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Wolf density and territory size in a low biomass ungulate prey system estimated with global positioning system (GPS) technology

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Abstract

Population density is a fundamental parameter for wildlife management. We estimated the density and territory size of wolves (*Canis lupus*) during 2009-2010 with locations acquired from global positioning system (GPS) collars. We conducted our study on the Yukon Flats of eastern interior Alaska, a region where moose (*Alces alces*) were the sole ungulate prey and occurred at low densities and biomass. We compared between winter (n=5 packs) and annual (n=2 packs) territory size and between minimum convex polygon and adaptive kernel methods. During November 2009 to April 2010, 6,215 GPS locations were obtained from five packs, and an additional 312 locations from two packs were obtained during April to November 2010. Pack sizes averaged five in November 2009 and 4.8 in March 2010. Average winter territory size for five packs was 1,378 km^2 with 95% adaptive kernel and 1,421 km^2 with minimum convex polygon. Annual territory size for two packs averaged 1,395 km^2 with 95% adaptive kernel and 1,515 km^2 with minimum convex polygon. Density was 3.7 wolves 1000 km^{-2} in fall and 3.5 in spring with 95% adaptive kernel, and 3.6 wolves 1000 km^{-2} in fall and 3.5 in spring with minimum convex polygon. Territories were large and differed by 3-8% between methods used to analyze the locations. Winter territory size described 85-99% of annual territory size for two packs. Densities were low, not sensitive to the method used to analyze the locations, and consistent with the low biomass ungulate prey system on the Yukon Flats.

Introduction

Fundamental to informed decision making and effective management of wildlife are population parameters, such as size, density, or productivity (Johnson et al. 1997, Williams et al. 2002, Mitchell et al. 2008, Gude et al. 2012). This information commonly arises from surveys of wildlife, which are often aligned with boundaries that correspond to management or administrative units (Mitchell et al. 2008, Ver Hoef 2008, USFWS 2012). For instance, wolf (*Canis lupus*) density has been measured on the Yukon Flats of eastern interior Alaska by surveying within Alaska Game Management Unit 25 and the Yukon Flats National Wildlife Refuge (Caikoski 2009). Wolves or wolf tracks were counted (Stephenson 1978, Caikoski 2009), and density was estimated by dividing by the area surveyed. However, a disadvantage of this method was that observations often occurred near the periphery of the survey boundary, and it was probable that a portion of the wolf territory occurred outside of this boundary. Wolves are highly mobile and may have large territories (Ballard et al. 1998, Fuller et al. 2003, Mech and Boitani 2003). If a significant portion of a territory is outside of the survey boundary, density, expressed as a count divided by the survey area, may be affected. Alternate methodology for estimating wolf density bases inference on the territory size or the population area occupied by wolf packs (Fuller and Snow 1988, Burch et al. 2005, Adams et al. 2008), rather than the survey area, but has not previously occurred in this region.

Measuring the population area includes estimating wolf pack territory size from locations of wolves, typically collected with radio telemetry and very high frequency (VHF) transmitters (Peterson et al. 1984, Fuller and Snow 1988, Burch et al. 2005, Adams et al. 2008). To acquire locations, aircraft were usually employed (Messier 1985, Fuller 1989, Ballard et al. 1997) because wolves commonly range long distances (Mech et al. 1998, Merrill and Mech 2000).

However, a disadvantage of aircraft was that practical considerations such as cost, weather, and daylight limited the number of locations that could be acquired (Fuller and Snow 1988, Mech et al. 1998, Burch et al. 2005). This limitation was particularly problematic in northern regions, such as Alaska, where low ungulate biomass frequently resulted in large territories (Fuller 1989, Ballard et al. 1998, Fuller et al. 2003, Mech and Boitani 2003), which required more locations to describe (Ballard et al. 1998, Burch et al. 2005). Consequently, sample sizes of locations have been inadequate in some instances or biased to periods when aerial tracking was possible (Ballard et al. 1997, Burch et al. 2005, Adams et al. 2008). Ballard et al. (1998) used satellite transmitters to ease these limitations, and recommended an average of 123 locations to describe annual territories where sizes were large. With the advent of global positioning system (GPS) collars, acquiring locations at regular intervals that greatly exceed minimum sample size recommendations has become relatively straightforward (Mills et al. 2006, Webb 2009, Tomkiewicz et al. 2010). This technology yields the opportunity to better estimate territory size and density, yet only a single estimate of territory size (Watts et al. 2010) and no estimate of density that utilized GPS locations has been reported for wolves in Alaska.

