University of Alberta

Seasonal Wolf Predation in a Multi-Prey System in West-Central Alberta

by

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Dedication

For my grandpa, Eric Thurston, whom inspired me since being a wee boy to appreciate the marvels of nature and the gift of life.

ABSTRACT

Estimating annual wolf kill rates and composition is important for assessing the impact of wolves on their prey and managing wolf-ungulate dynamics. Most studies have focused on kill rates of wolves in winter or single-ungulate dominated systems. I used high intensity GPS tracking combined with scat analysis to explored intra- and inter-seasonal variations in kill rates and prey composition of wolves in a multi-prey ungulate population. I found wolves in summer selected for neonate prey of all species with deer comprising the greatest proportion of both adult and neonate prey. Summer kill rates (0.21 ungulates/ adult wolf/day) were among the highest (~1.5-2.5 times) reported in the literature and were 2.5 times higher than winter rates (0.08±0.02), when wolves killed a greater diversity of predominately adult prey. Summer biomass consumption rates (4.22±0.36 kg/adult equivalent wolf/day) were lower than in winter (7.93±4.08), when wolves were less food limited. Seasonal differences in kill rates would have lead to significant underestimates (~29%) of annual kill rates when based on winter information only.

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International Foundation, and the University of Alberta all gave generously to ensure that this research went ahead.

Finally, I would like to pay tribute to the wild places of west-central Alberta where I worked, and especially to the wolves with which I worked.

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CHAPTER 1

GENERAL INTRODUCTION

Wolf management in Alberta historically has focused on control efforts through government sponsored bounties and paid trappers, liberal hunting and trapping seasons, and intensive poisoning campaigns. Wolves were eradicated across much of southern Alberta by the late 1800s (Cowan 1947), but recovered by the 1940s (Green 1951) only to face large-scale strychnine poisoning even in the National Parks during the 1950s because of concerns over spread of rabies, reduced game populations, and livestock predation (Gunson 1992). Since then public attitudes towards wolves across North America have become more positive (Kellert 1985) and government management regimes followed suit. Wolves recolonized Banff National Park in Alberta during the mid 1980s (Gunson 1992, Alberta Forestry Lands, and Wildlife 1991) and today wolves are widely distributed across Alberta with the exception of the Prairie Parkland regions. Except for endangered species protection and livestock deprivation (Gunson 1992, James 2004), wolf control to increase native ungulate populations has not been implemented in Alberta since 1966 (Gunson 1992). However, there are liberal regulations for hunting and trapping wolves on registered traplines, but province-wide harvests remain low (Robichaud and Boyce 2010). Locally, wolf populations remain high causing continued concern for their impact on prey populations (Alberta Forestry Lands and Wildlife 1991, Webb 2009).

Effective management of wolf- prey systems depends on an understanding of predation and the factors influencing it (Ballard et al. 1997, Adams et al. 2008, Fuller 1989, Hebblewhite 2005, Knopff et al. 2009). How wolf predation influences ungulate populations has been subject to public controversy and scientific debate for decades (NRC 1997, Mech and Peterson 2003). Research has shown that wolves have the potential to limit ungulate population (Messier 1994, Dale et al. 1994, Van Ballenberghe and Ballard 1994), and that these effects can cascade through a system (Hebblewhite 2005, Ripple and Bescha, 2004). Estimating predator kill rates and composition is important for assessing the impact of predators on their prey and managing wolf-ungulate dynamics (Sand et al. 2008). To date most studies have focused on kill rates of wolves in winter, due primarily to methodological problems for kill rate estimation in a snow–free environment (Mech and Peterson 2003). Until more recently, summer kill rates have been assumed to be lower than in winter (Messier 1994) based on reduced wolf body weights (Peterson and Page 1988, Seal and Mech 1983, Messier 1994).

Recent studies that have quantified summer kill rates by wolves show variable results. For example, Sand et al. (2008) reported kill rates of moose (*Alces alces*) in Scandinavia were 94 -116% higher in summer than winter yet biomass consumption rates were comparable to winter (Sand et al. 2005). In contrast, Metz et al. (*in prep.*) in Yellowstone National Park reported summer kill rates of elk (*Cervus canadensis*) were ~70 % higher than in winter while biomass consumption rates were 35% lower in summer than winter (Metz *et al.* 2011, Metz et al. *in prep.*). These contrasting results from single-prey dominated systems indicate a need to better understand how kill rates vary seasonally.

West-central Alberta provides a unique area to study summer wolf predation for several reasons. First, wolves exist in a multi-predator, multiple-prey system (Webb 2009), which contrasts from the few other studies that currently exist where summer kill rates have been quantified in single-ungulate dominated systems (Metz et al. 2011, Metz et al. *in prep.*, Sand et al. 2008). Second, winter but not summer kill rates have been studied in this area (Webb 2009), which provides an opportunity to compare winter and summer kill rates. Third, unlike other studies where wolf populations are either protected (Fritts and Mech 1981, Mech et al. 1998, Theberge and Theberge 2004, Peterson and Page 1988), subjected to control programs (Gasaway et al. 1983, Ballard et al. 1987, Hayes and Harestad 2000) or remote inaccessible trapped/ hunted population (Adams et al. 2008), wolves in this area are subject to liberal harvest regulations, which currently appears to result in a sustainable wolf population (Webb et al. 2011). Because harvests, of predominately non-reproductive wolves occurs through November-March (Webb et al. 2011:71%), population dynamics of wolves in this area are likely to differ from protected areas where mortality occurs year-round (Smith et al. 2006; 2010), or populations subjected to control programs which generally peak in spring and summer (Fritts et al. 2003). Differences in seasonal variation of wolf mortality and resulting pack structure and size likely affect pack stability and kill rates (Webb et al. 2011).

In this thesis I studied the summer predation of wolves in west-central Alberta and compared those rates to predation patterns of wolf packs in winter in the same area. Specifically, in Chapter 2 I quantified dynamics of wolf kill rates, biomass consumption, and species composition of ungulate prey killed by wolves during summer, where wolves are known to prey on multiple species of ungulates in winter (Webb 2009). In particular, I evaluated the relative importance of neonate ungulates in the diets of wolves and the intra-seasonal variation between adult and neonate prey. I hypothesized that neonates would be selected for during summer due to their high vulnerability, and as a result kill rates would be higher to allow wolves to meet the demands on the pack for feeding growing pups. To estimate kill rates of ungulate prey, I used the GPS-cluster approach for identifying adult kills and derived kill rates for neonates based on scats following the approaches of Mattioli et al. (2004) and Jedrezejewski et al. (2002). I compared pack cohesion rates in my study to those in Yellowstone and adjusted summer kill rates to account for pack cohesion following the approach of Metz et al. (2011).

