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The relationship of wolf and brown bear predation with moose population density and growth at Togiak National Wildlife Refuge and BLM Goodnews Block, Alaska, Progress report, 2014-2018

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Moose, *Alces alces,* Wolf, *Canis lupus,* Brown Bear, *Ursus arctos,* predation on moose.

ON THE COVER
A brown bear stalks a bedded moose, Togiak National Wildlife Refuge, southwestern Alaska.
Photograph courtesy of Togiak National Wildlife Refuge

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Project Description

In 2014, we initiated an investigation into the role of wolf (*Canis lupus*) and brown bear (*Ursus arctos*) predation in regulating the population dynamics of moose (*Alces alces*) on Togiak National Wildlife Refuge (Refuge), BLM Goodnews Block, and adjacent areas. We will relate the predation impact by wolves and bears on moose at varying levels of moose population density. We will use existing population estimates for brown bears, and through the use of radio telemetry, we will estimate the number and composition of wolf packs on the Refuge. We will model wolf and bear predation on moose based on the quantity of wolves and bears and diet composition of both species determined through analysis of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) stable isotopes. To date, we have gathered demographic and isotopic data on 25 wolves from nine wolf packs, and have collected approximately 400 brown bear hair samples. Genetic and isotopic analyses have been successfully performed on 139 bear samples. This reports our progress to date, and identifies the remaining data gaps.

Justification

Concern that wolf and bear predation is negatively affecting the Togiak Refuge area moose population is regularly voiced during public meetings by Federal Subsistence Regional Advisory Councils, state Fish and Game State Advisory Committees, and members of local communities. These concerns periodically result in requests for predator control. In recent years, there has been an increasing reliance on predator control programs by the Alaska Board of Game in order to increase ungulate abundance. This has increased the pressure on federal land managers to implement predator control, even though there are significant differences in management mandates between state and federal agencies. Regardless, information on predator/ungulate ecology becomes increasingly important for both state and federal land managers in order to support decisions on predator and ungulate management. This is particularly relevant in the case of Togiak Refuge and BLM Goodnews Block, where the moose population is growing, brown bears are moderately abundant, and the wolf population is probably growing.

Objectives:

1. Estimate the number, size, and productivity of wolf packs located on Togiak Refuge and BLM Goodnews Block.
2. Determine the distribution of wolf packs throughout Togiak Refuge and BLM Goodnews Block.
3. Determine the quantity of moose annually preyed upon by wolves and brown bears throughout Togiak Refuge and BLM Goodnews Block.
4. Describe the relationship of wolf and bear predation on moose to moose demographic performance.

Background

Moose population growth

The moose population on Togiak Refuge and BLM Goodnews Block is recently established, with the area virtually absent of moose until the early 1980s (Aderman et al. 2013). Colonization has proceeded from east to west (Fig. 1), and abundance changed from a minimum count of 4 moose observed in 1991 to a minimum population count of over 1,600 in 2011. Colonization is still occurring in unoccupied and sparsely occupied habitat in the western drainages of the area, and population growth is occurring rapidly there, while growth is slowing on the eastern half of the Refuge.

The study area can be considered to be composed of four sub-units in terms of moose colonization history, population density and trend (Fig. 2). Sub-unit A includes three watersheds located in GMU 17C: Wood, Snake, and Igushik watersheds. This region on the eastern edge of the study area is the area where moose colonization began in the early 1980s. Population density was last measured to be 0.45 moose/km^2 in 2011[1] (Togiak

[1] During the period 1995 – 2011, the moose population of Subunit A was surveyed on three occasions. The area is composed of 8 sample units (Aderman 2011), of which 4 were surveyed in 1995, 6 surveyed in 2006, and 8 surveyed in 2011, complicating trend analysis. Four sample units were the same in all three surveys. When population density in these units alone is considered, the population trend is relatively flat

Refuge unpublished data), and may have declined over the preceding 16 years. Sub-unit B includes the Togiak, Kulukak, and Ungalikthluk watersheds located in the central portion of GMU 17A, where moose colonization began approximately 20 years ago and where growth continues but is slowing. Density of moose per unit winter habitat was last measured to be 1.52 moose/km^2. Sub-unit C includes the Goodnews, Osviak, Matogak, and Quigmy watersheds, located at the southern extreme of GMU 18 plus the southwestern portion of GMU 17A. Colonization began approximately 10 years ago and population growth is currently proceeding rapidly and has not reached its asymptote (Fig. 2). Population density per unit winter habitat was last measured in 2012 as 0.25 moose/km^2. Sub-unit D includes the Kanektok and Arolik watersheds located in GMU 18, where colonization has just been initiated in the past few years, and where rapid growth is anticipated for the next decade. Winter habitat population density was last measured in 2013 at 0.09 moose/km^2.

Wolf-moose relationships

Wolf population density in the southeastern quadrant of Togiak Refuge varied from 0.05 – 0.53 wolves/100 km^2 from 2007-2012 (Walsh and Woolington 2014). These densities are comparable to wolf population densities summarized by Ballard and Van Ballenberghe (1997) in three studies in southcentral Alaska (0.18 – 0.36 wolves/100 km^2), but lower than that reported in two studies on Kenai Peninsula (1.10 wolves/100 km^2), and in a single study in southwestern Yukon, Canada (0.41 wolves/100 km^2). Mech et al. (1998) reported winter wolf population densities for Denali National Park over the years 1986 – 1994 as averaging 0.58 wolves/100 km^2 (range: 0.31 – 0.78 wolves/100 km^2). Thus, the wolf population density on Togiak Refuge is lower than most reported densities, although there is evidence that it is increasing.

From 1994 - 2010, Refuge staff recorded 52 wolf sightings Refuge-wide incidental to work unassociated with any formal wolf study (Togiak National Wildlife Refuge unpublished data). Of these, 63% occurred on the east-central portion of the Refuge, consistent with the highest concentration of moose (Fig. 1), suggesting that wolf population density may be a function of moose population density. During the period 2007 – 2012, Walsh and Woolington (2014) studied wolf predation on caribou (*Rangifer tarandus*) on the southeastern quadrant of the study area, and found that it was continuously occupied by two to three wolf packs, and that moose formed the primary diet component of all wolves, including one pack which was partially dependent upon caribou. Further, wolf prey selection changed in response to increasing caribou population density.

(moose/km2: 1995 – 0.74, 2006 – 0.90, 2011 – 0.70). Thus, population trajectory is flat or has declined slightly in subunit A.

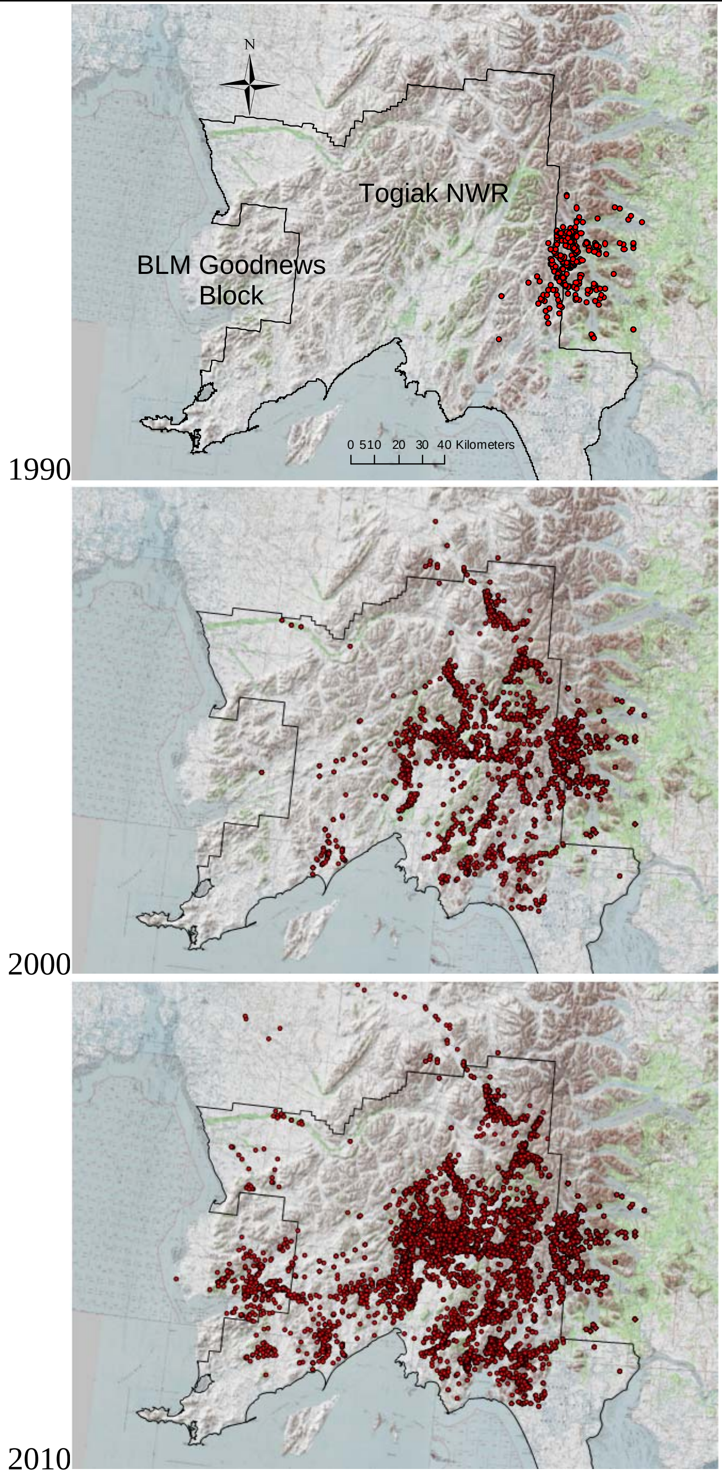

Figure 1. Change in distribution of moose on Togiak National Wildlife Refuge and and BLM Goodnews Block, 1990—2010. Points are cumulative radio telemetry locations of annual samples of ~30 cow moose.

