aderman 2009). Wolf peninsula-days were defined as any day in which at least one location occurred on the Peninsula. Seasons were defined as Winter: 1 December – 15 May; Early denning/caribou calving: 16 May – 30 June; Late denning: 1 July – 15 August; Late summer: 16 August – 15 September; and Caribou rut/post rut: 16 September – 30 November. A Chi-square goodness-of-fit test was used to determine whether there was a significant difference in the expected and observed times that wolves used the Peninsula, based on amount of time per season. If
significant differences were found, Bonferroni family of confidence intervals were used to
determine which seasons were different (Byers et. al 1984). An index to the potential level of
wolf predation on Nushagak Peninsula caribou was developed by calculating wolf peninsula-
days per season as such:

\[ PD_{\text{wolf}} = N_{\text{wolf}} \times (P_{cw} \times D) \]

where \( N_{\text{wolf}} \) was the number of wolves in packs using the Nushagak Peninsula in a given season,
\( P_{cw} \) was proportion of time that radio collared members of these packs used the Peninsula, and \( D \)
was the number of days in the season. Annual indices were calculated by summing the seasonal
numbers of wolf peninsula-days. Linear regression was used to determine trends over time in
annual and seasonal wolf use of the Nushagak Peninsula.

We determined den locations based on wolf location data during May-June. We determined
number of pups produced by making visual observations at den or near den locations during July.
We calculated parturition dates based on repeated failure of adult female GPS collars to record
locations during May, assuming that the parturient females were underground in their dens
during repeated times of location failure.

Caribou population size was estimated approximately twice annually using transect-based
minimum population counts in late winter (Aderman 2011) and by photograph counts taken after
post-calving aggregations in summer (Togiak Refuge unpublished data). We used linear
regression to determine relationships between annual wolf use of the Nushagak Peninsula and
caribou population size.

Results and Discussion

We captured a total of 19 individual wolves (Fig. 3) during eight capture periods (Table 1).
Fifteen wolves were recaptured on one or more occasions, for a total of 34 capture events.
Wolves were recaptured in order to replace collars with expended batteries (n = 8), exchange a
conventional collar for a GPS collar (n = 2) or re-collar wolves which broke off their collars (n = 5).
Wolves were surveyed via 75 radiotracking flights during the period March 2007 through
October 2011. Cumulative days of telemetry data for wolves instrumented with GPS collars was
4,326, for an approximate total of 35,000 individual locations.

Figure 3. Placing a GPS collar on Wolf 0701, 22 March 2007.
Two packs were identified in spring 2007 when the study began, and were referred to as Snake Lake Pack and Ualik Lake Pack. A third pack, named Weary River Pack, formed in 2008 when a young adult female from the Ualik Lake Pack dispersed to an area at the border of the Ualik Lake and Snake Lake Pack territories, found a mate, and established a pack territory.

Pack Histories, Size, and Production

Snake Lake Pack

2007
At the initiation of the study, the Snake Lake Pack was known to consist of two individuals: 
young adult male W0701 and young adult female W0704. They were located together on three subsequent locations, and were located apart from each other on three locations. W0701 was last seen 10 May 2007. Two searches expanded to an area approximately 30 km beyond the known range of W0701 did not detect the wolf. Subsequently, W0704 was located alone on nine
occasions until 28 November 2007. No pups were known to have been produced or survived in 2007.

2008
On 30 January 2008, a single, uncollared wolf was seen with W0704. She was seen with this wolf on four occasions through 2 April 2008. On 30 April, she was alone and was not seen with another wolf on the next four flights (through 10 October 2008). Thus, we assume that W0704 lost her mate in Spring 2008, just as happened in 2007. Also as in 2007, no pups were known to have been produced or survived in 2008.

2009
On 21 November 2008, W0704 was seen with a single companion. She was observed with this wolf on three subsequent occasions until spring 2009, at which time her mate was captured, collared with a GPS collar, and named W0901. She was recaptured at this time and her conventional collar was replaced with a GPS collar. The pair denned in the Killian Creek Valley (Fig. 4). Parturition date was determined to be 17 May 2009 (Appendix A) and seven pups were observed on 20 July 2009. W0901 remained on the air until his death on or soon after 24 June 2009. His skeleton was found near the den site, and his skull had wooden branches lodged between upper carnassials (Fig. 5). His death was assumed to be related to this.