In Chapter 3, I compared summer to winter predation by 4 different wolf packs with 3 objectives. First, I compared winter and summer species/age-specific kill rates and biomass composition of ungulates by wolves to test the hypothesis that wolf kill rates would be lower in winter than summer, but total biomass consumed would be higher in winter because more large-bodied prey would be killed compared to summer. Second, I evaluated whether these patterns of predation resulted in weight differences in winter compared to summer of a larger sample of wolves across the study area. Third, to explore potential mechanisms influencing seasonal differences in kill rates and biomass consumption, I assessed shifts in selection of ungulate prey species between seasons based on composition of kills and availability of prey from seasonal pellet group counts within pack home ranges. I assessed the hypothesis that because deer are likely to be most vulnerable due to the small body size of both the neonate and the defending adult, wolves would select more strongly for deer in summer than in winter compared to other species, when the rigors of winter may make the larger-bodied species more vulnerable. Finally, combining kill rates from both seasons I derived annual kill rates on ungulate prey for the purpose of future predator-prey modeling in this area.

LITERATURE CITED

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

Alberta Forestry, Lands, and Wildlife. 1991. Management plan for wolves in Alberta. Wildlife Management Planning Series No. 4. 89pp.

Ballard, W., L. Ayres, P. Krausman, D. Reed, and S. Fancy. 1997. Ecology of wolves in relation to a migratory caribou herd in northwest Alaska. Wildlife Monographs :5-47.

Cowan, I.M. 1947. The timber wolf in the Rocky Mountain National Parks of Canada. Canadian Journal of Research 25:139-174.

Dale, B., L. Adams, and R. Bowyer. 1994. Functional-response of wolves preying on barren-ground caribou in a multiple-prey ecosystem. Journal of Animal Ecology 63:644-652.

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

Fritts, S., and L. Mech. 1981. Dynamics, movements, and feeding ecology of a newly protected wolf population in northwestern Minnesota. Wildlife Monographs :6-79.

Fritts, S.H., Stephenson, R.O., Hayes, R.D., and Boitani, L. 2003. Wolves And Humans. In Wolves: Behavior, Ecology, And Conservation. Edited By L.D. Mech and L. Boitani. The University Of Chicago Press, Chicago. Pp. 289–316.

Gasaway, W., R. Stephenson, J. Davis, P. Shepherd, and O. Burris. 1983. Interrelationships of wolves, prey, and man in interior Alaska. Wildlife Monographs :1-50.

Green, H.U. 1951. The wolf of the Banff National Park, Alberta. Can. Nat. Park and Hist. Sites Sev. 58pp.

Gunson, J. 1992. Historical and present management of wolves in Alberta. Wildlife Society Bulletin 20:330-339.

Hayes, R., and A. Harestad. 2000. Demography of a recovering wolf population in the Yukon. Canadian Journal of Zoology-Revue Canadienne De Zoologie 78:36-48.

Hebblewhite, M. 2005. Predation by wolves interacts with the North Pacific Oscillation (NPO) on a western North American elk population. Journal of Animal Ecology 74:226-233.

James, A., S. Boutin, D.M. Hebert, and A.B. Rippin. 2004. Spatial separation of caribou from moose and its relation to predation by wolves. Journal of Wildlife Management 68: 799-809. National Research Council. 1997.

Jedrzejewski, W., K. Schmidt, J. Theuerkauf, B. Jedrzejewska, N. Selva, K. Zub, and L. Szymura. 2002. Kill rates and predation by wolves on ungulate populations in Bialowieza Primeval Forest (Poland) RID B-6823-2009. Ecology 83:1341-1356

Knopff, K.H., A.A. Knopff, M.B. Warren, and M.S. Boyce. 2009. Evaluating global positioning system telemetry techniques for estimating cougar predation parameters. Journal of Wildlife Management 73:586-597.

Mattioli, L., C. Capitani, E. Avanzinelli, I. Bertelli, A. Gazzola, and M. Apollonio. 2004. Predation by wolves (*Canis lupus*) on roe deer (*Capreolus capreolus*) in north-eastern Apennine, Italy. Journal of Zoology 264:249-258.

Mech, L.D., and R.O. Peterson. 2003. Wolf-prey relations. L.D. Mech, and L. Boitani, editors.

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:e17332.

Metz, M.C., J.A. Vucetich, D.W. Smith, D.R. Stahler, and R.O. Peterson. 2011. Seasonal patterns of predation for grey wolves in the multi-prey system of Yellowstone National Park. (*in prep).*

Peterson, R., and R. Page. 1988. The rise and fall of Isle Royale wolves, 1975-1986. Journal of Mammalogy 69:89-99.

Northern Research Council. 1997. Committee on management of wolf and bear population in Alaska. Wolves, bear and their prey in Alaska: Biological and social challenges in wildlife management. National Academies Home. Washington, DC.

Ripple, W., and R. Beschta. 2004. Wolves, elk, willows, and trophic cascades in the upper Gallatin range of southwestern Montana, USA. Forest Ecology and Management 200:161-181.

Robichaud, C. B., and M. S. Boyce. 2010. Spatial and temporal patterns of wolf harvest on registered traplines in Alberta, Canada. Journal of Wildlife Management 74:635-643.

Smith, D.W., Stahler, D.R., And Guernsey, D.S. 2006. Yellowstone Wolf Project: Annual Report, 2005. National Park Service, Yellowstone Center For Resources, Yellowstone National Park, Wyoming.

Smith, D.W., Bangs, E.E., Oakleaf, J.K., Mack, C., Fontaine, J., Boyd, D., Jimenez, M., Pletscher, D.H., Niemeyer, C.C., Meier, T.J., Stahler, D.R., Holyan, J., Asher, V.J., And Murray, D.L. 2010. Survival Of Colonizing Wolves In The Northern Rocky Mountains Of The United States, 1982–2004. Journal of Wildlife Management. 74(4): 620–634. Doi:10.2193/2008-584.

Sand, H., B. Zimmermann, P. Wabakken, H. Andren, and H. Pedersen. 2005. Using GPS technology and GIS cluster analyses to estimate kill rates in wolf-ungulate ecosystems. Wildlife Society Bulletin 33:914-925.