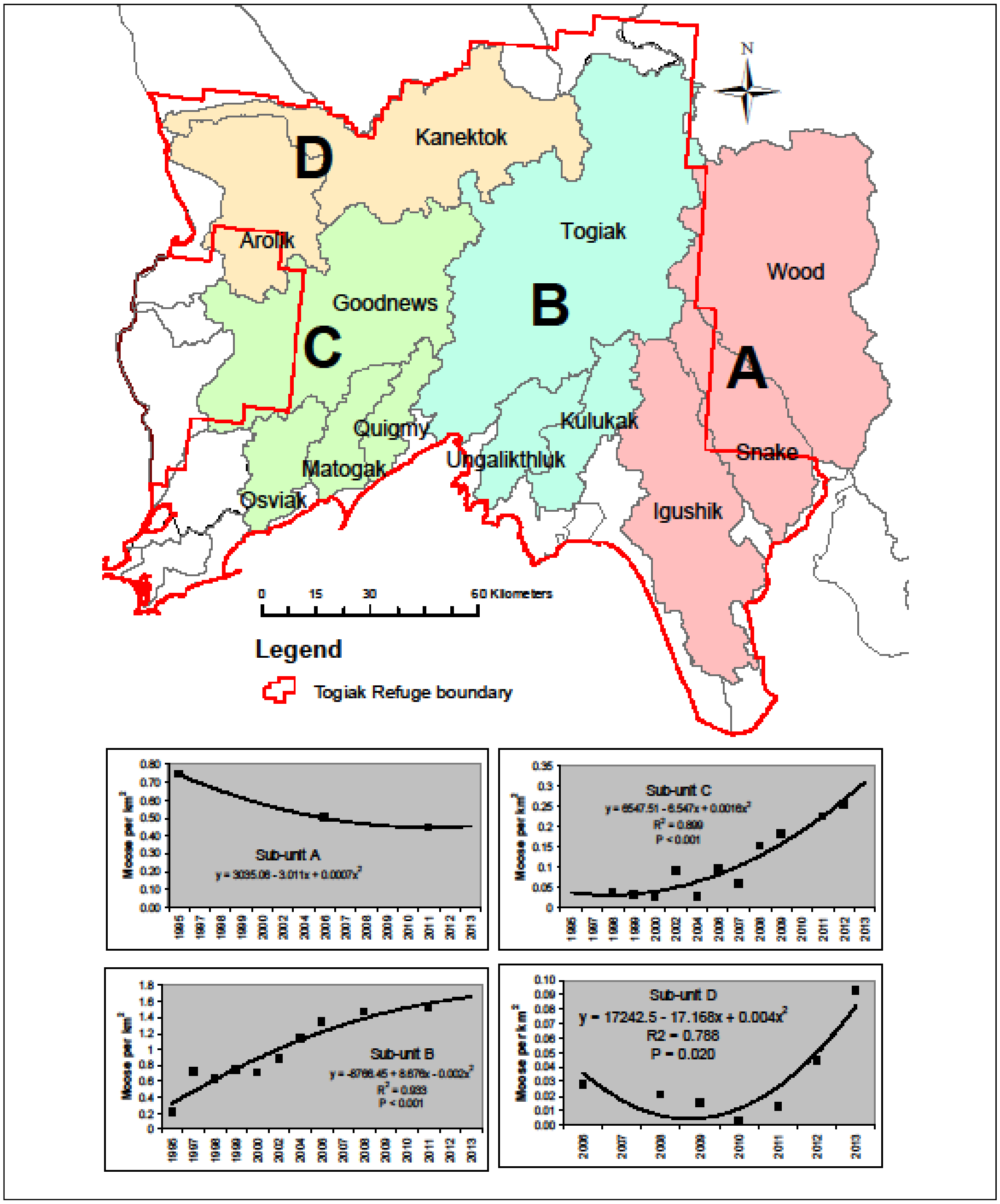

Figure 2. Subunits of study area divided into river watersheds with similar moose colonization history. Moose population density per km^2 winter habitat and population trend is shown in accompanying graphs.

Messier (1994) examined moose-wolf relationships over a broad range of moose population densities from 27 studies in order to test whether wolf predation can regulate moose population size, and found that wolf predation can be strongly density dependent at low moose population density levels (less than 0.65/km^2). Thus, at low moose population densities, wolf predation reduces moose population growth. It is likely that this relationship has not been the case during the rapid population growth of Togiak

Refuge/BLM Goodnews Block moose so far (Fig. 2), and this may be due to wolves occurring at low population density prior to colonization by moose. We assume that this is changing, and that the wolf population is increasing consistent with increasing moose abundance. Wolf predation clearly increased on the Nushagak Peninsula in response to an increasing caribou population (Walsh and Woolington 2014), and we expect a similar response to the increasing moose population on Togiak Refuge/BLM Goodnews Block.

Brown bear-moose relationships
The study area supports a moderate population density of brown bears distributed throughout the area relatively uniformly (Fig. 3). Walsh et al. (2010) reported an estimated population density of 40.4 bears/1000 km^2 (95% CI = 31.4-54.5); estimated density of independent bears was 27.3/1000 km^2 (95% CI = 21.4-34.4). Kovach et al. (2006) reported a population rate of increase of brown bears in a study area which included the north-central portion of this study area to range from 0.963 to 1.047 over a ten year period, suggesting relative stability. Given the reliability of Pacific salmon (*Oncorhynchus* spp.) as the primary protein source for this bear population, we hypothesize that bear population dynamics will be decoupled from moose population dynamics. It is unlikely that an increasing moose population will cause a commensurate increase in the bear population.

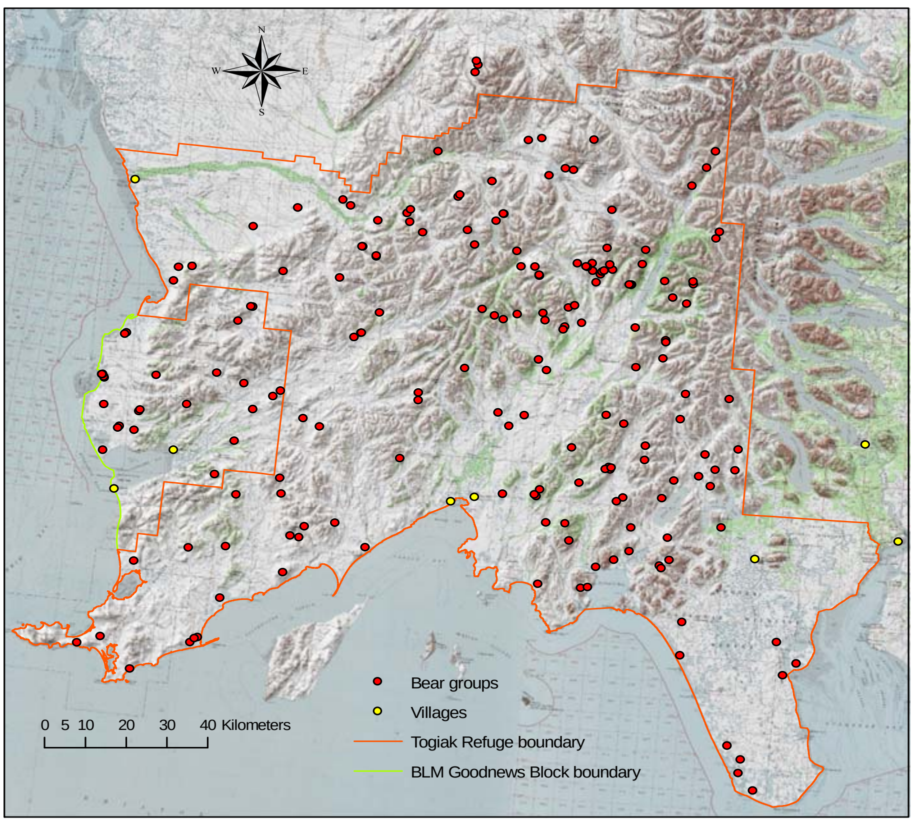

Figure 3. Distribution of bear groups found during population survey in 2004-2005 (figure from Walsh et al. 2010).