Territory size has also varied by the time period during which the locations were collected (e.g., winter only or annual) or method used to analyze the locations (e.g., kernel or convex polygon; Mech and Boitani 2003, Mech et al. 1998, Mills et al. 2006). However, the importance of these factors may be minimized or diminished with adequate sampling provided by GPS collars. For example, Ballard et al. (1998) reported that winter and annual territories averaged 980 and 1,430 km^2, respectively when locations were acquired with VHF transmitters, whereas estimates averaged 3,444 and 3,375 km^2 with satellite transmitters that provided greater sample sizes. Mills et al. (2006) compared performance of minimum convex polygon and adaptive kernel methods for estimating territory size. Their study demonstrated that the adaptive kernel method was robust across a range of sample sizes, but the minimum convex polygon method was not. As sampling intensity increased, bias in minimum convex polygon territory size was reduced, and at intervals of 0.25-day, estimates of territory size were 198 km^2 for adaptive kernel and 228 km^2 for minimum convex polygon. Mills et al. (2006) concluded that the adaptive kernel method should be the standard for measuring animal home ranges.

We used GPS locations from five wolf packs in eastern interior Alaska on the Yukon Flats during 2009-2010 to estimate density and territory size. We compared estimates of territory size based on adaptive kernel and minimum convex polygon methods, and whether winter territory size approximated annual territory size. Density was then estimated using both adaptive kernel and minimum convex polygon methods to define the population area. Notably, this study occurred in a region where moose (*Alces alces*) were the sole ungulate prey and occurred at some of the lowest densities in North America (Gasaway 1992, Caikoski 2010, Lake 2010), resulting in low ungulate biomass (Fuller 1989, Fuller et al. 2003). Thus, our results provide a valuable comparison with studies where ungulates occurred at higher biomass. Our results also have application to resource decisions by wildlife managers of the Yukon Flats and are useful for understanding the dynamics of wolves and their ungulate prey (Messier 1994, Hayes and Harestad 2000, Adams et al. 2010, Vucetich et al. 2011).

Study Area

The Yukon Flats (Alaska Game Management Unit 25, Yukon Flats National Wildlife Refuge) is a broad, relatively flat region of eastern interior Alaska stretching approximately 325 km from west to east and situated between the White Mountains to the south and the Brooks Range to the north. The Yukon Flats is characterized by a heterogeneous landscape bisected by the Yukon

River. Many wetlands, meadows of grasses (*Arctagrostis* spp., *Beckmannia erucaeformis*, *Bromus* spp., *Calamagrostis* spp., *Eriophorum* spp, *Glyceria* spp., *Hordeum jubatum*, *Poa glaucus*, *Triglochin* spp.), sedges (*Carex* spp.), and floating mats of bog vegetation (*Menyanthes trifoliata, Potentilla palustris, Caltha palustris, Equisetum* spp.) occur throughout. Forest stands consist of black spruce (*Picea mariana*), white spruce (*P. glauca*), balsam poplar (*Populus balsamifera*), quaking aspen (*P. tremuloides*), and paper birch (*Betula papyrifera*). Shrub stands of willow (*Salix* spp.) and alder (*Alnus* sp.) are interspersed, particularly around riparian corridors. Upland habitats (91 to 912 m) consist of alder, willow, dwarf birch (*B. nana*), Labrador tea (*Ledum decumbens*), crowberry (*Empetrum nigrum*), and blueberry (*Vaccinium uliginosum*).

Moose occurred at low densities in this region (Gasaway et al. 1992, Caikoski 2010, Lake 2010). Since 2001, the fall density from four separate surveys conducted over a 29,934 km^2 area extending from 66°04´N 149°20´W to 66°33´N 143°17´W ranged from 0.06 to 0.13 moose km^{-2} (Caikoski 2010, Lake 2010), and was 0.08 moose km^{-2} in the most recent surveys (2008 and 2010). Black bear (*Ursus americanus*) densities were high (Caikoski 2011). Grizzly bear (*Ursus arctos*) were present and thought to be at low densities (Bertram and Vivion 2002).

Methods

We placed seven GPS collars (Telonics model TGW-3580) on wolves in five packs during 2-3 November 2009. All collars were removed on 11-12 April 2010, and we replaced the collar on two wolves with another GPS collar. All captures (U.S. Fish and Wildlife Service Region 7 Animal Care Protocol no. 2008022) were conducted by darting from a Robinson R-44 helicopter and we remotely delivered (Palmer Cap-chur™) 540 or 572 mg of tiletamine HCL and zolazepam HCL (Telazol®; Fort Dodge Animal Health, Ford Dodge, IA; Ballard et al. 1991) to chemically immobilize wolves. We used tooth wear and staining, and body size to differentiate among young-of-the-year, yearlings, and adults (Gipson et al. 2000).

Collars were programmed to record eight locations per day during November 2009 to April 2010. To obtain data stored on the collar, we downloaded locations after retrieval. We then used a computer program (SAS Institute 2008, V 9.1.3) that converted location times from Coordinated Universal Time to Alaska Standard Time and adjusted the date accordingly. During April 2010 to November 2010, collars on two wolves were programmed to record a single location per day. These locations were uplinked via an Argos satellite antenna that was incorporated into the collar. Locations were then downloaded from a website (CLS America, Inc.), processed to an interpretable format with the ADC-T03 Argos data converter for Gen3 GPS, and then filtered with a program (SAS Institute 2008, V 9.1.3) that retained good and eliminated redundant locations, converted times from Coordinated Universal Time to Alaska Standard Time, and adjusted the date accordingly.