![Figure 4. Movements of W0901 during early denning (16 May – 30 June 2009) converging at den.](image)

W0704 was seen in a group of eight gray wolves on 8 September 2009, indicating that she had successfully raised all seven pups until then. On 10 September, she was seen accompanied by a black wolf, assumedly a male. On 18 December, she and 4-5 other wolves, including the black, were seen in the process of killing a moose cow and calf. In mid-December, a hunter killed a wolf (assumed to be one of the Snake Lake Pack pups) near Otter Creek, which occurs in the Snake Lake Pack territory. On 5 December 2009, W0704 was located with four gray pups.
2010
On 4 March 2010, W0704 was located with two pups and the black adult. On 30 March, she was
located with one pup, and in subsequent surveys, no 2009 pups were seen. It is possible that the
pups were shot or trapped, as hunter/trapper reports accounted for three pups taken December
2009 through March 2010.

In April 2010, W0704 was recaptured to replace the battery in her collar. She was accompanied
by the black young adult male, who was also captured, collared, and named W1001. The pair
used the same den as in 2009 (Fig. 3). Parturition date was determined to be 15 May 2010
(Appendix A) and five pups were observed on 29 July 2010.

W1001 was located on three additional occasions through 30 August 2010, then was heard (but
not seen) in the mortality mode on 25 October 2010 on a hillside near Snake Lake. His collar
collected locations normally for the first month after deployment, but gradually began to fail to
collect location data, with the last location collected on 14 September 2010. The VHF beacon
continued to transmit until 30 November, after which it went silent. At that time it was assumed
that W1001 had died, but this was later proven incorrect. As such, it is assumed that W1001
broke off his collar, and it later failed, perhaps due to damage sustained when broken off.

W0704 was seen on 25 October 2010 with six other wolves, including three blacks. The den
watch in July determined a total of five pups, including two blacks, so it is assumed that the third
black was W1001. On 30 November 2010, W0704 was seen with four other wolves (assumed to
be pups), including two blacks.

2011
On 9 February 2011, W0704 was seen with five other wolves, including two or three blacks, and
on 4 March 2011, she was seen with a single large black wolf, assumed to be W1001. On 24
March, W0704 was recaptured to replace the battery in her collar, and an uncollared adult black
male was captured with her (she was also accompanied by two other grays and one other black,
assumed to be pups). The black adult male was determined to be W1001 based on photo records
of his teeth which included a distinctively broken upper left canine.
W0704 and W1001 were seen on 27 April 2011 with two uncollared wolves (one black and one gray), then were not again seen on the subsequent five aerial surveys, although they were located and location data was downloaded. Unlike in the past two years, they denned in a new location in 2011 (Fig. 6) and the parturition date was approximately 17 May 2011. A den watch was attempted on 6 September 2011, but no wolves were seen. W0704 and W1001 were both seen accompanied by five wolves (three grays and two blacks) on 28 September, of which four or five were thought to be pups.

Figure 6. Movements of W1001 during early denning (16 May – 30 June 2011) converging at den.

Ualik Lake Pack

2007
At the initiation of this study, the Ualik Lake Pack was believed to consist of five individuals: W0702, W0703, and 3 other uncollared wolves. The wolves in this pack were generally united during winter months, and generally operated independently during non-winter months. Based on locations from W0703, the pack denned in the Ualik Lake valley (Fig. 7). The dominant female was not collared, so an accurate parturition date cannot be determined. Den observations on 31 July 2007 determined that six pups were produced.
In spring 2008, six wolves from the Ualik Lake Pack were captured and collared, including W0703, who had broken his collar in November 2007. W0801, the dominant female, was captured, as well as two young adult females (W0803 and W0804) and two young adult males (W0802 and W0805). Conventional collars were placed on W0804 and W0805, and GPS collars were placed on the others. The Ualik Lake Pack used the same den location it had used in the previous year (Fig. 8), and parturition occurred on 17 May 2008 (Appendix A). Den observations on 20 July determined the production of nine pups.