However, brown bears do constitute a significant mortality source for study area moose. Aderman et al. (2013) found brown bears responsible for 56% of mortality of cow moose >1 year old (25 of 45 total mortalities.) Other mortality sources included unknown causes (22%), illegal hunting (16%), and wolf predation (7%, Fig. 4). Ballard and Van Ballenberghe (1997) summarized the results of 10 studies of moose calf predation and found bear predation generally higher than wolf predation. In two studies in east central Alaska and southwestern Yukon, Canada, wolves were attributed with 15-18% of moose calf mortality while bears (both brown bears and black bears *U. americanus*) were attributed with 3-6% of calf mortality. Conversely, three studies in southcentral Alaska reported that moose calf mortality caused by brown bear predation ranged from 42-52% while wolf predation-caused mortality ranged from 2-6%. In two studies on the Kenai Peninsula, Alaska, moose calf mortality caused by bears (either brown bears or black bears) ranged from 34-44% while wolf-caused mortality ranged from 1-6%. In three studies in Canada, brown and black bear predation was attributed to 30-92% of moose calf mortality, while no wolf caused mortality was reported. So, in most cases where both bears and wolves prey on moose, bears are the more significant predator, and we hypothesize this to remain the case in this study area.

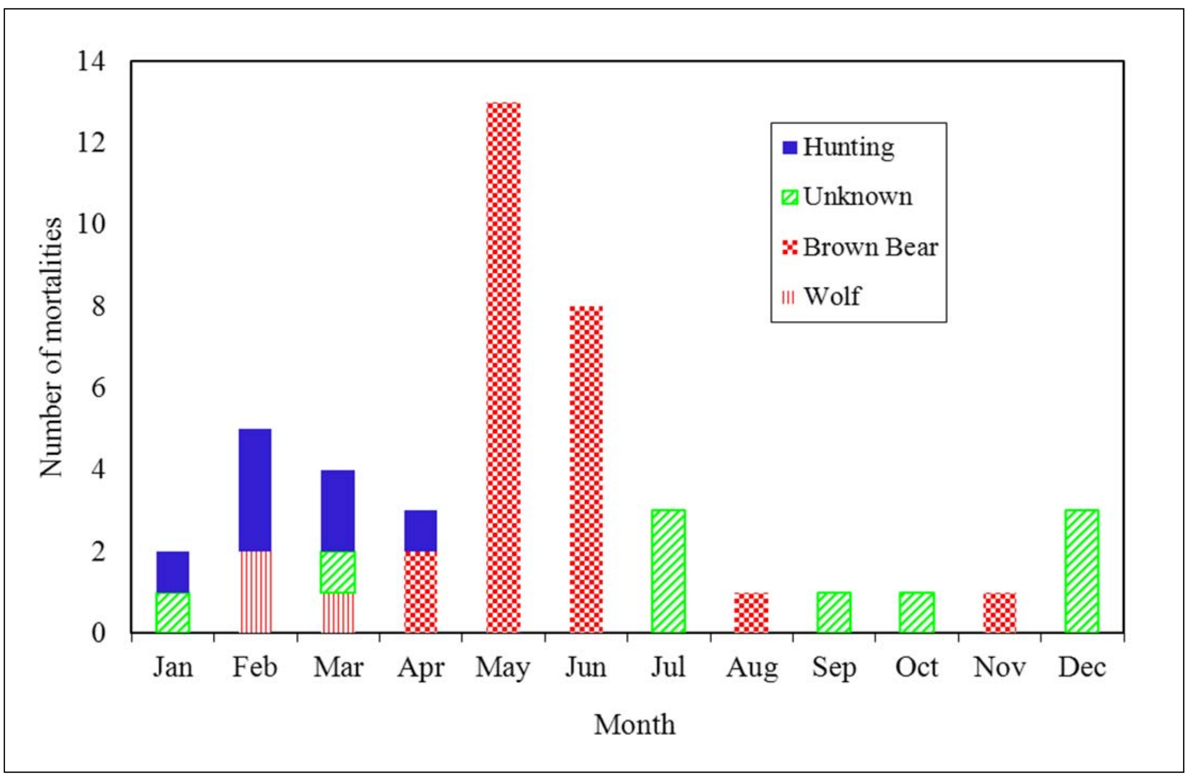

Figure 4. Timing and suspected causes of mortality of radio-collared female moose, southwestern Alaska, 1998-2011 (taken from Aderman et al. 2013).

Wolf/bear predation potential

No population estimate currently exists for wolves throughout Togiak Refuge or BLM Goodnews Block. However, for a study area including the southeastern quadrant of the

Refuge, Walsh and Woolington (2014) found an average pack territory of 3,231 km^2, an average winter pack size of 6.9 wolves, and an average population density of 2.3 wolves/1000 km^2. Extrapolating these metrics to the entire study area results in an estimate of 7 packs composed of a total of 49 wolves. Adding a 50% overlap of packs (Walsh and Woolington, unpublished data), and adding an estimated 20% of wolves not associated with packs, results in an estimate of 11 packs and an estimated total of 88 wolves. Thus, a conservative estimate for the entire study area is 7-11 packs totaling 49-88 wolves.

Using the brown bear population density reported in Walsh et al. 2010, there are an estimated 565-981 total brown bears in the study area. These include 385-619 independent bears (bears not dependent upon their mothers). So, based on numbers alone, there is approximately an order of magnitude more moose predation potential from brown bears than from wolves.

Alternate prey
Approximately 49.5% of the study area is covered with upland and lowland tundra communities. The tundra provides habitat to caribou, which serve as an alternate food to moose for predators. Caribou from the Mulchatna Caribou Herd migrate onto and away from the majority of the study area seasonally in variable numbers and calve in relatively low densities in portions of the study area, but are an unreliable food resource to wolves and bears. Caribou from the non-migratory Nushagak Peninsula Herd are a more reliable food source, but are largely restricted to the Nushagak Peninsula at the southeastern portion of the study area. From 2007 – 2012, Nushagak Peninsula caribou constituted approximately one third of the diet of a single pack of wolves (Walsh and Woolington, 2014). In addition to ungulates, both wolves and brown bears feed on salmon on the Togiak Refuge. Preliminary data on the carbon and nitrogen stable isotope ratios of bears and wolves suggest that both species consume considerable amounts of salmon but that the relative contributions varies markedly among the individuals of each species. Because salmon stable isotope signatures are distinct from both moose and caribou, our preliminary data demonstrate that we will be able to partition diets of both predators to moose, caribou and salmon with a high degree of confidence.

Study Area

The 2.1 million ha study area is centered at approximately 59.3^{o} N latitude, 160.4^{o} W longitude, and includes the Togiak National Wildlife Refuge and BLM Goodnews Block (Fig. 5). The area includes portions of two Alaska Department of Fish and Game (ADFG) Game Management Units, with GMU18 including the northwestern half of the study area and GMU17 including the southeastern half.

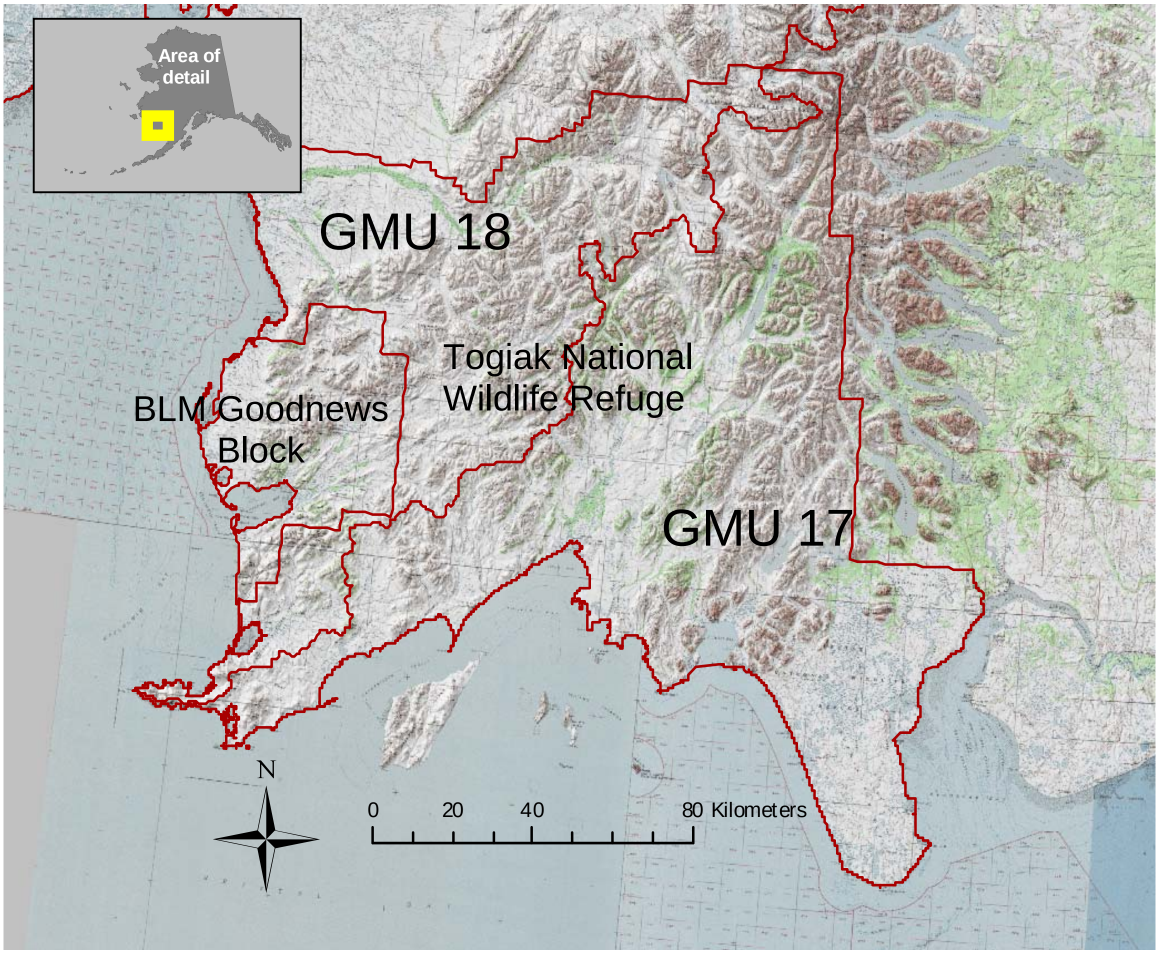

Figure 5. Study area, composed of Togiak National Wildlife Refuge, BLM Goodnews Block, and Game Management Units 17 and 18.