Territory Size Estimation

We used GPS locations from a single collar in each pack to estimate winter and annual territory size. Though we marked more than one wolf in two packs, only a single collar in each pack functioned throughout the winter months. We assumed locations from a single collar reflected the location of the pack during winter. We believed this assumption was reasonable as wolves are cohesive during the winter months (Peterson et al. 1984, Fuller and Snow 1988), often traveling and feeding together (Metz et al. 2011). During the summer months when wolves are less cohesive, both collars were attached to the breeding female. We estimated a winter (early November 2009 to mid-April 2010) territory size for five packs (Figure 1, Table 1) and an annual (early November 2009-early November 2010) territory size for two packs (Table 1). We used all locations per pack, but we eliminated obvious extraterritorial forays (n=6; Peterson et al. 1984, Ballard et al. 1998, Adams et al. 2008).

We estimated territory size with two methods. First, we surrounded the outermost locations for each pack with a minimum convex polygon (Fuller 1989, Ballard et al. 1998, Burch et al. 2005). Second, we estimated 95% adaptive kernel territory size by following the guidelines of Mills et al. (2006). We used the extension of Rodgers and Carr (1998), implemented in Arc View 3.3, to estimate territory sizes for each pack (Table 1). For adaptive kernel territory size, our objective was to produce a single polygon for each pack, and we followed the guidance of Mills et al. (2006) and Kie et al. (2010) and incrementally decreased (or increased) the bandwith parameter by 0.1 until a single polygon resulted.

Density Estimation

We estimated fall and spring wolf density following the radiotelemetry method advocated by Fuller and Snow (1988) and Burch et al. (2005) where the numerator was the highest count of wolves in instrumented packs and the denominator was the population area during winter. We defined the population area as the sum of pack territories and we deducted overlapping portions of territories from the population area (Figure 1). We calculated separate population areas using 95% adaptive kernel and minimum convex polygon methods (Table 2). Aerial counts were obtained by tracking wolves from fixed wing aircraft in early November and late March. The total number of wolves reflected the sum of wolves in five packs.

Results

We obtained a total of 6,215 locations from five wolf packs during early November 2009 to mid-April 2010 (Table 1). An additional 312 locations were obtained from two packs during April to November 2010 (Table 1). Location fix success was high during November 2009 to April 2010 ($\bar{x}$ =98%), but was lower during April to November 2010 ($\bar{x}$ =78%). This disparity was likely influenced by the denning period when both collared females were below ground caring for young and forest canopy cover during summer. Pack sizes ranged from two to 10 in early November 2009, with a mean of five (Table 1). March 2010 pack sizes ranged from two to eight, with a mean of 4.8.

During winter, mean 95% adaptive kernel territory size was 1,378 km^2 (range 732-2,681), and minimum convex polygon territory size was 1,421 km^2 (range 654-2,653; Table 1). Annual territory sizes for two packs averaged 1,395 km^2 (range 1,053-1,743) and 1,515 km^2 (range 1,198-1,832) for 95% adaptive kernel and minimum convex polygon, respectively (Table 1). Winter territory sizes described 85-99% of annual territory sizes for two packs (Table 1). When the winter datasets were reduced to a single rather than eight locations per day, winter territory sizes were 2% greater for adaptive kernel and 12% smaller for minimum convex polygon.

For estimating density, the total number of wolves was 25 in fall and 24 in spring (Table 2). The population area with 95% adaptive kernel was 6,767km^2, resulting in a density of 3.7 wolves 1000 km^{-2} in fall and 3.5 in spring (Table 2). The population area with minimum convex polygon was 6,927 km^2, resulting in 3.6 wolves 1000 km^{-2} in fall and 3.5 in spring (Table 2).

Discussion

Density of wolves on the Yukon Flats was low (range 3.5-3.7 wolves 1000 km^{-2}) due to small packs and large territories. Pack size averaged 5 and 4.8 in November and March, respectively, which compared to an average of 6.5 from 11 studies across North America where moose were the principal prey (Fuller et al. 2003). Territory size averaged 817 km^2 from 13 studies where moose were the principal prey (Fuller et al. 2003), whereas average territories in our study ranged from 1,378-1,515 km^2. When considering the work of Fuller et al. (2003), we suggest large territories were a response to the low biomass of moose, and that wolves maintained such territories in order to ensure an adequate supply of vulnerable prey (Peterson 1977). Fuller et al.

(2003) analyzed the relationship between ungulate prey biomass, territory size, and pack size across North America, and reported that biomass described 33% of the variation in territory size, but only 4% of pack size. We conclude that density of wolves on the Yukon Flats conformed to the positive correlation between wolf density and ungulate biomass (Fuller 1989, Fuller et al. 2003) due principally to large territories. In addition, our results provided a valuable confirmatory endpoint on this relationship, as both wolf and moose densities from the Yukon Flats corresponded to values among the lowest in Fuller (1989) and Fuller et al. (2003).