In fall of 2008, two wolves from the Ualik Lake Pack were captured and collared, including W0703, who had broken his collar for a second time in June 2008. W0803 was also recaptured, after having slipped her collar off on 23 April 2008.
2009
In spring of 2009, two wolves from the Ualik Lake Pack were captured and collared, including W0801 in order to replace her collar battery, and W0902, a young male. Based on coloration, W0902 was suspected to be W0802, who broke and lost his collar in fall 2008. W0805, who was fitted with a conventional collar in spring 2008, was last heard in February 2009, possibly dispersing outside the Ualik Lake Pack range.

W0703 and W0801 remained the leaders of the Ualik Lake Pack. Rather than denning in the Ualik Lake valley as in the past two years, they denned approximately 21 km southeast on the upper edge of the Nushagak Peninsula in the Tuklung River drainage (Fig. 9). Parturition occurred on 21 May 2009. Den observations on 20 July 2009 determined the production of three pups.

Figure 9. Movements of W0703 during early denning (16 May – 30 June 2009) converging at a new den site approximately 21 km from previous dens.

In fall of 2009, four wolves from the Ualik Lake Pack were captured, including W0703, in order to replace the collar battery. Also collared was young adult female (W0903), which appeared to be 1.5 years old, and young adult male (W0905), which appeared to be 2.5 years old. The fourth, a male pup, was released without a collar.

2010
In January 2010, young adult female W0903 was last heard, possibly dispersing from her natal range. In the spring of 2010, W0801 was recaptured to replace the battery in her collar.
Additionally, three other young adult wolves were captured and collared, including W1002 (female), W1003 (male), and W1004 (female). W1002 was relocated with the pack on the day following her capture, then was not located again until she was killed by a hunter on 15 March 2011 near Manokotak, within the Ualik Lake Pack range. A failed seal on the collar permitted moisture to enter, causing the collar to fail.
During the spring of 2010, four additional collared members of the Ualik Lake Pack were killed in traps or snares, including W0803, who apparently dispersed from her natal range in April 2009 and was snared near Bethel in February 2010, a straight-line distance of approximately 260 km (Fig. 10). Young male W0905 apparently dispersed, making extended trips to the northeast of his natal pack range to a distance of 213 km in January and February 2010, and was ultimately trapped near the village of Koliganek (Fig 11.) Young adults W0804 (female) and W0902 (male) were snared along with one uncollared adult (possibly from the Ualik Pack but also possibly an immigrant) near Warehouse Mountain, which is on the border of the Snake Lake and Ualik Lake Packs. Two uncollared juvenile wolves (assumed to be from the Snake Lake Pack) were also snared at this site.

The Ualik Lake Pack used the same den location it had used in 2009, and parturition occurred on 18 May 2010 (Appendix A). Den observations on 18 July determined the production of five pups.

A total of seven survey flights occurred from 30 June through 13 December 2010, with various numbers of wolves seen up to a total of 11, although never in a single group. W0703, W0801, W1003, and W1004 were located on most flights. In October 2010, W0703 was recaptured to replace the battery in his collar.

Figure 10. Locations and movements of young adult female W0803, April 2008-April 2009. The trip taken to the north of her home range occurred during a week in March 2009. Contact was lost in April 2009 and not regained until she was trapped near the arrow in February 2010.
In May and June 2010, young adult male W1003 made three trips outside the Ualik Lake Pack range, including a nine-day trip west to Goodnews Lake, a distance of ~100 km (Fig. 12). He made two shorter trips north to the vicinity of Ongivinuk Lake, then returned to his natal range and remained with the pack until October 2010, after which he was not relocated on subsequent aerial surveys. During 2010, searches were made on three occasions for dispersing wolves to a distance of 50 to 100 km surrounding the Ualik Lake Pack range. W1003 was assumed to have dispersed, but this was demonstrated to be incorrect on 15 March 2011, when he was killed by a hunter near Manokotak, within the Ualik Lake Pack range, in the company of his sister W1002, who was also killed. W1003’s collar had failed due to internal damage to the battery.

Figure. 12. Locations and movements of young adult male W1003, April -- October 2010. Movements include trips outside his natal range to the north and west. This wolf was ultimately shot within his natal range on 15 March 2011.
2011

On 9 February 2011, W0801, W0703, and W1004 were located with nine additional members of the Ualik Lake pack, indicating that the pack was composed of at least 12 individuals then. On 24 March, radio collars were replaced on W0801 and W1004 (whose collar had failed). Additionally, two one-year old male wolves were also captured, including W1102, who was collared, and W1103, who was not collared.