Located at the junction of the Bristol and Kuskokwim Bays of the Bering Sea, the study area climate can be considered sub-Arctic maritime near the coast, and transitioning to sub-Arctic continental toward the interior. Temperatures range from average daily low and high of -13.3 and -6.3 ^{o}C in December, the coldest month, to 8.6 and 16.9^{o} C in July, the warmest month at the nearest weather station, Dillingham, Alaska (climate data averaged 1951-2005, Western Regional Climate Center, http://www.wrcc.dri.edu/cgi-bin/cliMAIN.pl?ak2457, accessed October 2013). Annual precipitation averages 64.7 cm and snowfall averages 210.6 cm.

The Ahklun Mountains occupy the central portion of the study area while the Kanektok and Nushagak River lowlands occur to the northwest and southeast. The modern-day landscape, and thus the distribution of moose, wolves, and other biotic elements, is strongly influenced by glacial activity in the late Pleistocene. The study area includes 25 individual plant communities, which occupy ~84% of the total area, while the remaining 16% is covered by unvegetated cover types, such as snow/ice, water, or bare rock/gravel (Collins 2003). The predominant plant communities are upland herb tundra, lichen, and low or dwarf shrub communities from 11 community classes, and compose ~49.5% of the whole. The second-most predominant communities are the tall shrub types dominated by willow (*Salix*), alder (*Alnus*) and mixtures of the two, and compose ~19.4% of the total study area. Four wetland community types account for ~12.2% of the total, and four deciduous forest communities covering ~2.4% of the total area occur predominantly in riparian zones. Spruce (*Picea*) and spruce/deciduous forest types account for less than 1% of the total area, and are restricted to the southeastern quarter of the study area.

The study area contains all or most of 11 river watersheds as well as portions of five adjacent watersheds. Including tributaries, the area includes all or portions of 35 major rivers and hundreds of small streams (Lowe et al. 2013). Riparian hardwood forests and shrub communities are key habitats for moose, particularly in winter, at which time habitat is most limited. Winter moose habitat represents approximately 11.7% of the entire study area (Aderman and Lowe 2011). Thus, the majority of the study area provides little or no value to moose during winter.

Methods

Objective1. Estimate the number, size, and productivity of wolf packs located on Togiak Refuge and BLM Goodnews Block.
Objective 2. Determine the distribution of wolf packs throughout Togiak Refuge and BLM Goodnews Block.

We estimate that there is sufficient habitat in the study area to support 7-11 wolf packs, assuming similar area requirements of wolf packs investigated 2007-2012 (Walsh and Woolington, 2014). However, given that some pack ranges will include portions of both the study area and adjacent areas, the true number of wolf packs potentially preying on Togiak Refuge moose is likely to be more than 7-11. To address Objectives 1 and 2, we will attempt to capture and radio-collar wolves from at least 50% of packs. We will delineate pack ranges as the study progresses, and infer the existence of un-instrumented packs based on the distribution and size of gaps between known packs. We will attempt to confirm inferences on the presence and size of un-instrumented packs using aerial surveys to search for tracks or wolves. We will estimate pack territory size by calculating minimum convex polygons (Environmental Systems Resource Institute 2012) from two or more wolves per pack for a period of one or more years.

We have attempted to maintain 2-3 radio collars per pack. From 2015-2017, collar models were Lotek © Iridiumtrack M Basic satellite-interfaced GPS radio collars. Collars were pre-programmed to collect locations every 2 hours and had an expected lifetime of 3 years. Data were received by satellite, then transferred once daily to the internet and were available remotely through Lotek Wireless GPS WEB Service (https://webservice.lotek.com/default.aspx). After 2017, we discontinued using the Lotek collars and began using Vectronic© Vertex Lite-2D Iridium collars. Radioed wolves have been aerially tracked periodically in order to determine size and composition of packs.

Capture was performed during winter months. Capture operations included spotter crews in one or more fixed-wing aircraft in communication with a capture crew in a helicopter. Upon locating a group of wolves, the spotter crews directed the helicopter to the location, then maintained visual contact with wolves after they were darted. Wolves were captured using doses of 572 mg of Telazol dissolved in 2.6 ml of water and delivered with a 3 cc Palmer™ TM dart with .75” barbed needle. Darts were fired from a Palmer™ capture rifle charged with Very Low Power (brown) .22 charges. Wolves were sexed, weighed, aged by tooth wear (Gipson et al. 2000) and development of the epiphyseal closure of the distal end of the radius and ulna (Rausch 1967) into three age classes: juvenile (< 1 year), young adult (1-2 years), mature adult (>2 years), and a hair sample was collected for stable isotope analysis. To determine pup production, we have determined parturition timing using radio-location fix failure associated with parturient females going into dens (Walsh et al. 2016), then performed den watches through direct observation when dens were located. Animal care and handling was performed consistent with the Animal Welfare Act as Amended, (P.L. 91-579) under Alaska Department of Fish and Game IACUC protocol 2015-01.

Objective 3. Estimate the quantity of moose annually preyed upon by wolves and brown bears throughout Togiak Refuge and BLM Goodnews Block.

Stable isotope analysis

Objective 3 will be accomplished through simulation modeling of wolf and bear predation on moose based on proportion of moose in wolf and bear diets. A preliminary step to the modeling is stable isotope analyses of predator tissues. Stable isotope analyses of N and C will be performed at the University of Washington IsoLab using a Finnigan MAT 253 isotope ratio mass spectrometer. Isotope analyses and diet calculations will be done in collaboration with Daniel Schindler, University of Washington.

Isotope analyses will require obtaining tissue samples from brown bears, wolves, moose, and other components of the bear-wolf-moose trophic web (e.g., caribou and salmon). Isotopic ratios of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) provide a means to estimate a time-integrated estimate of predator diets because consumer isotope signatures reflect the isotope signatures of their prey and well-described fractionation rates. Isotope signatures of different prey items are often statistically distinct because of their specialized trophic habits, thereby permitting the estimation of their relative contributions to the mixture observed in the tissues of a predator.

Stable isotope analyzes have been successfully used to apportion wolf diets (Szpanski et al. 1999, Darimont and Reimchen 2002, Darimont et al. 2007, Adams et al. 2010) and bear diets (Hobson et al. 2000, Jones et al. 2006, Mowat and Heard 2006), and to demonstrate wolf and bear trophic relationships with other mammalian species (Jacoby et al. 1999, Urton and Hobson 2005). Because isotopic signatures differ regionally as a function of the specific mix of elements of the regional food web, it is necessary to characterize other elements (plant and animal taxa) of the wolf-bear-moose web. Thus, other common bear and wolf food items, including caribou, beavers (*Castor canadensis*), salmon, berries, sedges, and others will also be characterized. An existing database of Togiak Refuge isotopic data (Walsh and Schindler, unpublished data) including >200 analyzed samples is available for this study. Preliminary data (Fig. 6) demonstrate a high degree of isotopic resolution among the important prey species for bears and wolves in this study area. In particular, moose appear to have isotope signatures with $\delta^{13}C$ values of about -26‰ reflecting a diet of willow, caribou around -23‰ reflecting a diet of lichens, and salmon around -21‰ reflecting their marine signature. There is also wide spread in the $\delta^{15}N$ among prey with salmon being distinctly enriched (approximately 12‰ relative to the ungulates (moose approximately 2‰, caribou approximately 4‰), again reflecting the marine-derived origin of their tissues. We will augment this existing database with additional samples collected during this study. We expect that the isotope values of bears and wolves, after correction for trophic fractionation, will fall between the values observed for moose, caribou and salmon. The proximity of the isotope signature of a predator to each of its primary prey is proportional to the relative importance of each of the prey to the predator diet. If, after preliminary analysis, additional discrimination is determined necessary, we will incorporate a third isotope (e.g., sulfur) or lipid analysis. A Bayesian isotope mixing model (Parnell et al. 2013) will be used to estimate the relative contributions of moose, salmon and caribou to the diets of each individual predator sampled. This model will also produce estimates of the uncertainty in the diet contributions given the observed variation in prey from each of the taxa.