Density estimates (range 4.4-5.3 wolves 1000 km^{-2} in 2006 and 2009) from aerial wolf surveys (Stephenson 1978, Caikoski 2009) conducted separate from this study, but occurring on the Yukon Flats, all exceeded those we estimated (range 3.5-3.7 wolves 1000 km^{-2}). We believe this disparity was principally from wolf pack observations on the periphery of the survey area boundary, and associated difficulty with determining the effective area covered by such packs, as it was likely their territories extended beyond the survey boundary. We use results from the most recent aerial survey (2009) and territory size estimated in this study to illustrate this point. In the 2009 aerial survey, 24 packs were reported within 22,220 km^2 of the survey area (Caikoski 2009). At territory size estimated in this study (1,378 km^2), 24 packs would occur in an area of 33,072 km^2, which was 33% greater than the survey area. We conclude that some observations made on the periphery likely inflate density. Nonetheless, although aerial surveys may overestimate density compared to telemetry based methods, they are useful to management because they can cover a larger region, are significantly cheaper, and effectively enumerate wolves, including some single, transients that may constitute 10-15% of the population (Fuller 1989, Fuller et al. 2003), but may not be accounted for by telemetry based studies (Burch et al. 2005, Adams et al. 2008, this study). Therefore, we propose that on the Yukon Flats, telemetry based methods may be most appropriate for estimating density of resident, territorial wolves. Aerial surveys may be most appropriate for enumerating the total number of wolves that have occupied the survey area, with the caveat that some territories likely extend outside the survey area. This is analogous to the superpopopulation approach where the superpopulation is the total number of animals that enter the sampled population (Williams et al. 2011).

Wolf density is useful to managers when considering proposals related to wolf harvest. Recently, much research has been devoted to understanding how human induced mortality affects wolf population dynamics. Several threshold rates of human caused annual mortality that did not impact wolf populations have been reported, including 29% (Adams et al. 2008), 24% for non-Northern Rocky Mountain populations (Creel and Rotella 2010), 34% (Webb et al. 2011), and 48% (Gude et al. 2012). Therefore, from a November density of wolves on the Yukon Flats (3.7 wolves 1000 km^{-2}), 0.89 wolves 1000 km^{-2} could be harvested at minimum mortality rates (24%; Creel and Rotella 2010). At maximum rates (48%; Gude et al. 2012), this value would be 1.8 wolves 1000 km^{-2}. Annual harvest in this region from 1996-2012 (Alaska Game Management Unit 25D; Caikoski 2009; Jason R. Caikoski, Alaska Department of Fish and Game, personal communication) averaged 0.46 wolves 1000 km^{-2} (21 wolves 45,731 km^{-2}) and ranged from 0.09 to 0.92 wolves 1000 km^{-2} (4-42 wolves 45,731 km^{-2}). We conclude that in most years wolves were lightly harvested and only occasionally moderately harvested. This conclusion could have been skewed if a significant number of harvested wolves went unreported each year. However, this was unlikely because harvested wolves must be sealed in Alaska, and fur buyers and tanneries cannot accept unsealed pelts, providing an incentive to report harvest. Furthermore, we suggest this assessment of harvest was conservative because density did not include single, transient wolves that may form a large portion of the harvest, likely due to increased naivety and susceptibility (Adams et al. 2008). We believe harvest will remain light on the Yukon Flats because large territories require that hunters and trappers travel long distances to encounter significant numbers of wolves. Use of fixed-wing aircraft for travel could overcome large territories, but we suggest that significant harvest from ground or air methods is unlikely barring economic subsidies from the government, a dramatic increase in the price of wolf pelts, or decrease in gasoline prices.

Wolf densities, when combined with prey densities (i.e., predator to prey ratio), were used in three systems to predict prey growth rate (Vucetich et al. 2011). Information of this type is desired by managers of the Yukon Flats due to interest in characterizing the impact of wolf predation. Vucetich et al. (2011) described how in two of three systems, predator to prey ratios were negatively related to the annual prey growth rate. Replicating the calculations of Vucetich et al. (2011), resulted in a predator to prey ratio on the Yukon Flats of 3.2 wolves to 100 moose. This value was within the range reported in other studies (Messier 1994, Vucetich et al. 2011). Moreover, 3.2 wolves to 100 moose was associated with prey growth rates that approximated zero in two systems with comparable ratios, although Vucetich et al. (2011) noted that confidence intervals on such a prediction were broad. However, consistent with the prediction, no growth in the moose population on the Yukon Flats has been detected since at least the 1960s (Bentley 1961, Gasaway et al. 1992, Caikoski 2010, Lake 2010). The predator to prey ratio was calculated using 3.7 wolves 1000 km^{-2}, and 114 moose 1000 km^{-2}, which reflected a density of 80 moose 1000 km^{-2} in fall surveys (Lake 2010), adjusted by a detection estimate of 0.7 for interior Alaska (Keech et al. 2011). We conclude that although wolf densities on the Yukon Flats are among the lowest in North America (Gasaway et al. 1992, Messier 1994, Fuller et al. 2003), the ratio of predator to prey is comparable to other systems that reported negligible prey growth rate, which is further supported by counts of moose in aerial surveys on the Yukon Flats. This result is contrary to previous thought by some who posited that a low wolf density on the Yukon Flats translated to low predation impact by wolves. We suggest that as wolf and moose densities are estimated in future surveys, the above calculation can be used to track changes in predator to prey ratios.