Sand, H., P. Wabakken, B. Zimmermann, O. Johansson, H.C. Pedersen, and O. Liberg. 2008. Summer kill rates and predation pattern in a wolf-moose system: Can we rely on winter estimates? Oecologia 156:53-64.

Seal, U., and L. Mech. 1983. Blood indicators of seasonal metabolic patterns in captive adult gray wolves. Journal of Wildlife Management 47:704-715.

Theberge, J.B., and M.T. Theberge. 2004. The wolves of Algonquin Park: a 12 year ecological study. University of Waterloo, Department of Geography Publication Series 56, Waterloo, Ontario, Canada.

Vanballenberghe, V., and W. Ballard. 1994. Limitation and regulation of moose populations - the role of predation. Canadian Journal of Zoology-Revue Canadienne De Zoologie 72:2071-2077.

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

Webb, S.L., M.R. Dzialak, J.J. Wondzell, S.M. Harju, L.D. Hayden-Wing, and J.B. Winstead. 2011. Survival and cause-specific mortality of female rocky mountain elk exposed to human activity. Population Ecology 53:483-493.

CHAPTER 2

SUMMER DYNAMICS OF WOLF PREDATION ON UNGULATES IN A MULTI-PREY SYSTEM

As reintroduced and recolonizing wolf populations expand across North America, they have the potential to reduce ungulate populations and alter prey community structure by influencing adult mortality and recruitment rates (Ballard et al.1981, Kunkel and Mech, 1994, Barber- Meyer et al. 2008). Approaches to determine wolves' impact on ungulate populations include quantifying either cause-specific mortality of ungulates or wolf kill rates. While cause-specific mortality rates indicates predation levels (e.g. Bender et al. 2007, Frair et al. 2007, Barber-Meyer et al. 2008), this approach requires collaring a large number of ungulates, in particular neonates, which can be impractical if multi-prey species are of interest. Alternatively, wolf kill rates have been estimated for major prey items by locating ungulate kills using fixed-wing aircraft (Mech 1966, 1974, Peterson et al. 1984, Ballard et al. 1997), snow tracking (Hebblewhite 2000, Kunkel and Pletsher 2001), and more recently with the use of clusters of GPS locations from collared individuals (Zimmermann et al. 2007, Webb et al. 2008, Knopff et al. 2010, Tambling et al. 2010).

Most wolf predation studies to date have focused on kill rates of wolves in winter, yet annual kill rates are required to understand predator-prey dynamics. Until more recently, summer kill rates have been assumed to be lower than in winter (Messier 1994) based on reduced wolf body weights (Peterson and Page. 1988, Seal and Mech 1983, Stahler et al.2006, White and Garrott 2005, Messier

1994), or increased scavenging in summer than winter (Peterson et al. 1984). Recent studies that have quantified summer kill rates of wolves show variable results. For example, Sand et al. (2008) reported kill rates of moose in Scandinavia that were 94 -116% higher in summer than winter but neonates comprised almost 90% of all moose kills. In Yellowstone, Metz et al. (*in prep.*) reported summer kill rates of elk that were ~70 % higher than in winter with neonates comprising 63%.

In temperate systems neonate prey would be expected to comprise a high proportion of the diet of wolves in summer because wolves are opportunistic and will respond to a rapid increase in abundance of vulnerable neonates after the birth pulse (Messier and Crete 1985, Sand et al. 2008, Jedrezejewski et al. 2002, Metz et al. 2011). However, abundance and vulnerability of neonates changes over the summer (Testa et al. 2000, Mech and Peterson. 2003), and kill rates and proportion of neonates in the diet is likely to reflect this dynamic. For example, in Minnesota neonate white-tailed deer comprised 80% of the diet in June based on scat analysis but this dropped to 50% in July (Fuller 1989). In Yellowstone, Metz et al. (*in prep.)* found the proportion of neonate elk in wolf kills varied over the summer with a peak of 80% of the total kill in mid June and declined through July. However, Sand et al. (2008) identified that kill rates of neonate and or yearling moose increased over the summer season. To date the dynamics of summer predation have been described primarily in these systems dominated by a single large prey (Sand et al. 2008, Metz et al. 2011). In systems with multiple ungulate prey, dynamics of summer kill rates may be more complex due to switching of prey. For example, Jedrezjewski et al. (2002) found kill rates of neonate wild boar (*Sus scrofa*) increased over summer, but kill rates of red deer (*Capreolus capreolus)* declined over summer.

In this study, I quantified total, adult and neonate dynamics of summer kill rates by wolves in a montane system in west-central Alberta, where wolves are known to prey largely on ungulates including moose (*Alces alces*), elk (*Cervus elaphus*), two species of deer (*Odocoileus virginianus*, *O. hemionu*s) and feral horses (*Equus caballus*) in winter (Webb 2009). Because all 5 species give birth in mid-May to early June, I expected a general peak in kill rate of neonates in mid-summer that reflected the trade-offs in growth rates of neonate prey and growing wolf pups, as reported in systems dominated by a single, large ungulate (Sand et al. 2008, Metz et al. 2011). At the same time, because vulnerability is likely related to prey body size, I expected neonates of small prey (i.e. deer) to remain a relatively high proportion of the diet later into the season than large prey (i.e. elk, moose, horses). I explored the implications of the dynamics of kill rates for consumption of prey biomass per wolf considering the changing requirements of growing pups.

To determine kill rates and subsequent prey biomass consumption, I used intensive GPS monitoring (i.e. 15-min relocations) of wolf movements to identify location clusters and visited all of these to locate kills. A major advantage in using the GPS cluster approach is that it does not rely on weather conditions and provides continuous monitoring that has the potential to detect a higher proportion of the kills (Merrill et al. 2010). On the other hand, the GPS cluster approach may not detect small prey due to their short handling times or to lack of finding evidence of a kill at a site (Jedrezejewski et al. 2002, Smith et al. 2004, Sand et al. 2005, Webb et al. 2008, Palacios and Mech 2011). If all wolf scats could be collected during the period when kill rates were monitored, they could be used to adjust for undetected kills because neonate hair can be identified in scats; however, finding all scats is problematic because only a proportion of the scats are typically collected. By supplementing searches for kills of radio-collared wolves with detailed analysis of scat, Jedrezjewski et al. (2002), identified up to 41% of wolf kills were detected only from scats, representing mostly small-bodied prey. Adopting the idea of Jedrezjewski et al. (2002), I combined the ratio of the relative number of neonates to the relative number of adults consumed, as determined in scat analyses (Mattioli et al. 2004), and used this scat-based ratio with the known number of adult kills from field visitations of wolf GPS clusters, to derive the total number of neonates killed per tracking session.