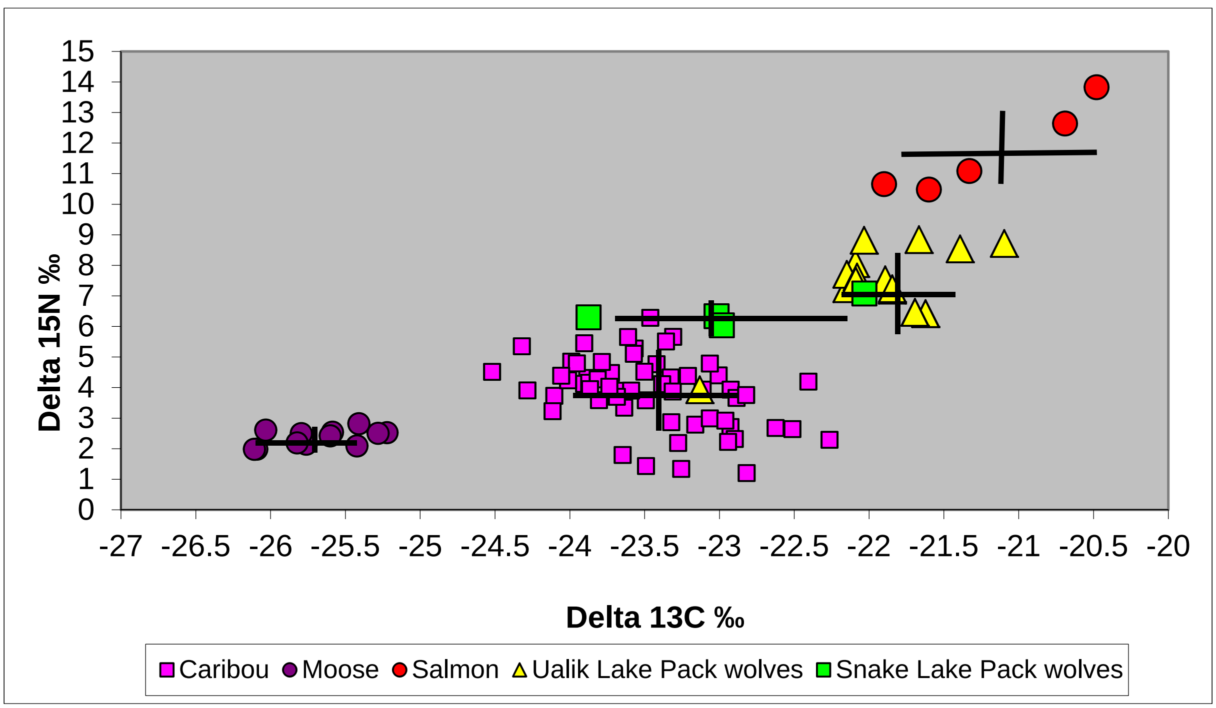

Figure 6. Example of isotopic separation of wolves from two Togiak Refuge packs in relation to diet components. Ualik Lake Pack diet includes moose, caribou and salmon, while Snake Lake Pack includes moose and salmon only. Cross bars indicate one standard deviation around mean $\delta^{13}C$ and $\delta^{15}N$ values. Salmon isotopic values from Johnson and Schindler 2008, remaining data from Walsh and Schindler, unpublished.

The analysis will be partitioned into subunits of the study area which correspond to differing regions of moose colonization history and current population density and trend (Fig. 2). For each subunit, we will attempt to analyze samples from a minimum of 10 wolves. Given the far greater population density of brown bears over wolves, we will analyze a minimum of 20 bears per subunit. We will analyze a minimum of 10 moose from each subunit, although we expect that moose isotopic signatures will be similar enough that moose from the entire study area can be considered a single population, and thus combined. We will also analyze representative samples of primary moose forage taxa (*Salix glauca, S. alexensis, S. pulcra, S. arbusculoides, S. barclayi)*. We currently have sufficient moose, wolf, and forage samples from Unit A, so isotope sampling will be focused on the remaining units with additional samples from Unit A added opportunistically.

Moose isotopic tissues will be hair samples from the existing database, as well as additional samples collected incidental to moose capture operations associated with a moose radio telemetry study (Aderman et al. 2011) which will occur simultaneously with this study. Wolf isotopic tissues will be guard hair samples collected from captured and hunter/trapper killed wolves to represent diet during hair growth (spring through fall, Young and Goldman 1944). Additionally, whole blood (a metabolically active tissue in which elements turn over in a matter of weeks, Rubenstein and Hobson 2004) will be collected to characterize winter diet.

Because bears are primarily active spring through fall, and inactive during winter, hair samples alone will be used to characterize diet. Guard hair samples will be collected from hunter killed bears and hair collected from hair snares following the methods of Beier et al. (2005). Hair snares will be deployed during July-August at locations near the center of each subunit at sites where bears concentrate to capture salmon (lake shores and stream banks). Snares will be deployed for approximately 8-14 days each. Lakes will be accessed by float-equipped airplane and streams will be accessed by inflatable boats. Hair snaring was consistent with the Animal Welfare Act as Amended, (P.L. 91-579) under Alaska Department of Fish and Game IACUC protocol 2014-22.

Because of evidence that moose predation by brown bears may differ by sex, with males more carnivorous than females (Jacoby et al. 1999, Mowat and Heard 2006), gender was determined for bear hair samples using DNA analysis. Bears were genotyped at 11 microsatellite loci: G1A, G1D, G10B, and G10L (Paetkau and Strobeck 1994); G10C, G10M, G10P, and G10X (Paetkau et al. 1995); G10H and G10J (Paetkau et al. 1998); and UarMu50 (Taberlet et al. 1995) to identify unique bears; and an amelogenin gender determination marker (Ennis and Gallagher 1994) (Table 1). Total genomic DNA was isolated from 1-10 hairs from each snare sample, prioritizing guard hairs with visible root bulbs. If guard hairs were not present, under fur was used. Approximately 5mm was trimmed from the proximal end of the hair, and DNA was isolated Qiagen QIAamp® DNA Investigation kits, with an overnight Proteinase K digest. Polymerase chain reaction (PCR) amplifications were carried out in 10 µl reaction volumes using 2 µl DNA, 2.5 mM $MgCl_2$, 0.2 µg/µl BSA, 1 mM dNTPs, 0.12–0.6 µM labeled forward primer, 0.12–

0.6 µM reverse primer, and 0.05 U/µl *Taq* polymerase. Applied Biosystems Veriti thermal cyclers were used for PCR with 1 cycle of 2 min at 94^o; 45 cycles of 15 sec at 94^o, 15 sec at 53^o (microsatellite loci) or 60^o (amelogenin) and 30 sec at 72^o, with a final extension for 30 min at 72^o. The PCR products were separated with an Applied Biosystems 3730 Genetic Analyzer using a polymer denaturing capillary system. Size scoring was completed using GeneMapper® Software ver 5.0. Applied Biosystems GeneScan™-600 LIZ® size standard, 20-600 bases, were loaded as internal size standards. Two researchers scored alleles independently. Error checking followed the guidelines of Paetkau (2003), with one modification. Three separate PCRs were conducted for each sample. An individual was scored as a heterozygote if one of three scores was a heterozygote and a homozygote if all three scores were homozygotes or if 2 of the three scores were homozygotes and the third was a blank. Individuals with no scores for more than four loci were deleted from further analysis. The program GenAlEx 6.502 (Peakall and Smouse 2012) was used to detect matching genotypes and to calculated probability of identity.

Moose mortality modeling

We will estimate the total quantity of moose preyed on by wolves and bears by developing a simulation model (Table 1) which incorporates the diet apportionment from the stable isotope analysis with the following demographic and physiological parameters:

1. <u>Seasonal predator days</u>

Predation potential for bears and wolves will be derived separately by species for study area subunits. Time budget for wolves in potential contact with moose will be determined by calculating the number of wolves by season present in each subunit. A wolf-subunit-day is defined as a day in which at least one location occurred within the subunit, so in the case of a wolf pack that uses multiple subunits, its time will be apportioned based on proportion of locations. Seasons for wolves are defined as Winter: 1 December – 15 May; Early Denning/Moose Calving: 16 May – 30 June; Late Denning: 1 July – 15 August; Late Summer: 16 August – 15 September; and Fall (moose rut/post rut): 16 September – 30 November. An index to the potential level of wolf predation on moose will be developed by calculating wolf subunit-days per season as such:

$$PD_{wolf} = N_{wolf} * (P_{mw} * D) \qquad (1)$$

where N_{wolf} is the number of wolves in packs using the subunit in a given season, P_{mw} is proportion of time that radio collared members of these packs used the subunit, and D is the number of days in the season. Annual indices will be calculated by summing the seasonal numbers of wolf subunit-days.