Density estimates benefited from use of GPS technology that enabled us to obtain sample sizes of locations that greatly exceeded recommendations for estimating territory size (Fuller and Snow 1988, Mills et al. 2006, Ballard et al. 1998). Comparison between adaptive kernel and minimum convex polygon methods for estimating territory size revealed a difference of 3-8%, which we interpret as reflecting adequate sample sizes for both methods (Mills et al. 2006). Territory size estimated with winter locations appeared to approximate annual territory size, as large territory size occurred regardless of whether winter only or annual locations were used (Ballard et al. 1998), and for two packs we observed that winter territory size described 85-99% of annual territory size. Territory size could have been biased by lower location fix success in summer, although 39% of failed acquisitions were during May when breeding females were caring for newly born young and movement was likely restricted (Mech et al. 1998). Winter territory size differed by 2-12% depending on whether estimation was based on eight locations or a single location per day. This result has practical application to planning for future studies. Due to battery constraints, GPS collars must balance longevity with the number of locations acquired per day, among other factors. Where territory estimation is the study objective, collar longevity may be extended by programming collars to record a single location per day.

Adams et al. (2010) documented use of salmon (*Oncorhynchus* spp.) by wolves in Denali National Park within interior Alaska. Consequently, in a portion of the Park, wolf densities were only 17% less (4.4-5.8 wolves 1000 km^{-2} vs. 5.8-7.2 wolves 1000 km^{-2}) despite ungulate densities that were 78% lower. Such differences resulted in a three-fold difference in predation rates, which has important implications for wolf-ungulate relations (Adams et al. 2010). On the Yukon Flats, moose are the sole ungulate prey of wolves, but each summer more than a million chum (*O. keta*) and Chinook (*O. tshawytscha*) salmon are counted traveling up the Yukon River (JTC 2011). These salmon are potentially available to wolves during fall and spring in the numerous tributaries that branch from the Yukon River, and during this study a wolf pack on the Yukon Flats was observed adjacent to a stream that contained salmon, presumably foraging (Nikki Guldager, U.S. Fish and Wildlife Service, personal communication). Knowledge of whether wolves on the Yukon Flats benefit numerically from use of an alternate food subsidy would be valuable, as such use may perturb the system from equilibrium conditions (Gasaway et al. 1992), and may inflate densities and the impact of predation.

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Literature Cited

Adams, L. G., R. O. Stephenson, B. W. Dale, R. T. Ahgook, and D. J. Demma. 2008. Population dynamics and harvest characteristics of wolves in the central Brooks Range, Alaska. Wildlife Monographs 170:1-25.

Adams, L. G., S. D. Farley, C. A. Stricker, D. J. Demma, G. H. Roffler, D. C. Miller, and R. O. Rye. 2010. Are inland wolf-ungulate systems influenced by marine subsidies of Pacific salmon? Ecological Applications 20:251-262.

Ballard, W. B., L. A. Ayres, K. E. Roney, and T. H. Spraker. 1991. Immobilization of gray wolves with a combination of tiletamine hydrochloride and zolazepam hydrochloride. Journal of Wildlife Management 55:71-74.

Ballard, W. B., L. A. Ayres, P. R. Krausman, D. J. Reed, and S. G. Fancy. 1997. Ecology of wolves in relation to a migratory caribou herd in northwest Alaska. Wildlife Monographs 135:1-47.

Ballard, W. B., M. Edwards, S. G. Fancy, S. Boe, and P. R. Krausman. 1998. Comparison of VHF and satellite telemetry for estimating sizes of wolf territories in northwest Alaska. Wildlife Society Bulletin 26:823-829.

Bentley, W.W. 1961. Moose population inventories – Interior and Arctic Alaska. Alaska Wildlife Investigations.

Bertram, M. R., and M. T. Vivion. 2002. Moose mortality in eastern interior Alaska. Journal of Wildlife Management 66:747-756.

Burch, J. W., L. G. Adams, E. H. Follmann, and E. A. Rexstad. 2005. Evaluation of wolf density estimation from radiotelemetry data. Wildlife Society Bulletin 33:1225-1236.

Caikoski, J. R. 2009. Units 25A, 25B, 25D, and 26C Wolves. *In* P. Harper (editor). Wolf Management Report of Survey and Inventory Activities 1 July 2005–30 June 2008. Alaska Department of Fish and Game, Project 14.0. Juneau, AK. Pp. 248-256. Available online at http://www.adfg.alaska.gov/static/home/library/pdfs/wildlife/mgt_rpts/09_wolf.pdf (accessed 10 December 2012).