Applying these methods I tested the following 3 hypotheses: (1) Total kill rates of neonates peaked in mid-summer and this corresponded with an inverse change in adult kill rates. (2) The ratio of neonate to adult kills of small prey (deer) remained higher later into the summer than any of the large prey (i.e., elk, moose, feral horse) because they remained relatively more vulnerable for a longer period than other species. (3) As a result, biomass consumed by wolves (kg ungulate/metabolic-rate-adult equivalent kg wolf/day) remained constant across the summer despite the change in kill rates. Based on estimates of prey availability, I also assessed whether wolves were selecting for neonate prey or killed them more or less at random.

STUDY AREA

The study area is located on the central eastern slopes of the Rocky Mountains of Alberta (52^{o} 27’N, 115^{o} 45’W) and consists of 3434 km^2 that was delineated by the home ranges of four wolf packs (Fig. 3.1). Elevation ranges from 900 m in the eastern foothills to 3,600 m in the steep mountains in the western portion of the study area. Conifer forests dominate (45.7%) the landscape including large stands of lodge pole pine (*Pinus contorta*) and white spruce (*Picea glauca*) interspersed with mixed conifer-deciduous (10.3%) of aspen (*Populus tremulodies*), open grassland (13.9%), and clearcuts (5.2%). The high elevations in the western portion of the study area consist of subalpine meadows (9.4%), bare rock and permanent ice or snow (15.5%). Extensive forest harvesting and oil and gas development together with associated seismic exploration lines and roads occur throughout the majority of the provincial lands except for high elevation areas in the western mountainous region.

Historically, wolves along the eastern slopes of the Rocky Mountains of Alberta were subject to government sponsored bounties, government paid hunters and trappers, liberal hunting and trapping seasons, and intensive poisoning campaigns that resulted in a decline in wolf numbers during the 1900s to 1920s. Wolf recovery occurred during the late 1960s and the 1970s (Gunson 1992, Alberta Forestry Lands, and Wildlife 1991) with wolf density in this area estimated at 22.3 wolves/ 1000 km^2 in the foothills to 9.68 wolves/ 1000 km^2 in the mountainous west portion of the study area in 2004-2006 (Webb 2009). Currently wolves are managed as a furbearer and big-game animal on provincial lands. They are also subject to a 10-month hunting season August to May or June, depending on location and a 6-month trapping season (October - March) with no harvest quotas. Webb et al. (2011) reported annual harvest rates of wolves in this area of 0.34, which appeared sustainable because the harvest was comprised mostly (71%) of pre-reproductive aged wolves.

Major ungulate prey for wolves in this area includes elk, moose, white-tailed deer, mule deer and feral horses (which were present throughout the study area. Bighorn sheep (*Ovis canadensis*) were present only in isolated areas. Domestic livestock (primarily cattle) were available throughout the study period but limited to the Clearwater wolf pack's home range only. Other carnivores including bobcat (*Lynx rufus*), lynx (*L. canadensis*), cougar (puma concolor), coyote (*Canis latrans*), wolverine (*Gulo gulo*), black bear (*Ursus americanus*) and grizzly bear (*U. arctos*) were present as potential prey and/or competitors for wolves.

METHODS

I modeled the seasonal change in kill rates and biomass consumed of the major ungulate prey species of radio-collared wolves in 4 different packs. Kill rates were estimated in two steps. First, I used intensive monitoring of movements of GPS-collared wolves to find clusters of locations and visited the cluster sites to identify kill sites of adult ungulate prey. Second, because the cluster approach underestimates kills rates of neonate ungulate prey, I multiplied the species-specific ratio ($RNP_N : RNP_A$) of the relative number of neonates (RNP_N) to the relative number of adults (RNP_A) as determined from scat analysis by the number of adult kills to estimate kill rates of neonate prey. For all analyses I expressed kill rates on a per adult wolf basis, where adult wolves included all non-pups. Using species and age-specific kill rates, I then derived estimates for biomass consumed per metabolic-rate-adult equivalent kg wolf assuming a fixed body mass for adult prey and wolves, but a varying body mass for neonate prey and wolf pups to account for growth, differences in metabolic-rate of pups, and variable wolf pack sizes reflecting pack differences and decreased survival of pups over the summer. Ungulate prey was classified as adults (yearling and adult) or neonates for all analysis because we could distinguish only between adult and neonate hair in scats.

Capture and Monitoring of Wolves

Kill sites were estimated for one GPS-collared wolf continuously monitored in 2008 and 6 wolves alternately monitored in 3 packs in 2009 ($n = 4$ packs). Wolves were captured either with a modified foothold trap during the summer of 2008 or by helicopter netgunning during the winter of 2009 (University of Alberta Animal Care Protocols No. 411601). Captured wolves were physically restrained using a noose pole and/or ‘Y-stick’ and collared with remote-downloadable GPS collars (Lotek 4400S, Lotek Engineering, Newmarket, ON). GPS-collared wolves were relocated at 15-min intervals for a minimum of 14-days (mean tracking sessions = 16.0 days, SD = 2.63, *n* = 17) per month followed by 15 days of 2-hr interval locations. This facilitated the highest frequency of sampling wolf locations while still sampling each wolf in each month from May – August. Although monitoring periods longer than the 15 days of a tracking session may have reduced the influence of sampling error (Knopff et al. 2009), 15 days was a compromise between length of monitoring period and increasing the number of different wolf packs and months that could be monitored. Locations were downloaded at the end of each tracking session from the ground using a hand-held Lotek download unit. Successful fix rates across the 4 packs averaged 90% (range: 85-97%). Based on this fix success rate and sampling interval, data from Metz et al. (2011) indicate that even at my lowest fix success rate I would have located > 90% of small (adult deer) and 95% of large bodied (adult elk, moose and horse) prey items. Positional error was not evaluated in this study, but Hebblewhite et al. (2006) reported that in an adjacent area 95% of locations from Lotek 4400S collars fell within 114 m of the true position.