Time budget for bears in potential contact with moose will be determined by estimating the number of bears present in each subunit based on subunit area and an assumed bear population density of 40.4 bears/1000 km^2; estimated density of independent bears: 27.3/1000 km^2 (density estimate from Walsh et al. 2010). Seasons for bears are defined as Winter (denning): 1 December – 15 April; Summer (active): 16 April – 30 November. An index to the potential level of bear predation on moose will be developed by calculating bear subunit-days per season as such:

$$PD_{bear} = N_{bear} * D \qquad (2)$$

where N_{bear} is the estimated number of bears in the subunit in a given season, and D is the number of days in the season.

2. Proportion of moose in predator diets. We will use the biomass proportions of moose vs. other items in wolf and bear diets based on our stable isotope analyses.

3. Proportions of moose cows, bulls, and calves in wolf and moose diets seasonally. We will use values from the literature to apportion wolf and bear predation of moose by gender and by season.

4. Weight of cow, bull, and calf moose. We will use existing weight data for Togiak Refuge 10-month old moose calves (Aderman et al. 2013), and model weight at other age stages by fitting weight to age with the sigmoidal Gompertz growth equation (Zullinger et al. 1984):

$$M(t) = A \times e^{-e^{-K(t-I)}} \qquad (3)$$

where M = weight (g), t = age (days), A = asymptotic weight (kg), K = growth constant (day^{-1}), and I = the inflection point at which weight gain slows. Values for K (0.0039 g/d), A (324 kg), and I (150 days) are taken from Zullinger et al. 1984 for moose. In a similar study, we compared results from this equation with two competing growth models (von Bertalanffy and logistic equations, Zullinger et al. 1984) and found the Gompertz equation fit better with known average Nushagak Peninsula 10-mo old caribou weights (Walsh and Woolington, unpublished data).

5. Predator daily meat consumption (or more appropriately, availability, as not all of a prey animal killed by wolves or bears is consumed). Eighteen studies in North America resulted in an average daily availability of 5.4 kg wolf/day (sources cited in Peterson and Ciucci 2003). We will use these studies to determine both an average daily availability, as well as measures of uncertainty around the average. A literature search for brown bear daily consumption rates is ongoing.

Table 1. Example of simulation model quantifying moose predation by wolves during winter season, assuming 3 packs of wolves averaging 7 wolves/pack in a 9,000 km^2 subunit. Values are hypothetical.

Identifier	Parameter	Derivation	Value
A	Number of wolves		21
B	Days in season		180
C	Wolf/days/season	(A * B)	3,780
D	Proportion of moose in diet		0.8
E	Proportion of cows preyed on		0.1
F	Proportion of calves preyed on		0.75
G	Proportion of bulls preyed on		0.15
H	Weight cows (kg)		408
I	Weight calves (kg)		204
J	Weight bulls (kg)		499
K	Wolf meat consumption/kg/day		5.4
L	Wolf/moose predation days	(C * D)	3,024
M	Total moose weight consumed	(K * L)	15,180
N	Total cow weight consumed	(E * M)	1,518
O	Total calf weight consumed	(F * M)	10,626
P	Total Bull weight consumed	(G * M)	3,036
Q	Cows consumed	(N / H)	4.0
R	Calves consumed	(O / I)	54.4
S	Bulls consumed	(P / J)	4.9

Objective 4. Describe the relationship of wolf and bear predation on moose to moose demographic performance.

The predator-prey relationship between wolves, bears, and moose on the study area could be top-down (i.e., wolves and/or bear predation is a primary force in regulating moose population size and composition) or bottom-up (i.e., moose population density controls the population dynamics, distribution, and prey selection of wolves and/or bears), or there could be some combination of the two. Walsh and Woolington (2014) described a bottom-up predator-prey relationship between wolves and caribou on the southeastern portion of Togiak Refuge, and we hypothesize a similar relationship between wolves and moose. However, we hypothesize the converse in the bear-moose relationship, with bear predation exerting more demographic force on the moose population, than moose availability driving bear population density, prey selection, or distribution. Thus, we will test the following hypotheses:

1. Ho: Moose population density is independent of wolf population density across a spatial gradient of varying density.
2. Ho: Moose population is independent of proportion of moose in wolf and bear diets across a spatial gradient of varying density.

Relationships between moose population density and predator density and diet proportions will be examined by regressing moose population density, survival, and calving percentage with wolf and bear population density and proportion of moose in diet across the four subunits of different population size and trends, in a framework of generalized linear models. When appropriate, hierarchical models (e.g., mixed effects models) will be employed to control for spatial or temporal autocorrelation in the data.

Additional insight into the relative influence of bear- and wolf-related predation mortality on moose population dynamics will be provided by developing a stage-based moose population matrix model and examining vital rate elasticities through Life Stage Simulation Analysis, following methods outlined in Wisdom et al. 2000 (see Raithel et al. 2007 for an application on large ungulate taxa). Vital rates for the population projection model will be informed through Togiak Refuge data sets, literature search, and information on wolf- and bear-related predation resulting from analyses outlined above.

Results

Objective1. Estimate the number, size, and productivity of wolf packs located on Togiak Refuge and BLM Goodnews Block.
Objective 2. Determine the distribution of wolf packs throughout Togiak Refuge and BLM Goodnews Block.

Pack Narratives 2015-2017

2015

We captured and collared four wolves, all aged to be juveniles, from two packs during the period 24-28 March 2015 (Table 2). A lack of snow hampered wolf capture. Unlike most years, when snow cover is near its peak in late March, snow was absent at elevations below approximately 300 m, thus not permitting snow tracking. Anticipating the difficulty in locating wolves, we increased the number of observation aircraft from two to five.

Table 2. Physical and demographic data of wolves captured 2015-2017 on Togiak National Wildlife Refuge and BLM Goodnews Block.

Date	ID	Pack	Sex	Age	Weight kg	Color	Pack size at capture
24-Mar-2015	W1501	Togiak Lake	F	1.0	34.0	Gray	4
25-Mar-2015	W1502	Togiak Lake	M	1.0	45.4	Gray	4
27-Mar-2015	W1503	Snake Lake	F	1.0	38.6	Black	2
28-Mar-2015	W1504	Togiak Lake	M	1.0	40.8	Gray	4
22-Mar-2016	W1601	Ualik Lake	F	1.0	34.0	Gray	6
22-Mar-2016	W1602	Ongoke River	F	1.0	35.4	Gray	2
22-Mar-2016	W1603	Ongoke River	F	1.0	35.8	Gray	2
23-Mar-2016	W1604	Ualik Lake	F	1.0	37.6	Gray	6
23-Mar-2016	W1605	Ualik Lake	M	3.0	50.3	Gray	6
23-Mar-2016	W1606	Togiak Lake	M	4.0	43.5	Gray	7
23-Mar-2016	W1607	Togiak Lake	F	4.0	55.3	Gray	7
23-Mar-2016	W1608	Togiak Lake	F	1.0	36.3	Gray	7
23-Mar-2016	W1502	Togiak Lake	M	2.0	43.5	Gray	7
23-Mar-2016	W1609	Kwethluk River	M	2.0	46.7	Gray	1

20-Mar-2017	W1701	Ongivinuk River	F	3.0	43.1	Gray	6
20-Mar-2017	W1702	Ongivinuk River	F	2.0	41.7	Gray	6
20-Mar-2017	W1703	Ongivinuk River	F	3.0	38.6	Gray	6
20-Mar-2017	W1704	Upper Kanektok River	F	1.0	38.6	Gray	12
20-Mar-2017	W1705	Upper Kanektok River	M	3.0	49.9	Black	12
20-Mar-2017	W1706	Upper Kanektok River	M	4.0	47.2	Gray	12
20-Mar-2017	W1707	Upper Kanektok River	F	3.0	48.5	Gray	12
21-Mar-2017	W1708	Goodnews River	M	5.0	64.0	Gray	6
21-Mar-2017	W1709	Goodnews River	F	4.0	41.3	Gray	6
21-Mar-2017	W1710	Goodnews River	M	2.0	45.8	Black	6
21-Mar-2017	W1606	Togiak Lake	M	5.0	37.2	Gray	11
22-Mar-2017	W1712	Ongoke River	M	1.0	44.9	Black	7
22-Mar-2017	W1602	Ongoke River	F	2.0	43.5	Gray	7
22-Mar-2017	W1713	Lower Kanektok River	M	4.0	49.0	Gray	3
21-Mar-2018	W1801	Ongoke River	M	2.0	42.2	Gray	7
21-Mar-2018	W1802	Ongoke River	F	1.0	39.0	Gray	7
22-Mar-2018	W1803	Kwethluk River	F	3.0	34.5	Gray	1
22-Mar-2018	W1804	Ongivinuk River	M	1.0	42.6	Gray	9
22-Mar-2018	W1805	Ongivinuk River	F	2.0	41.7	Gray	9
23-Mar-2018	W1606	Togiak Lake	M	6.0	39.5	Gray	2
23-Mar-2018	W1806	Togiak Lake	F	5.0	50.8	Gray	2
23-Mar-2018	W1807	Goodnews River	M	4.0	54.4	Gray	5
23-Mar-2018	W1808	Goodnews River	F	4.0	44.9	Gray	5
23-Mar-2018	W1809	Matogak River	F	2.0	41.7	Gray	2
23-Mar-2018	W1810	Matogak River	M	3.0	47.6	Gray	2
24-Mar-2018	W1811	Ualik Lake	F	3.0	41.7	Gray	3
24-Mar-2018	W1812	Ualik Lake	M	1.0	44.5	Gray	3

Three of the collared wolves were captured approximately 5 km north of Togiak Lake, thus the pack was named Togiak Lake Pack. The fourth wolf was captured approximately 1 km north of Snake Lake. It was a member of a different pack, named Snake Lake Pack. Both packs included at least one additional uncollared wolf, but these are probably underestimates of the correct pack composition.