Caikoski, J. R. 2010. Units 25A, 25B, and 25D Moose. *In* P. Harper (editor). Moose Management Report of Survey and Inventory Activities 1 July 2005–30 June 2007. Alaska Department of Fish and Game, Project 1.0. Juneau, AK. Pp.611-642. Available online at http://www.adfg.alaska.gov/static/home/library/pdfs/wildlife/mgt_rpts/10_moose.pdf (accessed 10 December 2012).

Caikoski, J. R. 2011. Unit 25D Black Bear. *In* P. Harper (editor). Black Bear Management Report of Survey and Inventory Activities 1 July 2007–30 June 2010. Alaska Department of Fish and Game. Project 17.0 Juneau, Alaska. Pp.257-261. Available online at http://www.adfg.alaska.gov/static/home/library/pdfs/wildlife/mgt_rpts/11_blb.pdf (accessed 10 December 2012).

Creel, S., and J. J. Rotella. 2010. Meta-analysis of relationships between human offtake, total mortality, and population dynamics of gray wolves (*Canis lupus*). Plos One 5(9). Available online at http://www.plosone.org/article/info%3Adoi%2F10.1371%2Fjournal.pone.0012918 (accessed 10 December 2012).

Fuller, T. K. 1989. Population dynamics of wolves in north-central Minnesota. Wildlife Monographs 105:1-41.

Fuller, T. K., and W. J. Snow. 1988. Estimating winter wolf densities using radiotelemetry data. Wildlife Society Bulletin 16:367-370.

Fuller, T. K., L. D. Mech, and J. F. Cochrane. 2003. Wolf population dynamics. *In* L. D. Mech, and L. Boitani (editors). Wolves: behavior, ecology, and conservation. University of Chicago Press, Chicago, USA. Pp. 161-191.

Gasaway, W. C., R. D. Boertje, D. V. Grangaard, D. V. Kellyhouse, R. O. Stephenson, and D. G. Larsen. 1992. The role of predation in limiting moose at low densities in Alaska and Yukon and implications for conservation. Wildlife Monographs 120:1-59.

Gipson, P. S., W. B. Ballard, R. M. Nowak, and L. D. Mech. 2000. Accuracy and precision of estimating age of gray wolves by tooth wear. Journal of Wildlife Management 64:752-758.

Gude, J. A., M. S. Mitchell, R. E. Russell, C. A. Sime, E. E. Bangs, L. D. Mech, and R. R. Ream. 2012. Wolf population dynamics in the U.S. Northern Rocky Mountains are affected by recruitment and human-caused mortality. Journal of Wildlife Management 76:108-118.

Hayes, R. D., and A. S. Harestad. 2000. Wolf functional response and regulation of moose in the Yukon. Canadian Journal of Zoology 78:60-66.

Johnson, F. A., C. T. Moore, W. L. Kendall, J. A. Dubovsky, D. F. Caithamer, J. R. Kelly, and B. K. Williams. 1997. Uncertainty and the management of mallard harvests. Journal of Wildlife Management 61:202-216.

JTC (Joint Technical Committee of the Yukon River US/Canada Panel). 2011. Yukon River salmon 2010 season summary and 2011 season outlook. Unpublished report on file at Alaska Department of Fish and Game, Division of Commercial Fisheries, Anchorage.

Keech, M. A., M. S. Lindberg, R. D. Boertje, P. Valkenburg, B. D. Taras, T. A. Boudreau, and K. B. Beckmen. 2011. Effects of predator treatments, individual traits, and environment on moose survival in Alaska. Journal of Wildlife Management 75:1361-1380.

Kie, J. G., J. Matthiopoulos, J. Fieberg, R. A. Powell, F. Cagnacci, M. S. Mitchell, J-M Gaillard, and P. R. Moorcroft. 2010. Philosophical Transactions of the Royal Society of Biological Sciences 365:2221-2231.

Lake, B. C. 2010. Moose Population Survey of the Western Yukon Flats - November 2010. Yukon Flats National Wildlife Refuge, Fairbanks, AK. Available online at http://alaska.fws.gov/nwr/yukonflats/pdf/lake_moose_report_nov_2010.pdf (accessed 10 December 2012).

Lake, B. C., M. R. Bertram, N. Guldager, J. R. Caikoski, and R. O. Stephenson. 2011. Wolf kill rate on moose across winter in a low density ungulate prey system. Unpublished report on file at the Yukon Flats National Wildlife Refuge, Fairbanks.

Mech, L. D., and L. Boitani. 2003. Wolf social ecology. *In* L. D. Mech, and L. Boitani (editors). Wolves: behavior, ecology, and conservation. University of Chicago Press, Chicago, USA. Pp. 1-34.

Mech, L. D., L. G. Adams, T. J. Meier, J. W. Burch, and B. W. Dale. 1998. The Wolves of Denali. University of Minnesota Press, Minneapolis.

Merrill, S., and L. D. Mech. 2000. Details of extensive movements by Minnesota wolves (*Canis lupus*). American Midland Naturalist 144:428-433.