Kill Site Identification and Adult Ungulate Kill Rates

***Kill site identification**:* Kill sites were identified using GPS-movement clusters (Anderson and Lindzey 2003, Webb et al. 2008, Knopff et al. 2009) where a cluster along a movement path was defined as two, 15-min locations occurring within 200 m of each other. This definition resulted in a higher frequency of clusters that were examined for kills compared to other studies (i.e., Sand et al. 2008: two 30-min locations within 200 m; Metz et al. 2011: two 30-min locations within 100 m). All GPS-clusters were uploaded to hand-held GPS units and visited in the field 1-20 days (mean = 8.76, SE = 0.27) after the wolves were first located at the cluster. In addition, for each 2-week tracking session, 20 - 35% of all single points (*n* = 4126) were randomly selected and visited in the field, which resulted in locating 6 kills. Because all kills were neonates (2 elk and 4 deer) and I assumed all adult kills were identified with this intensive level of site visitation.

At each cluster a two-stage search strategy was used to find evidence of an ungulate kill. An intensive search by two persons was conducted within a 50-m radius of the centroid of each GPS location in a cluster. If nothing was located, a second search followed procedures described by Webb et al. (2008) where a search was conducted within a 200-m search radius from the geometric center of the cluster. A cluster was classified as a kill site where there was evidence of an animal being killed by a wolf, which included hide, bones, hair, and/or rumen, and the remains were estimated to be of an age that matched the date when wolves were at the kill site. The prey was assumed to have been killed by the wolf when tracks of appropriate freshness and/or only wolves tracks were presence (Peterson and Ciucci 2003, Sand et al. 2008, Webb et al. 2008), the carcasses was disarticulated and scattered rather than having been cached as resembling cougar or bear kill (Logan and Irwin, 1985, Elgmork, 1982), and the hide was not eaten, indicating a wolf kill.

I encountered non-wolf killed carcasses (moose = 4, deer = 8, elk = 2, horse = 1, cow = 1) that were believed to have died outside of the study period and/or there was evidence that the animal had been killed by something other than a wolf. On a per pack basis, non-wolf kills occurred in a ratio of non-kills: kills of 1: 9.5 (SD = 1.08). The most common examples were when the carcass remains indicated (1) a cougar kill based on bite marks, hemorrhaging on the neck, and caching ($n = 2$), (2) a hunter-killed animal based on bullet wounds or knife lacerations or unnatural location (i.e. parking lot) of carcass ($n = 3$), or (3) if a carcass' age greatly preceded the date the wolf spent at the cluster ($n = 13$). These carcasses were not included in the estimation of kill rates. In all but 3 of these 16 cases, it also was assumed that carcasses provided minimal biomass because of the state of decomposition of the carcasses (only dried skeletal bones and hair remained), and thus, were not included in estimates of biomass consumption. In 3 cases the kills were fresh and wolves spent (> 12 hrs) at the carcass I included these into biomass consumed rates.

Prey remains at the kill site were identified to species and sex by anatomical, skeletal, and pelage characteristics (Stelfox 1993). I assigned prey to two age classes: neonate or adult (≥1 yr) based on size of bone /skull remains, degree of epiphysis fusion of bone remains, and tooth eruption and wear (Stelfox 1993). All kills of adult prey were identified to species; however, in cases where the sex of the prey killed could not be identified (44%), kills were recorded as ‘adult unknown’. I also recorded neonate kills when found, and used clumps of short hair to confirm species identification where necessary. I assigned a date to a confirmed wolf kill based on the date of the first GPS location at the kill site.

Adult kill rates: Kill rates of each adult ungulate prey (number prey/collared wolf/day) species were estimated by locating kills along the movement path of a GPS-collared wolf and dividing the number by the number of days in a tracking session. However, a single collared wolf may not indicate the average kills per individual/pack due to low pack cohesion in summer (Metz et al. 2011). Therefore, I adjusted kill rates for pack cohesion based on pack attendance at kill sites following Metz et al. (2011). I first estimated wolf attendance at kill sites using data from this study when there were two GPS-collared wolves in each of the 4 packs. Due to one dispersal and 3 collar failures, the number of kills made while both collars were functioning was small: 14 small prey and 7 large prey killed. Following the approach of Metz et al. (2011), I calculated the probability of detecting a kill for a pack as 71% for small prey (<130 kg) and 86% for large prey (≥130 kg). This was similar to the probability of detecting 73% for small (<130 kg) and 93% large (≥ 130 kg) prey in Yellowstone during summer. Because of the general similarity, I applied the correction of Metz et al. (2011) due to their larger sample size to derive adjusted numbers of adults killed and used these estimates to calculate kill rates of adults KR_A (ungulates/wolf/day).

Scat Analysis and Neonate Kill Rates

I estimated the number of neonates killed of each ungulate prey species in each tracking session in 4 steps. First, I collected fresh wolf scats during a tracking session and identified the proportion of neonates and adults in the scat based on hair analysis. Second, I determined the equivalent total scats of neonate and adult prey in the scat following a modified version of the approach presented by Mattioli et al. (2004), and converted these to prey biomass consumed following Weaver (1993). Third, I converted the biomass consumed to relative number of adult (RNP_A) or neonate (RNP_N) prey consumed using fixed adult and variable by date neonates body masses of prey following Mattioli et al. (2004). Finally, I calculated the RNP_N :RNP_A ratio of prey consumed from scats and multiplied it by the number of known adult prey killed (K_A) identified from cohesion-adjusted GPS located kills to derive the number neonate kill (K_N).

Scat collection and analysis: During each tracking session, fresh wolf scats were collected along GPS-movement paths (n = 79), dens (n = 74), rendezvous sites (n = 40), kill sites (n = 67) and non-kill cluster sites (n = 86). Floyd et al. (1979) found wolves defecated 8-56 hrs after consumption of prey; thus, given 76% of my kills had handling times < 8 hrs, I assumed scat collected at kill sites would not be related to that kill. Because 24% of the handling times of kills extended this period and as a precaution, scat collection was limited to 2 scats at all kill sites. Freshness of scats was based on color, consistency and dryness in relation to the site (sunny or shaded) and previous weather conditions (Kennedy and Carbyn 1981, Jedrezejewski et al. 2002). By collecting fresh scat in close proximity to wolf GPS locations, it aided not only in assigning approximate dates, but also reduced possible confusion with scats from sympatric canid species such as coyotes and red foxes (Latham 2009). Scats < 25 mm in diameter were excluded because of potential misidentification with coyotes (Reed et al. 2004). Samples were placed in labeled plastic bags indicating location and date stored at -20° C until scat analysis.