To determine pup production, on 12 July 2015 two of us were dropped off by helicopter in Killian Creek Valley north of Snake Lake near the den site used by the Snake Lake Pack in 2010. We saw no wolves, and assumed we were not at the active den site. We suspected the Togiak Lake Pack denned about 1 km southwest of Togiak Lake based on telemetry data. So, on 14 July 2015 we performed a den watch at the Togiak Lake Pack den and verified that three pups were present.

During the remainder of 2015, the Togiak Lake Pack wolves remained on the air. Of the three, W1502 made occasional trips outside the pack territory, as defined by the location data from all instrumented pack members. The radio collar from W1503 (the Snake Lake

Pack wolf) went into the mortality mode for unknown reasons on 21 December 2015 in a steep canyon. With less than a year's data from a single wolf, we assume the pack territory may be larger than that indicated by her locations.

2016

Wolf W1504's collar went off the air for unknown reasons (assumed collar failure) on 26 January 2016, and W1501 did the same on 7 March 2016. Thus, by the time we attempted recapturing wolves in 2016, we were down to a single collared wolf. Snow conditions in 2016 were slightly better than 2015, but still there were large areas without tracking snow. We captured and collared 10 wolves during four field days during the period 22 – 28 March 2016. The capture crew included one helicopter and two observation aircraft.

From the Togiak Lake Pack, we recaptured W1502 and replaced his collar. Additionally, we captured three packmates, including one juvenile female, a ~4 year old male assumed to be the dominant male, and a ~4 year old female assumed to be the breeding female. We captured two juvenile females in the Ongoke River Valley and named their pack Ongoke River Pack. We captured four wolves in the Ualik Lake Valley over a period of two days, and assumed all were from the same pack (named the Ualik Lake Pack). However, W1609, a ~2 year old male, departed the Ualik Lake Pack territory and traveled north to the Kwethluk River north of Togiak Refuge. This wolf was apparently on a dispersal trip when captured, and not a member of the Ualik Lake Pack. Over the period of the next year, its locations defined a territory we identified as the Kwethluk River Pack (Fig. 8), although it made four dispersal trips during the period from the time of capture on 23 March 2016 until 17 July 2016, returning to his natal territory after each trip. From 17 July 2016, it remained in its natal territory through the remainder of the 2016.

Radio telemetry data suggested the presence of dens in the Togiak and Ualik Lake Packs, so we performed den watches on 1 and 2 July 2016. We verified a minimum of 8 pups and 6 adults in the Togiak Lake Pack and a minimum of 4 pups in the Ualik Lake Pack. The Togiak Lake Pack dominant female (W1607) was instrumented, so we were able to determine that parturition date was 12 May 2016.

W1605, the Ualik Lake Pack dominant male's collar failed 2 November 2016. This wolf was later killed by a trapper in No Lake Creek Valley on 8 April 2018. W1601 and W1604 remained in the Ualik Lake Pack territory throughout 2016. W1603 (Ongoke River Pack) experienced a collar failure on 2 September 2016, while packmate W1602's collar functioned throughout the year. W1607, the dominate female from the Togiak Lake Pack, was killed by a hunter on 6 September 2016. W1608, a juvenile female from Togiak Lake Pack, experienced a collar failure on 15 November 2016. W1606, the Togiak Lake Pack dominant male remained in the Togiak Lake Pack territory throughout 2016.

2017

Snow conditions were better in 2017 than the previous years, and so during the period 20-22 March 2017, we captured 14 and collared 13 wolves. Capture crews consisted of the helicopter crew and two observation aircraft. The collar on W1602 (Ongoke River Pack) had failed on 8 February 2017, but we were able to capture and recollar her. At age 3, W1609, the Kwethluk River Pack male successfully dispersed to and joined the Ongoke River Pack in March 2017. His collar failed on 26 May 2017. We recaptured and collared W1606, the Togiak Lake Pack dominant male, and did not capture any additional packmates. We captured three wolves from the Ongivinuk River Valley and identified their pack as the Ongivinuk River Pack. We captured four and collared three wolves from a pack we identified as the Upper Kanektok River Pack. W1601, captured as a juvenile in 2016 from the Ualik Lake Pack, dispersed to the lower Kanektok River valley on 9 February 2017. On 21 March 2017, we captured an adult male with her and identified them as in the Lower Kanektok River Pack. We captured and collared three wolves in the Goodnews River valley, and identified them as belonging to the Goodnews River Pack. W1708 was an ~5 year old and assumed dominant male. W1709 was an ~4 year old and assumed dominant female, and W1710 was a 2 year old male pack member.

Based on numbers seen during capture operations in March 2017 and a subsequent radio telemetry flight, minimum pack sizes were Togiak Lake Pack 11; Ongivinuk River Pack 6; Ongoke River Pack 7; Goodnews River Pack 6; Lower Kanektok River Pack 3; Upper Kanektok River Pck 12; for a minimum of 44 in these packs. Additionally, we found sign or other evidence of wolves on Nushagak Peninsula/Ualik Lake area (9 wolves in November 2016); Matogak and associated drainages; lower Togiak.

Den watches were performed 10-26 July 2017 at suspected den sites of four packs. We found a minimum of 6 pups at the den site of the Ongivinuk River Pack; 6 pups at the Goodnews River Pack, and 2 pups at the Ongoke Pack. However, high temperature (mid-70 degrees F) on the day we observed the Ongoke Pack may have minimized time in the open by pups seeking cooler temperature in the shade, so it is possible that more pups were produced. We accessed these dens via helicopter, but attempted to perform a den watch at the Upper Kanektok River Pack by hiking in from the Kanektok River. We were seen approaching by an adult wolf, and so abandoned the effort to perform the den watch, although telemetry data clearly indicated denning activity, with a parturition date of 14 May 2017 for dominant female W1707.

Pack territories and demographics

During the period March 2015 through March 2018, we collected approximately 107,000 wolf locations from 25 instrumented wolves from nine packs. Pack territory size was estimated to average 3,478 km^2 in area (range: 1,652 to 6,107, Fig. 7, Table 3). Pack sizes varied between packs and over time (Table 3) from 1 to 16 wolves, and averaged 7.4 wolves in winter, when packs were at their annual minimum to 11.8 wolves in summer, after pups were produced. The total known number of wolves using Togiak Refuge and BLM Goodnews Block varied from 67-106, but this is likely an underestimate. Based on tracks and observations of wolves in areas outside of known territories, we suspect 2-3 more packs are present in the Matogak/Osviak River drainages, the lower Togiak River drainage, and possibly in the Ungalikthluk River drainage.

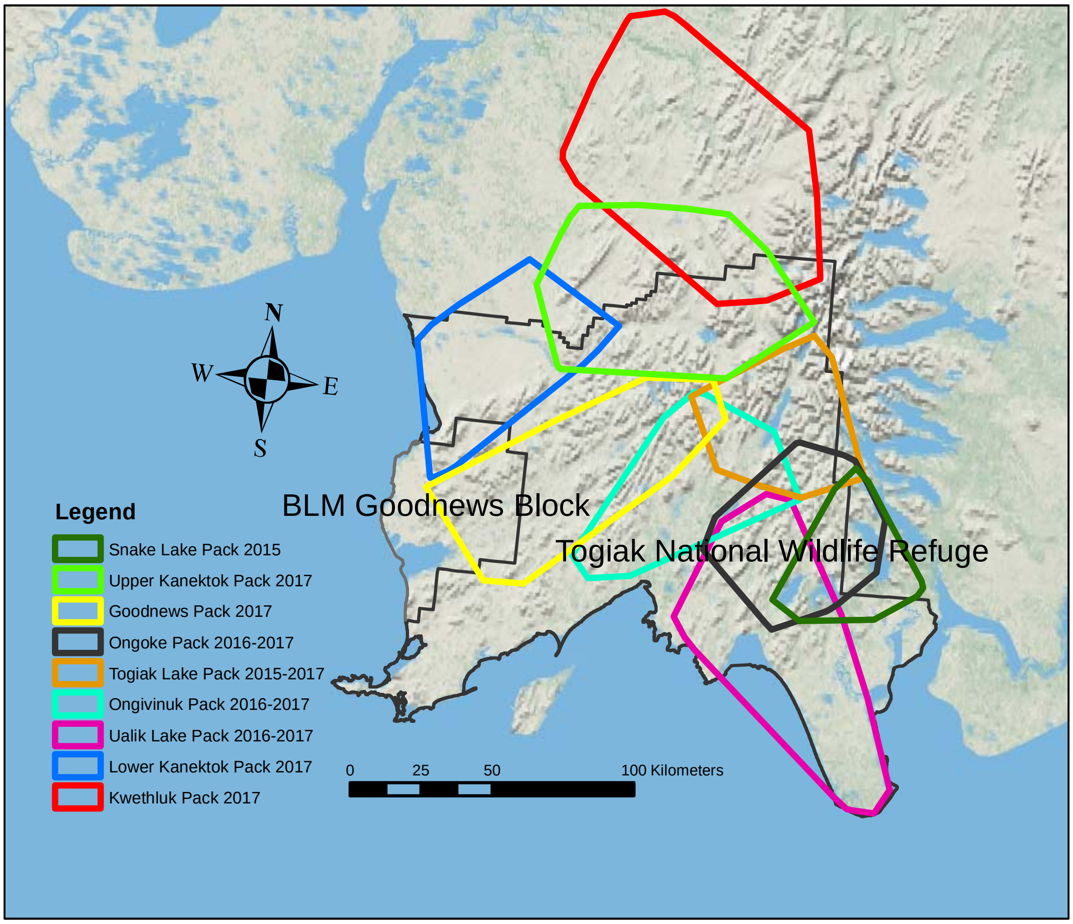

Figure 7. Locations of radio-collared wolf packs Togiak National Wildlife Refuge and BLM Goodnews Block, southwestern Alaska, 2015-2017.