In 2011, W0801 selected a new den site (Fig. 13) and parturition occurred on 22 May 2011 (Appendix A). Additionally, on the day previous, W1004, a 3-year old female and daughter of W0801, denned and had pups at a location 31 km to the south, but still within the Ualik Lake Pack range (Fig. 13, Appendix A). Backdating the parturition date of these two wolves by 63 days (the expected wolf gestation period) results in breeding dates of 19 and 20 March 2011. To infer the sire, location data for W0801, W1004, and W0703 (the Ualik Lake Pack dominant male), were analyzed for proximity for 10 days prior to and after the calculated breeding dates. From 16 – 29 March 2011, all three wolves were co-located or within a few hundred meters of each other. For the precise time of estimated breeding, all three wolves were co-located continuously for 53 consecutive locations from 0100 h 18 March 2011 until 1600 h 24 March 2011. It thus seems likely that W0703 mated with both females, even though he was the sire of W1004.

![Fig. 13. Locations, approximate travel paths, and den sites of W0801 (red) and W1004 (blue) from 25 March – 17 October 2011.](image)

During the 2011 denning period, W0801 showed similar fidelity to her den site as in previous years, until while on an assumed foraging trip on 23 June 2011, encountered W1004’s den apparently for the first time. This was W0801’s first long-distance trip from her new pups in
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2011. Her subsequent 42 consecutive locations from 1600h 23 June 2011 until 0400h 29 June 2011 were at the center of W1004’s den site. During this time, W1004 spent approximately half of her time at the den site, and half of her time making short distance, short duration trips away from the den. It appeared that W0801 “adopted” her daughter’s pups, assumed a motherhood role, and W1004 reverted temporarily to the role of helper. On 3 July, after a 4-day period back at her own den, W0801 returned to W1004’s den, remaining there for five days, then returned to her home den, then repeated a pattern of alternating time between dens until 10 September 2011. During this period, W1004 remained at her own den, whether or not W0801 was present. However, the distance and duration of trips made by W1004 throughout this period suggested that she actively hunted and delivered food to the den, often appearing in the role of a helper rather than mother. W1102, a two-year old male in the Ualik Pack, served as a helper at W0801’s den up to the point that W0801 first encountered W1004’s den. W1102 accompanied W0801 to the new den, then remained there, apparently making regular food deliveries to W1004’s pups throughout the remainder of the denning season, and no longer assisting at W0801’s den.

No den watches were made via ground observation at either W0801 nor W1004’s den. A total of four pups were seen with W0801 on an aerial survey on 25 August, and a total of four or five were observed with her on 28 September. W1004 was seen on three aerial surveys after parturition (13 July, 28 August, and 28 September) but no pups were observed until 17 October 2011, at which time W1004 and W1102 were seen with four pups at a caribou kill site. On the same day, W0801 was seen with five other wolves, including four pups, approximately 2 km away. Subsequently, during the months of November and December 2011, W1004 was generally co-located with W0801, W0703, and W1102, indicating that they functioned as a single pack.

Weary River Pack

2008

W0702 originated in the Ualik Lake Pack. She was instrumented with a conventional collar and was estimated to be 3 years old in spring 2008. On 7 March 2008, she was located approximately 19 km east of the Ualik Lake Pack border, deep within the Snake Lake Pack territory. She was subsequently located in the Ualik Lake Pack territory alone on 2 April, then in the company of the pack on 11 April. On 30 April, she was located in the Weary River valley with another uncollared wolf. They were approximately 50 km from the remainder of the Ualik Lake Pack. She was located three times in May and June in the Weary River valley, although was not observed, nor was a mate observed, on these occasions. On 24 July 2008, she was observed with four pups near her suspected den site, and thus confirmed the establishment of a new pack. She was located without visual observation in August in the same vicinity, then was seen on 18 September with three pups in the Picnic Beach area, located on the west-central edge of the Ualik Lake Pack. She was captured near the Picnic Beach area and her conventional collar was replaced with a GPS collar on 24 September. She remained in this general vicinity until 28 September, then moved to the Weary River, Ongoke River, and Amanka Lake area. This area occurred within the Ualik Lake Pack territory, but was on the periphery.