Mitchell, M. S., D. E. Ausband, C. A. Sime, E. E. Bangs, J. A. Gude, M. D. Jimenez, C. M. Mack, T. J. Meier, M. S. Nadeau, and D. W. Smith. 2008. Estimation of successful breeding pairs for wolves in the Northern Rocky Mountains, USA. Journal of Wildlife Management 72:881-891.

Messier, F. 1985. Social organization, spatial distribution, and population density of wolves in relation to moose density. Canadian Journal of Zoology 63:1068-1077.

Messier, F. 1994. Ungulate population models with predation: a case study with the North American moose. Ecology 75:478-488.

Metz, M. C., J. A. Vucetich, D. W. Smith, D. R. Stahler, and R. O. Peterson. 2011. Effect of Sociality and Season on Gray Wolf (*Canis lupus*) Foraging Behavior: Implications for Estimating Summer Kill Rate. Plos One 6(3). Available online at http://www.plosone.org/article/info%3Adoi%2F10.1371%2Fjournal.pone.0017332 (accessed 22 November 2011).

Mills, K. J., B. R. Patterson, and D. L. Murray. 2006. Effects of variable sampling frequencies on GPS transmitter efficiency and estimated wolf home range size and movement distance. Wildlife Society Bulletin 34:1463-1469.

Peterson, R. O. 1977. Wolf ecology and prey relationships. U.S. National Park Service scientific monograph series No. 11. U.S. Government Printing Office, Washington, D.C., USA. Available online at http://www.nps.gov/history/history/online_books/science/11/index.htm (accessed 23 January 2013).

Peterson, R. O., J. D. Woolington, and T. N. Bailey. 1984. Wolves of the Kenai Peninsula, Alaska. Wildlife Monographs 88:1-52.

Rodgers, A. R., and A. P. Carr. 1998. HRE: The Home Range Extension for ArcView. Ontario Ministry of Natural Resources, Centre for Northern Forest Ecosystem Research, Thunder Bay, Ontario, Canada.

SAS Institute. 2008. Version 9.1.3. SAS Institute, Cary, North Carolina, USA.

Stephenson, R. O. 1978. Characteristics of exploited wolf populations. Unpublished report on file at Alaska Department of Fish and Game, Juneau.

Tomkiewicz, S. M., M. R. Fuller, J. G. Kie, and K. K. Bates. 2010. Global positioning system and associated technologies in animal behavior and ecological research. Philosophical Transactions of the Royal Society of Biological Sciences 365:2163-2176.

United States Fish and Wildlife Service (USFWS). 2012. Waterfowl population status, 2012. U.S. Department of the Interior, Washington, D.C. USA. Available online at http://www.fws.gov/migratorybirds/NewReportsPublications/PopulationStatus/Waterfowl/StatusReport2012_final.pdf (accessed 10 December 2012).

Ver Hoef, J. M. 2008. Spatial methods for plot-based sampling of wildlife populations. Environ Ecol Stat 15:3-13.

Vucetich, J. A., M. Hebblewhite, D. W. Smith, and R. O. Peterson. 2011. Predicting prey population dynamics from kill rate, predation rate, and predator-prey ratios in three wolf-ungulate systems. Journal of Animal Ecology 80:1236-1245.

Watts, D. E., L. G. Butler, B. W. Dale, and R. D. Cox. 2010. The Ilnik wolf *Canis lupus* pack: use of marine mammals and offshore sea ice. Wildlife Biology 16:144-149.

Webb, N. F. 2009. Density, demography, and functional response of a harvested wolf population in west-central Alberta, Canada. Ph.D. Dissertation, University of Alberta, Edmonton, Alberta.

Webb, N. F., J. R. Allen, and E. H. Merrill. 2011. Demography of a harvested population of wolves (*Canis lupus*) in west-central Alberta, Canada. Canadian Journal of Zoology 89:744-752.

Williams, K. A., P. C. Frederick, and J. D. Nichols. 2011. Use of the superpopulation approach to estimate breeding population size: an example in asynchronously breeding birds. Ecology 92:821-828.