Table 3. Estimated upper (summer) and lower (winter) numbers of wolves in Togiak NWR and BLM Goodnews Block in 2017; and estimated minimum convex polygon territory sizes 2015-2017.

Pack	Estimated number	Territory size (km^2)
Snake Lake	8-12	1,652
Lower Kanektok River	1-6	2,885
Kwethluk River	12-16	6,107
Upper Kanektok River	10-14	4,579
Togiak Lake	11-15	2,248
Goodnews River	4-10	3,888
Ongoke River	7-9	2,756
Ongivinuk Lake	6-12	2,836
Ualik Lake	8-12	4,346
	Total: 67-106	Average: 3,478

Wolf mortality and collar life

Of the 25 wolves instrumented 2015-2017, we documented 7 mortalities. Of these, 6 were the result of human hunting or trapping and one was for unknown causes, but probably not human- associated mortality given timing and location. Of 26 deployed collars, six functioned until the wolf died or the collar was replaced, and averaged 431 days of service. Twenty-one collars failed prematurely, averaging 264 days of service. The functional range of collars was 7 to 709 days.

Objective 3. Estimate the quantity of moose annually preyed upon by wolves and brown bears throughout Togiak Refuge and BLM Goodnews Block.

DNA and Stable isotope analyses

Brown bears

In 2014, brown bear hair snaring occurred from 23 July through 11 September, during which time a total of 189 snares were set. Of these, 107 captured bear hair (Figure 8), for a catch rate of 0.57. An additional 11 hair samples were obtained from hunter harvests. In 2015, snaring occurred 10 August through 11 September and resulted in 189 snare sets which captured 126 bear hair samples. In 2016, snaring occurred 29 July through 13 September and resulted in 64 snare sets which captured 28 bear hair samples. Over the three years, a total of 442 snare sets yielded 261 samples. No snaring occurred during 2017—instead, samples collected from 2014-2016 were analyzed and summarized.

Figure 8. Brown bear hair sample, Togiak National Wildlife Refuge, southwestern Alaska.

Of the 261 snare samples containing hair and 11 hunter harvest samples, 187 were successfully genotyped (i.e., scores achieved for 8 or more markers and no evidence of more than one bear in a DNA sample; 84% of these were scored at all loci). Thirty-six multilocus genotypes were matches. Eight genotypes matched at all but one or two loci but differences were consistent with allele dropout. These were conservatively dropped for isotope analysis, for a total of 143 unique bear samples with gender identification (58 males, 85 females). The average number of alleles per locus was 7, average observed heterozygosity was 0.70, and probability of identity was $0.6x10^{-8}$ for 8 loci. Of the 143 unique bear samples with gender identification, isotopic analysis was successful on 139. Of these, 84 were females and 55 were males. We have not yet reached the target sample size of 20 bears in all study subunits (Table 4, Fig. 9), so additional sampling is necessary.

Table 4. Number of unique male and female brown bears successfully genotyped and isotope analyzed by study sub-unit, Togiak National Wildlife Refuge and BLM Goodnews Block, 2014-2016.

Sub-unit	Male	Female	Total
A	18	42	60
B	6	5	11
C	21	24	45
D	10	13	23
Total	55	84	139

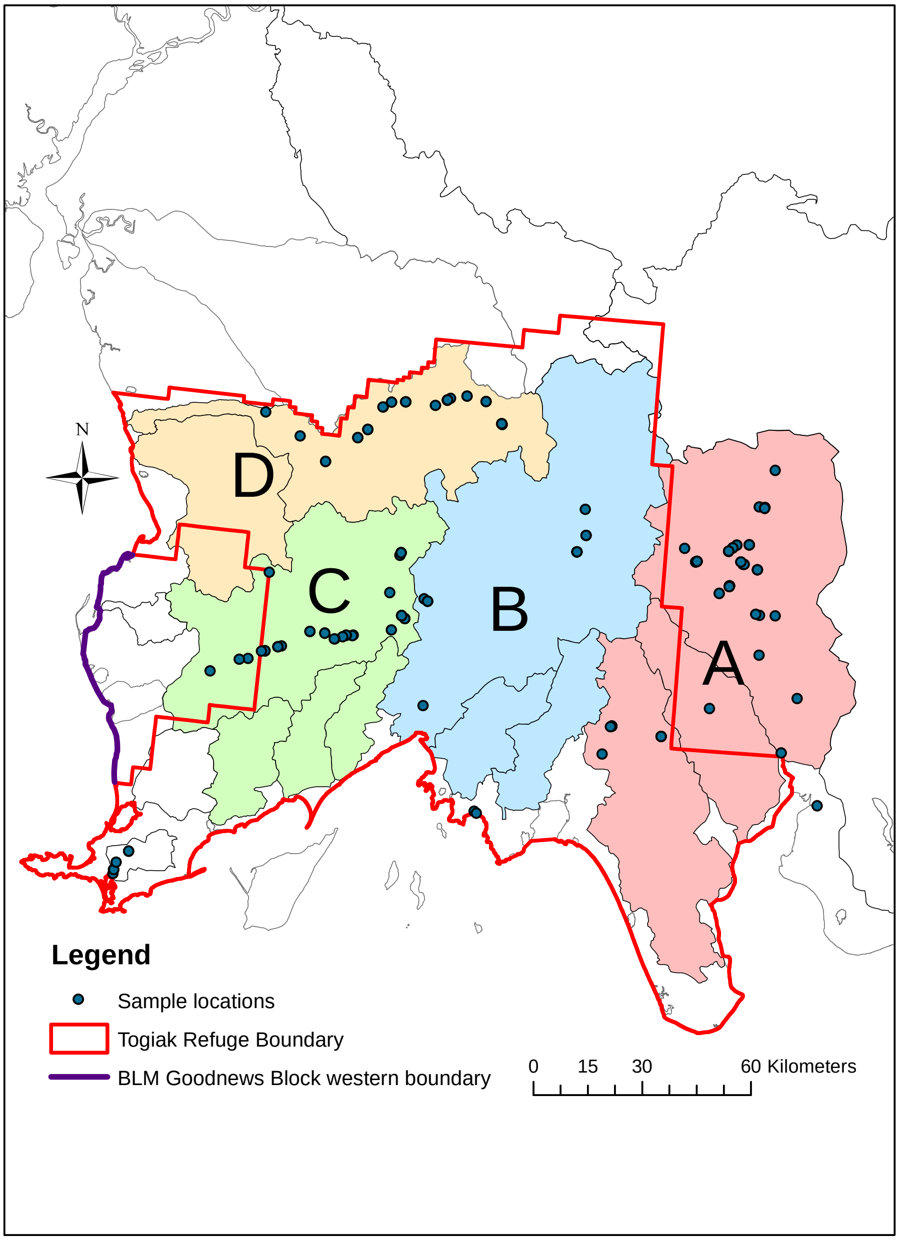

Figure 9. Location, by study area subunit, of brown bear hair samples successfully genotyped and isotope analyzed, 2014-2016, Togiak National Wildlife Refuge and BLM Goodnews Block.

Wolves

Wolf hair and blood samples were collected from all wolves captured during the course of this study (Table 5). Additionally, hair and blood were collected during a previous wolf study that occurred in study sub-units A and B from 2010-2013. As with brown bear hair sampling, we have not yet reached the target sample size of 10 wolves per study subunit, so additional sampling is needed.

Table 5. Wolf isotope samples collected during wolf studies since 2010 on Togiak National Wildlife Refuge and BLM Goodnews Block. Samples are summarized by study sub-unit, by tissue type (hair or blood), and those collected in current study (2015-2018).

	Hair		Blood	
Sub-unit	2015-2018	2010-2018	2015-2018	2010-2018
A	12	50	11	23
B	19	23	14	14
C	7	7	6	6
D	6	6	6	6
Total	44	86	37	49

Objective 4. Describe the relationship of wolf and bear predation on moose to moose demographic performance.

Nothing to report.

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