Prior to analysis in the lab, scat samples were autoclaved (121^{O}C for 60 min), washed in a 0.5-mm sieve, and dried for 24 hours under a flume (Reynolds and Aebischer 1991). Twenty hairs per scat sample were randomly selected for identification and identified as to species and age (neonate or adult) using published hair identification keys for adult ungulates (Adorjan and Kolenosky 1969, Moore et al. 1974, Kennedy and Carbyn 1981, De Marinis et al. 2006, Mattioli et al. 2004), and an additional reference collection of hairs from neonate ungulates as part of this study (Jones et al. 2009). The reference hairs were collected at monthly intervals from captive, new born animals at the Calgary Zoo, Calgary Alberta, Northwest Trek Wildlife Park, Washington and Yukon Wildlife Preserve, Yukon, in order to account for changes in hair structure over time. Data from white-tailed deer and mule deer were pooled due to the difficulty in distinguishing between species (Moore et al. 1974). Two trained analysts were given blind tests with 30 scat samples (Ciucci et al. 1996, Mech and Boitani 2003, Mattioli et al. 2004) and had accuracy levels of $\geq$ 95%. Because this study focused on ungulate prey, all other non-ungulate prey (e.g. *Sciuridae*, *Leporidae, Mustelidae* and *Castoridae)* were pooled into a group called 'Other' that accounted for < 5% of hairs identified.

To estimate prey biomass consumed based on scats I used the equation provided by Weaver (1993). This required the delineation of the number of scats of each prey species. Because some scats (54%) contained more than one prey category (species and age), I used the general approach of Mattioli et al. (2004) to obtain the equivalent total number of scats per prey category. I used the relative number of identified hairs rather than the relative volume because it was not possible to identify scat contents without microscopic analysis of individual hairs.

In a test with 100 scats where I determined composition based on complete volumetric analysis of separated contents and 20 randomly selected hairs, I found no difference in relative amounts of the 4 ungulate prey in scats (species: $F_{1,3}$= 0.54, $P = 0.74$). Assuming the 20 randomly selected hairs/scat represented the scat content, I summed the total number of hairs per prey category and divided by the number of hairs identified per scat ($n = 20$) to calculate an equivalent number of scats of each prey category required, similar to Mattioli et al. (2004) for volumetric content.

Prey biomass and relative number consumed from scats: Using the data on equivalent number of scats per prey category, I estimated the biomass of neonate and adult prey consumed for each prey species per tracking session using the regression equation of Weaver (1993):

$$y = 0.439 + 0.008x \qquad \text{Eq 1}$$

that converts body mass of prey (kg) (x) to mass of prey (kg) (y) consumed per collectable scat. For adults, I used constant seasonal mean yearling/adult weights to calculate biomass per collectable scat. For neonates of a species, I used variable weights across tracking seasons to account for seasonal growth (Table 2.1). For each prey category, I then multiplied y by the equivalent number of scats containing that species category to estimate the total biomass consumed (Table 2.2-2.5). To derive the relative number of neonate ($RNP_{N_{ij}}$) and adult ($RNP_{A_{ij}}$) prey killed in each species-age class (i) per tracking session (j), I divided the consumable scat biomass by the assigned weight of that class (Table 2.1). This value is relative because I did not collect all the scats of wolves during the each tracking session.

Number of neonate prey consumed: I assumed the scats collected were unbiased as to kills of adults and neonates and derived the species-specific ratio (RNP_N:RNP_A) of relative number of neonates killed per adult killed per tracking session. To estimate the number of neonates killed, I multiplied this ratio by K_A identified from cohesion adjusted GPS clusters to obtain the number of neonates killed (K_N).

Although uncommon, three situations occurred where the necessary data were missing and it became problematic to calculate RNP_N:RNP_A or K_N for a tracking session. (1) When an adult species was identified in the scat but not found by GPS located kills, I assumed the adult hair was due to an undetected scavenge event with a handling time too short to create a GPS cluster. In these cases I excluded scats containing adult hair from the analysis. (2) When an adult species was found at a GPS cluster, but not in the scat, I assumed adults could have been killed because we did not collect all scats. In this case I used the mean RNP_N:RNP_A from tracking sessions where it was possible and used this value to estimate $K_{N_{ij}}$. To test the accuracy of both approaches I compared the neonate estimates from tracking sessions where both calculations were possible and found no difference in the estimated K_{Nij} (paired $t_{11} = -0.549$, $P = 0.59$). (3) When I found adult hair but no neonate hair in the scat, I assumed no neonates were killed.

Species-specific and Total Kill Rates

Species-specific kill rates (prey killed/wolf/day) were the sum of KR_A and KR_N. Total kill rate (KR_T) was the sum of kill rates across species (total prey killed/adult wolf/day). I used these values to assess my hypotheses. Standard deviations (SD) reported for kill rates across packs was based on a ratio estimator (Hebblewhite et al. 2003) which is considered to be more accurate than the inter-kill method (Hebblewhite et al. 2003, Cooley et al. 2008).

To evaluate changes in KR_N, KR_A and KR_T over the season, I first tested for differences between months using an ANOVA using all 17 tracking sessions and blocking by pack. I used Bonferoni post-hoc comparisons to determine which months differed ($\alpha = 0.10$). Because I hypothesized KR_N would peak and then decline while KR_A would show the opposite pattern, I compared a linear, asymptotic and quadratic model fit to seasonal changes in these kill rates. The model with the most support was selected using Akaike's Information Criterion corrected for low sample size (AIC_c, Burnham and Anderson 2002). I also accessed the differences in the average species-specific ratios of neonate to adult kills (K_N:K_A) by month to evaluate whether timings of neonate kills were consistent with my hypothesis that neonates of small prey comprised a higher proportion of the kills made by wolves later in the season than large prey. For all statistical analysis I used STATA SE 10.0 (StataCorp, College Station, TX).