W0702 was heard but not seen on two subsequent occasions. She was killed by a hunter on 13 December, after having killed a moose near the Manokotak airport. All of her pack mates were killed by hunters and trappers within the next few weeks, based on harvest reports.
2010

On 21 January 2010, young adult female W0804 (member of the Ualik Lake Pack instrumented with a conventional collar) was located at a moose kill site approximately 10 km from the remainder of the Ualik Lake Pack, which included 10 individuals at that time. The moose kill was located on the border of the Ualik Lake Pack and Snake Lake Pack territories. No locations were recorded from any other members of the Ualik and Snake Lake Packs at this kill site at that time, or at any time thereafter, suggesting that neither pack killed or consumed the moose. On 22 January 2010, W0804 was observed with an uncollared adult wolf approximately 19 km northwest of the moose kill site in the Weary River valley. The Weary River valley forms the border between the two packs, and had not been occupied by an independent pack since December 2008. It is possible that W0804 had mated with a new immigrant, and they were in the process of establishing a territory in the Weary River valley.

W0804 was last located in the Weary River valley on 4 March 2010. However, both W0804 and an uncollared young adult male were killed in snares in March 2010 near Warehouse Mountain, which is also part of the border between the two established packs.

Pack size

Pack size has varied from a single wolf to 15 individuals (Table 2). Pack sizes were highest in summer, after pups are produced, and lowest in springtime, when mortality and dispersion reduced numbers.
Table 2. Known number of wolves per packs by season, 2007 through 2011. Pups were not distinguished from adults in Fall and Winter.

<table>
<thead>
<tr>
<th>Pack</th>
<th>Season</th>
<th>Age</th>
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<td>Pups</td>
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<td>Adults</td>
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<tr>
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<td>Adults</td>
<td>5</td>
<td></td>
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</tr>
</tbody>
</table>

Use of Nushagak Peninsula

Overall time budget
We recorded no occasions in which the Snake Lake Pack ventured onto the Nushagak Peninsula (Fig. 12). However, in 2010, W0704 (and likely her pack mates) traveled to the southernmost point documented for this pack, almost to the village of Dillingham (Fig. 14).
Figure 14. Range of the Snake Lake Pack from spring 2007 through 2010. This includes W0701 (original dominant male) from 23 March – 10 May 2007, W0901 (the third dominant male) from 5 April – 24 June 2009, W1001 (fourth dominant male) from 4 April – 15 September 2010, and W0704 (dominant female) from 5 April 2009 – 4 March 2011.

The Weary River Pack spent virtually all of its time off the Peninsula. Of the 80 days which W0702 was instrumented with a GPS collar, she spent only four on the Peninsula (Fig. 15.)

Figure 15. Movements of W0702, dominant female of the Weary River Pack, from 25 September until her death on 13 December 2009.
The Ualik Lake Pack regularly used the Nushagak Peninsula (Fig 16). Use was concentrated in the vicinity of Picnic Beach, with a decreasing concentration with increasing distance south. In the years 2007-2009, there were no locations documented east of the Igushik River and south of the village of Manokotak. The area is primarily lowland tundra, with little caribou or moose use, and little winter cover. However, on multiple occasions, individuals from the local community reported seeing wolf tracks in this area, and from November 2009 – February 2010, W0905 (young adult male) used this area on several occasions (Fig. 17). The Ualik Lake Pack mated pair did not venture into this area, nor did we document any other pack members there, so it is not clear whether this area is part of the Ualik Lake Pack territory, or whether it was used by one or more wolves in the process of dispersing. Regardless, W0905 was documented to use this area, as was W0704 from the Snake Lake Pack (Fig. 14).

Figure 16. Range of the Ualik Lake Pack from 2007 through 2010, including all locations from W0703, W0801, W0802, and W0803, W0903, and W1004. The dispersal trips of W0803, W0905, and W1003 are not used to define this range.
Figure 17. Locations (yellow points) and movements of W0905 east of the Igushik River outside the known range (red) of the Ualik Lake Pack.