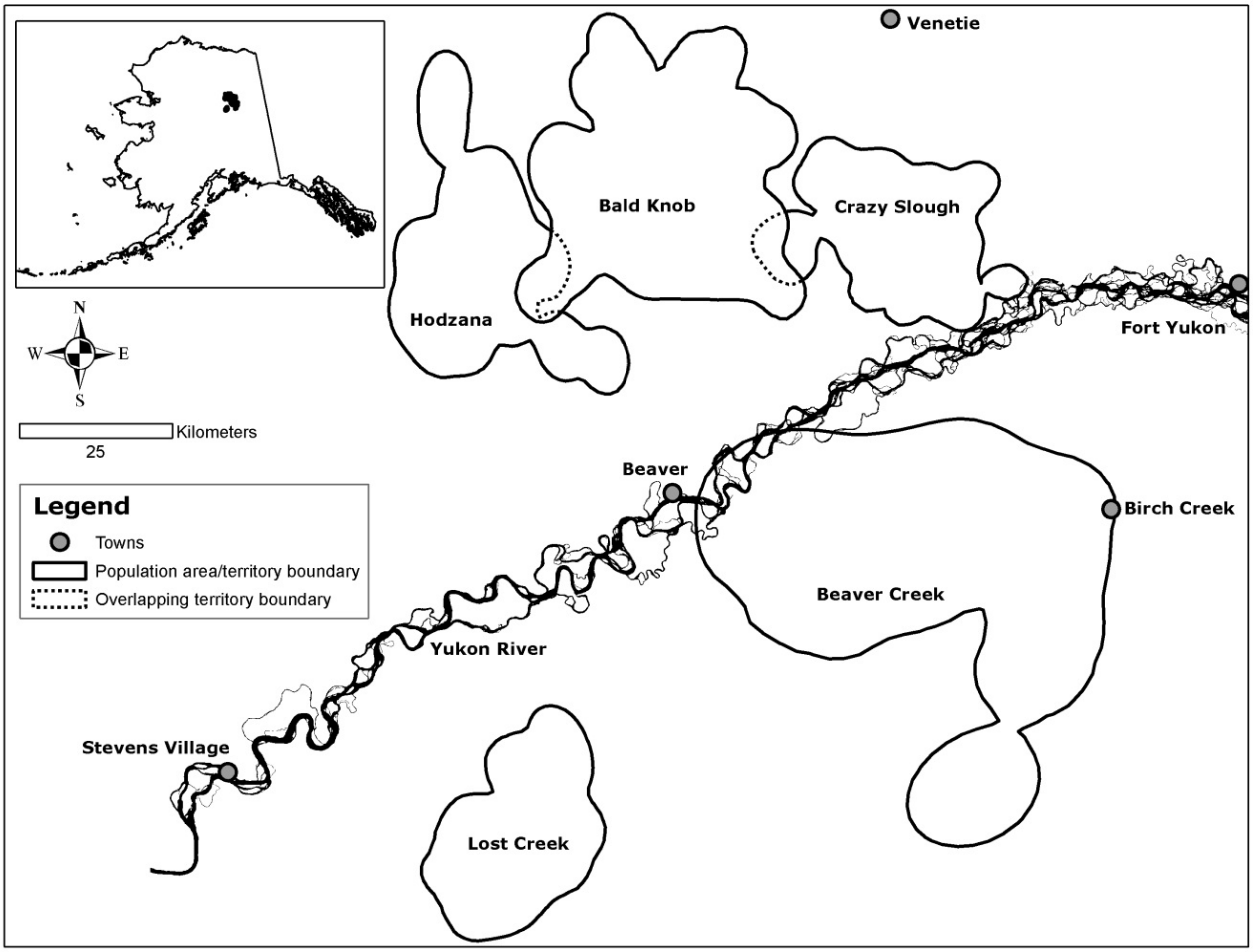
Williams, B. K. J. D. Nichols, and M. J. Conroy. 2002. Analysis and Management of Animal Populations. Academic Press, San Diego.

Table 1. Territory and pack sizes of five wolf packs on the Yukon Flats, Alaska. For five packs, estimates were presented for the winter period (November 2009-April 2010), and for two packs annual (November 2009-November 2010) estimates were presented. Pack sizes were from November 2009.

Period	Pack-packsize	# locations	95% Adaptive kernel (km^2)	Minimum convex polygon (km^2)
Winter	Bald knob-4	1,221	1,621	1,824
	Beaver creek-10	1,249	2,681	2,653
	Crazy slough-4	1,257	842	957
	Hodzana-5	1,259	1,013	1,017
	Lost Creek-2	1,229	732	654
	$\overline{X}$-5	1,243	1,378	1,421
Annual	Bald knob-4	1,367	1,743	1,832
	Hodzana-5	1,425	1,053	1,198
	$\overline{X}$	1,396	1,395	1,515

Table 2. Fall and spring densities of wolves on the Yukon Flats, Alaska, November 2009 and March 2010.

Period	Population area method	Population area (km^2)	# wolves	Density (wolves 1000 km^{-2})
Fall	95% Adaptive kernel	6,767	25	3.7
	Minimum convex polygon	6,927	25	3.6
Spring	95% Adaptive kernel	6,767	24	3.5
	Minimum convex polygon	6,927	24	3.5



Venetie
Bald Knob
Crazy Slough
Hodzana
Fort Yukon
N
W
E
S
Kilometers
25
Legend
Towns
Population area/territory boundary
Overlapping territory boundary
Beaver
Birch Creek
Beaver Creek
Yukon River
Stevens Village
Lost Creek

Figure 1. Wolf pack territories and population area during winter (November 2009-April 2010) on the Yukon Flats, Alaska. Boundaries were developed with 95% adaptive kernels. For the Hodzana and Crazy Slough packs, overlapping territory boundaries were depicted with the dotted line. For the remaining packs, territory and population area boundaries were equivalent.