Prey Biomass Consumed

Daily ungulate biomass consumed during a tracking session (BCR_j, kg ungulate/metabolic-rate-adult-equivalents kg /day) was calculated as:

$$BCR_j = \frac{\sum K_{Aij} B_{Ai} K_{Nij} B_{Nij}}{\sum W_A B_A + W_W B_W + W_{Pj} (B_{Pj}{}^{3/4} / B_L{}^{3/4})} / D \qquad \text{Eq 2}$$

where K_A and K_N for prey species i during tracking a session j are corrected kill rates as defined above; B_{Ai} is the constant mass (kg) of the adult prey of species i derived from the literature (Table 2.1) and B_{Nij} is the variable mass of neonate prey of species i during tracking session j derived from growth curves (Table 2.1): W_A and B_A are static number and mass (kg) of adult alpha wolves: W_W and B_W is the static number and mass of non-alpha adults and yearlings; W_{Pj} is the varying number of pups per tracking session based on counts of pups at den sites and assuming an average monthly survival rate during summer of 0.70 (Webb and Merrill 2011); B_{Pj} is the varying mass of a pups in tracking session j predicted from growth curves derived using data from the study area (Appendix I) and scaled to metabolic adult equivalents following Metz et al. (2011); and D is number of days of monitoring in a tracking season.

In the above equation I assumed wolves consumed only a portion of the biomass of prey killed during a tracking session: 65% of the mass of large-bodied (> 100 kg, adult moose, elk, horse), 75% of medium-bodied (20-100 kg, adult deer or neonate elk, moose, horse), and 90% of small-bodied prey (< 20 kg, neonate deer) (Glowacinski and Profus 1997, Hayes et al. 2000, Jedrzejewski et al. 2002, Sand et al. 2008).

Number of adult and yearling wolves in a pack was based on counts during either wolf captures (spring only), aerial telemetry flights, observations of wolf packs and/or tracks throughout the summer, which together typically provided observations at least once per month. Although counts varied, after excluding cases where subsequent counts were higher, pack counts supported stable pack sizes. Pack sizes were one pack of 3 adults and 3 packs of 6 adult wolves. I did not incorporate adult mortality because Webb (2009) found 95% of wolf mortalities occurred during the fall and winter hunting and trapping season. On the other hand he reported emigration rates of ~11% in May to August, which I assumed were offset largely by immigration. Average weights of adult alpha female and male wolves were determined for this study area (40.8 ± 4.80 kg, n = 6 from this study, 12 from Webb 2008), as was the weight of the remaining adults and yearlings (33.0 ± 5.5 kg, n = 7 from this study, 26 from Webb 2008).

For pups, I assumed from the literature a mean summer survival rate of 0.7, and therefore, I evaluated a range of survival rates (0.5, 0.7 and 0.9) and found these did not alter my conclusions. I present these results in Appendix II. I adjusted the average mass of pups during a tracking session based on the following growth curve derived from data collected during den site visits and from wolves trapped throughout the summer (Appendix I):

$$y = 22.91 / (1 + \exp(-(x-74.70) / 25.36)) \qquad \text{Eq 3}$$

where y is neonate mass (kg) and x is days since birth (27 April, Mech, 1970, pers. commun., Nathan Webb). Estimates from this model closely resembled estimates from a number of other studies (Appendix I). I then adjusted the cumulative weight of neonates to metabolic rate adult wolf equivalents (Metz et al. 2011) to express on prey consumption on an adult wolf basis.

To test the hypothesis whether wolf BCR_j remained constant across the summer months, I first used an ANOVA blocking by pack to test for monthly differences (May-August) and Bonferoni post-hoc comparisons to determine in which months biomass consumed differed ($\alpha = 0.10$). To evaluate variation of biomass consumption of adults ($BCRj_A$) and neonates (BCR_{jN}) across summer I compared a linear, asymptotic, exponential and quadratic model fit to seasonal changes in these rates. The model with the most support was selected using Akaike's Information Criterion corrected for low sample size (AIC_c, Burnham and Anderson 2002).

Neonate Prey Selection

To assess whether wolves were likely to select for neonate prey, I compared the proportions of neonates killed by wolves to an estimate of the proportion of neonates in the population post-birth pulse (Husseman et al. 2003, Knopff et al. 2009). To estimate the species-specific proportion of neonates in the population, I followed the approach of Knopff et al. (2009). For each of the 4 ungulate species, I assumed 80% were female, species-specific fecundity rates were 2.0, 1.0, 1.3 and 0.8 neonates/adult for deer, elk, moose and horse, respectively (Selfox 1993). I also assumed that mortality rate was similar and constant across the summer.

RESULTS

Wolves were monitored for a total of 267 wolf days (67 days/wolf, SD = 11.5, *n* = 4) in 17 tracking sessions between 20 April to 26 August that averaged

16 days /session (SD = 2.63, range: 9-20). Summer wolf pack sizes including pups averaged 10.35 SD = 2.17 (range: 7-13) and excluding pups averaged 5.25 SD = 1.50 (range: 3-6).

Scat Analysis

A total of 364 wolf scats were collected from 15 May to 26 August 2008 and 20 April to 17 August 2009 within the home ranges of the wolf packs monitored in those years.

***Prey composition of scats*:** Scat composition based on mean frequency of hairs across packs indicated deer occurred $\geq$3x greater in scats than the other species with adults (48%) and neonates (52%) comprising about the same proportion of the hair (Table 2.3 -2.5).

***Ratio of neonates to adults in scats*:** The ratio of RNP_N:RNP_A differed across species ($F_{2,33} = 6.65$, $P = 0.003$) with deer (5.46, SE =1.25) over 3 times higher ($P = 0.03$) than elk (1.42, 0.36), and moose ($P = 0.007$) (1.33, 0.57). Elk and moose did not differ. Feral horses represented < 3% of scats and because the difference between adult horse and neonate hair was indistinguishable ratios were not calculated for horse.

Kill Composition and Rates

Based on over 15,500 clusters inspected among the 4 packs over 267 wolf days, I found a total of 55 adult kills (deer 78%, elk 9%, moose 11%, horse 2%) and 77 neonate kills (75% deer, 9% elk, 13% moose, 3% horse). After adjusting each tracking session for undetected neonates based on the RNP_N:RNP_A , and $K_{A,}$

the total number of neonates killed was 224 (deer 82%, elk 10%, moose 7%, feral horse 1%).

Total kill rates (KR_T) averaged across all 4 packs in summer was 1.07 ungulates/pack/day (SD = 0.16, range: 0.34 - 1.77). This equated to 0.21 ungulates/adult wolf/day (SE =0.06, range: 0.06 - 0.38) or 0.18 ungulates/ metabolic-rate-adult equivalent wolf/day (SD =0.08, range: 0.05 - 0.36). Kill rates of neonates (0.17/adult wolf/day, SD = 0.06) was almost three times higher than adults (0.05, SD = 0.02, paired $t_{16} = -3.80$, $P < 0.01$).