**Seasonality of wolf use of Nushagak Peninsula**

Although wolves were often co-located, there was much variability in their individual use of the Nushagak Peninsula (Fig. 18). Use of the Peninsula varied from a little as 10% of the time by W0803 (which was tracked for 239 days from April 2008 through May 2009) to 63% of the time by W1102 (which was tracked for 208 days from March through October 2011). More representative of annual time budgets on the Peninsula are W0703 and W0801, which were tracked for 1,133 and 1,285 days, and which used the Peninsula for 39 and 29% of their time respectively.

![Proportion of time on Peninsula](chart.png)

Fig. 18. Proportion of time individual wolves from the Ualik Lake Pack used the Nushagak Peninsula, 2007 – 2011.
On an annual basis, over the five years of study, the wolves which used the Nushagak Peninsula averaged 36% of their time there, and 64% off the Peninsula (Table 3). Peninsula use varied from a high of 46% in 2007 to a low of 21% in 2008. However, given that the sample size in 2007 was a single wolf with less than a full year of location data, trends in pack use are likely more representative from 2008. Since 2008, there has been a significant increase in wolf year-round use of the Nushagak Peninsula ($r^2 = 0.962$, $P = 0.019$, Fig. 19).

<table>
<thead>
<tr>
<th>Year</th>
<th>Wolf</th>
<th>Winter 1 Dec-15 May</th>
<th>Early denning/ caribou calving 16 May-30 Jun</th>
<th>Late denning 1 Jul-15 Aug</th>
<th>Late summer 16 Aug-15 Sep</th>
<th>Caribou rut and post rut 16 Sep - 30 Nov</th>
<th>Total year</th>
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<td>9</td>
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<td>37</td>
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<td>36</td>
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<td>34</td>
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</tr>
<tr>
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<td>153</td>
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<td>36</td>
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<td>427</td>
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<td>% time on Peninsula</td>
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<td>0.32</td>
<td>0.63</td>
<td>0.70</td>
<td>0.54</td>
<td>0.36</td>
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Table 3. Wolf days by season on and off Nushagak Peninsula from 2007 through 2011.
Wolf use of the Nushagak Peninsula was not proportional seasonally. Ualik Lake Pack wolves spent only 8% of their time on the Peninsula during winter, and as much as 70% of their time there in late summer. During the caribou calving season, Ualik Lake Pack wolves used the Peninsula 32% of their time, and spent 68% of time elsewhere.

Our seasonal division of the year was not equal, with Winter totaling 45% of the year, while Late Summer only accounting for 8% of the year. Accounting for this unequal season length, the time that wolves spent on the Peninsula was not proportional to the amount of time per season ($\chi^2 = 936.0$, d.f. = 4, $P < 0.001$). Use of the Peninsula in Winter was significantly ($P < 0.01$) lower than expected, while time on the Peninsula in all other seasons was significantly ($P < 0.01$) higher than expected (Table 4, Fig. 20). Stated differently, wolves avoided the Peninsula in winter, and preferred it during other times of year.

Table 4. Simultaneous confidence intervals using the Bonferroni approach for wolf time on the Nushagak Peninsula, 2007 – 2011. Time spent on the Peninsula was significantly ($P < 0.01$) higher than expected in all seasons except winter, in which it was significantly lower.

<table>
<thead>
<tr>
<th>Season</th>
<th>Expected proportion of time</th>
<th>Actual proportion of time $P_i$</th>
<th>Bonferroni intervals for $P_i$</th>
<th>Direction of difference</th>
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<tr>
<td>Late summer</td>
<td>0.085</td>
<td>0.184</td>
<td>0.183</td>
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<tr>
<td>Rut/post-rut</td>
<td>0.208</td>
<td>0.344</td>
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Use of the Nushagak Peninsula during the early denning/caribou calving season varied from no use to 56% of their time in 2011. This suggests that wolf predation on caribou calves was highly variable, but demonstrated an increasing trend. However, overall the majority of wolf predation must have been focused on other prey, such as moose calves, during the course of this study. Wolf use of the Nushagak Peninsula also demonstrated a clear increasing trend throughout this study during the late denning, late summer, and fall seasons.

It is possible that wolves were focused on bull caribou during the fall. Mech et al. (1998) found that bull caribou was the predominant prey type taken by wolves in Denali National Park August through October. They attributed this to bull caribou being in poor nutritional condition and often injured during and after the rut. Consistent with this, over the course of the study we observed 11 incidents of wolf predation on caribou while conducting aerial telemetry surveys, and of these, six occurred in October and five of the six were adult bulls (Figs. 21, 22).
We also observed a total of 23 incidents of moose predation by wolves during the course of conducting aerial telemetry surveys (Fig. 22). The majority of moose predation was observed to occur during winter, and secondarily, during fall. The combined total of moose and caribou kills observed was 34, and of these, moose accounted numerically for 68% and caribou accounted for 32%. As previously reported, wolves spent a combined total of 32% of their time on the Nushagak Peninsula, and 68% of their time off the Peninsula, suggesting the proportion of time on and off the Peninsula can serve as a relative index to moose and caribou predation.

Caribou population estimates since the onset of this study have demonstrated an increasing trend (Fig. 23). For the years 2008-2011, wolf peninsula-days were directly related to the size of the
caribou population ($r^2 = 0.96, p = 0.021$, Fig. 24). Data from 2007 was not included, as the sample size included a single GPS collared wolf in the Ualik Lake Pack, whose time totaled ~65% of the year.

Figure 23. Nushagak Peninsula Caribou Herd population estimates, 1988-2011. Red line indicates the initiation of this study.

Fig. 24. Relationship of caribou population counts and total estimated time spent on Nushagak Peninsula by Ualik Pack wolves, 2008-2011.
Conclusions to date

Wolf use of the Nushagak Peninsula has increased from 2008 until 2011. This increase in use occurred in the non-winter seasons, and in particular in late summer and fall. Caribou population size increased during the same time that wolf use of the peninsula increased, suggesting that wolves capitalized on an increasingly abundant food source. However, wolf predation was not a primary population driver for caribou—on the contrary, caribou abundance was a primary control for wolf habitat use.

The Snake Lake Pack has not produced known dispersers, but generally has experienced a level of mortality that has prevented pups from moving beyond the yearling age class. The stability in this pack has been a function of the dominant female, who has survived four mates and two to four litters of pups.

The Ualik Lake Pack has produced two known dispersers, and it is probable that 2-3 additional young adults dispersed from the natal range annually during the course of this study. This pack has consistently had pup survival to young adulthood, such that there has continuously been adult pack members additional to the breeding pair.

During the study period, the Ualik Lake Pack was the sole wolf pack that regularly used the Nushagak Peninsula. This pack varied in size within and over years, but was consistently the most successful of the three packs studied. It produced and raised pups each year and maintained the largest pack territory. The Snake Lake Pack was reduced to a single individual for much of this study, and likely failed to produce pups in two of four years. The Weary River Pack developed, produced pups, and was killed in a period of less than one year.

The Ualik Lake Pack was potentially in contact with caribou 32% of the time, and not in contact for 68% of the time. Incidental observations of wolf predation on moose and caribou suggest that wolf time budget on and off the Peninsula relates directly to the number of moose and caribou killed by wolves, supporting the idea that caribou have accounted for about a third of the Ualik Pack diet.

Mech et al. (1998) found variability in annual and monthly prey proportions, with moose predominating wolf diets in some years, while caribou predominated the diet in others. This variability appears to be true in this study as well, based on wolf temporal use of the Nushagak Peninsula. Of the four caribou calving seasons covered by this study so far, the Ualik Lake Pack time on the peninsula varied from no use to 50%. The most consistent use of the Peninsula by wolves occurred in summer and fall. This may be related to predation on bull caribou which are weakened or injured by stresses involved in breeding, but likely includes other classes of caribou or other prey species.

Next Steps

We will continue following the time budgets of wolf packs in the vicinity of the Nushagak Peninsula through Spring 2012. During times of wolf activity on the Peninsula, we will estimate potential caribou predation based on published caribou predation rates. We will refine this estimate by using stable isotopes of carbon and nitrogen contained in wolf hair to estimate the proportion of moose, caribou, and salmon in the diets of Ualik Lake Pack wolves.
Acknowledgements

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References


Appendix A. Breeding and parturition timing

Breeding and parturition timing were determined based primarily on collar success rate in calculating locations, and secondarily on wolf behavior while denning.

GPS collars were scheduled to obtain locations every three hours. Locations were not collected when, at the appointed time, the collars were obscured for approximately 90 seconds from the satellites, such as when in dense vegetation, when obscured by terrain, or underground. During the period 10 April--16 May 2008, Ualik Pack dominant male W0703’s collar was scheduled to collect locations on 533 occasions, but failed to record locations on 12 occasions. During this same period of time, Ualik Pack parturient female W0801’s collar was scheduled to collect the same number of locations, but failed to record them on 139 occasions (Fig 1).

The distribution over time of failed locations appeared random for W0703 (Fig. 1), while there was a clear grouping for W0801 (Fig. 1). We assume this grouping of locations for W0801 was primarily associated with being underground while denning, and thus can be used to infer an accurate estimate of the timing of parturition. We assume that parturition occurred near the beginning of the block of time when W0801 was continuously out of satellite contact. W0801’s collar failed to collect locations in a continuous group in May and June 2011, but the timing was later and the duration of the failed locations was shorter than in other years, or with other wolves. Analysis of W0704’s location history at this time indicated that she moved normally throughout her pack range until 17 May (Fig. 3a), at which time movement ceased for three days, then
Figure 2. Timing of successful and unsuccessful attempts by GPS collars to calculate locations of three parturient female wolves on Togiak National Wildlife Refuge, 2008-2011. Locations were scheduled at 3-h intervals. Blue squares represent date and time of locations successfully received. Red squares represent date and time that locations were not successfully collected.

exhibited a pattern of short distance, short duration trips from the putative den location (Fig. 3b) consistent with attending newborn pups. After mid-July, W0704’s daily travel remained centered at the den, although trip distances increased (Fig. 3c). Our interpretation of these data is that W0704 gave birth to her pups above ground, or in a shallow den that allowed the GPS collar to function normally. We assume parturition occurred on 17 May 2011, at which point she remained stationary for three days, then exhibited minimal movement for the next three days, then gradually increased the number and duration of trips from the den. On 3 June, W0704 moved approximately .9 km to the east, at which point her collar failed to record locations 18 times out of 54 attempts, and after which collar success rate gradually increased. We interpret this as W0704 moving her pups to a new location (often referred to as a rendezvous site), then either digging a den or locating an existing shelter which prevented normal GPS collar function.
Figure 3. Locations and approximate travel paths of W0704 before (a., 17 April – 16 May 2011), during (b. 17 May – 13 June 2011), and following (c., 14 June – 13 July 2011) parturition and early denning.

With the exception of W0704, we assigned parturition dates to the days when the GPS signal was first lost for eight or more continuous location attempts (Fig. 4).
Figure 4. Assumed parturition dates of wolves on Togiak National Wildlife Refuge, 2008-2011 (green lines).

With a sample size of three wolves over a four year period, little can be inferred concerning parturition and mating. However, the data suggest high synchrony between wolves, and over time (Table 1.) All parturition dates combined have a range of only eight days (15-22 May). Assuming an average gestation period of 63 days, the mating dates for these wolves are estimated to occur 13-20 March.

Table 1. Estimated parturition dates of three wolves, 2008-2011, Togiak National Wildlife Refuge, Alaska.

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</tr>
<tr>
<td>2011</td>
<td>22 May</td>
<td>17 May</td>
<td>21 May</td>
</tr>
</tbody>
</table>
Using similar methodology to estimate parturition date with GPS collars collecting six locations per day on three parturient female wolves in the spring of 2010, Bryce Lake, Yukon Flats National Wildlife Refuge estimated parturition dates of 3, 5, and 9 May 2010 (personal communication, Bryce Lake). Thus, although similar to Togiak Refuge wolves in that parturition dates were highly synchronous among wolves within Yukon Flats Refuge, there was a difference in timing between the two areas. The average parturition date in 2010 for the Yukon Flats Refuge wolves was 6 May, while the average for Togiak Refuge was approximately 19 May, a 13-day difference.

At approximately 66°20’N latitude 146° 0’W longitude, the Yukon Flats Refuge is approximately 1,100 km northeast of Togiak Refuge, and located in the interior of Alaska instead of on the coast. Springtime plant phenology at Yukon Flats Refuge is advanced by a few weeks over that of Togiak Refuge, and it is likely that parturition in wolves is timed to respond to this.