Total adjusted kill rate (KR_T) differed among months *(*$F_{3,13} = 3.48$, $P = 0.04$), but this was attributed only to differences between June and August *(*$P = 0.04$ (Fig. 2.4*).* Total kill rates of both adults (KR_A) and neonates (KR_N) differed among months (KR_A: $F_{3,13} = 5.83$, $P = 0.01$; KR_N:$F_{3,13} = 5.33$, $P = 0.01$). KR_A was higher in May than in June through August ($P < 0.05$), while KR_N was higher in June than in May ($P = 0.05$) and August ($P = 0.011$) but not July.

The model explaining the most variation in the change in KR_N and KR_A across the summer was quadratic and explained ~50% of the variation (Table 2.6, Fig. 2.1). KR_N peaked in early July and declined rapidly in late July early August, whereas in KR_A there was a reverse trend with kill rates declining in May and remaining low through June and July with a slight increase in August. The ratio of K_N:K_A for elk was higher earlier in the season than the other species, while K_N:K_A was higher for deer late in the season (Fig. 2.2).

Prey Biomass Consumed

Total prey biomass consumed ($BCR_{T},$ kg/ metabolic-rate equivalent adult kg/day) averaged 0.15 (SD = 0.02, range: 0.08 - 0.30) across packs or 5.20 kg/adult equivalent wolf/day (SD = 0.94, range: 2.96 - 10.90). Prey biomass consumed across packs averaged 52 ±32% (range 17-94%) deer, 25±21% (range 5-40%) moose, 19±14% (range 2-36%) elk, and 4±7% (range 0-15%) horse. Adult prey 70% (range: 52%- 78%) comprised 2 times the biomass of neonate prey 30% (range: 22-48%), (0.14, SE = 0.007 vs. 0.04, SE = 0.02, paired t_{16} = 3.94, $P < 0.001$). BCR_A ($F_{3,13} = 8.28$, $P = 0.002$) and BCR_N ($F_{3,13} = 5.07$, P = 0.015) both differed across summer months and although BCR_A decreased from May to July ($P = 0.003$) and August ($P = 0.003$, BCR_N increased between May to June ($P = 0.067$) and July ($P = 0.021$) (Fig. 2.4). BCR_T across summer months differed ($F_{3,13} = 4.04$, $P = 0.031$) with BCR_T decreasing between May and July (P = 0.073) and August ($P = 0.066$).

Change in biomass consumption of neonate prey over summer was best described by a quadratic equation (Table 2.7, Fig. 2.3). Biomass consumption rates of adults was equally well described by the exponential and quadratic models, performing equally well ($\Delta_i AIC_c < 4$), although the exponential model had a higher r^2.

Wolf Selection for Neonates

In June through August, wolves selected for neonate prey of each species. Based on overlap in the confidence limits, wolves did not select for neonates of any species more or less than any other species: elk: 1.71, CI 1.37 – 2.04; moose:

1.41, CI 0.90 – 1.91; and deer: 1.27, CI 1.08-1.45. Selection for horse (1.92 CI 0.001-3.25), was high, but the sample size was small (*n* = 2 neonates, 1 adult) and may not provide a reliable estimate

DISCUSSION

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I found summer kill rates of ungulate prey were at the high end of those reported in the few studies that have attempted to quantify wolf kill rates for summer. Specifically, average kill rates in this study (0.18 prey/adult equivalent wolf/day, SD 0.08) were about 2.5 times higher than in Yellowstone NP (0.07 prey/adult equivalent wolf /day, SE 0.011, Metz et al. *in prep.*) where elk are the primary ungulate prey species and comprise >85% of the ungulate kills in summer. Summer kill rates reported by Metz et al. (*in prep.*) and those reported here were both adjusted for pack attendance. I used the probability of pack attendance (PA) at a kill in summer reported by Metz et al. (*in prep.*) because they had a larger sample of collared wolves for deriving PA. Given the differences in abundance and body size of the primary prey of wolves in this study (deer) compared to in YNP (elk), pack cohesion might be expected to be lower. This was not supported for small prey in this study compared to YNP (0.71% vs. 0.73%), but for large prey (0.86% vs. 0.93%), respectively. However, if I had used PA values derived on my large size prey, the kill rates I report would have been even higher.

In contrast to this study, Metz et al. (*in prep.*) did not correct for neonates that may have been missed. In this study, I included 5 neonate kills that were found at 15min single points relocations, a total of 24% (n = 16) of neonate kills were located with GPS, had handling time of ≤ 30 min. Metz et al. (*in prep.*) searched 30% of all single, 30min relocations in 2008 and located 9 neonate kills, which could reflect as much as ~27 neonates or 19% of GPS located neonate kills that season. Assuming an equal number of kills across years and packs this would result in an increase in summer kill rates of ~ 31% to 0.1 ungulate/adult equivalent wolf/day, which is still lower than in this system. However, Metz et al. (*in prep.*) argued against incorporating these kills because they believed that they did not appear to provide significant biomass and were likely scavenge events due to the limited time (30min) spent at the site.

In Scandinavia where moose are the primary ungulate prey, Sand et al. (2008) identified 8% of moose kills at single relocations (30 min) indicating that wolves were able to kill and consume/carry off prey in ≤30 min and they included these kills in their kill rates as in this study. Sand et al. (2008) included pups in kill rates calculations reporting higher summer kill rates (0.19 prey/wolf/day) than this study (0.10 prey/wolf/day) if we also included pups, but their rates also included non-ungulate species (25.6% of kills). Assuming an equal proportion of ungulates kills across packs this equates to ~0.15 ungulates/wolf/day, a rate that still appears higher than the 0.10 ungulates/wolf/day in this study. Considerably smaller pack sizes (5.0 SD 2.9, range: 1-9) in Scandinavia compared to this system (10.3 SD 2.17, range: 7-13) is likely to be one reason for higher mean per wolf kill rates in Scandinavia. When comparing adult (mean = 2.8, SD = 0.70) kill rates excluding the three non-reproductive packs from Sands et al. (2008) study, kill rates were lower (0.16 ungulate/adult wolf/day, SD=0.06) than adult (mean = 5.2, SD = 1.5) kill rates in our study (0.21 ungulate/adult wolf/day, SD=0.06).

In a multi-prey system in Poland, Jedrezejewski et al. (2002), who incorporated scat analysis to correct for missed small prey when wolf kill rates were determined with VHF tracking, also reported lower summer ungulate kill rates (0.51 prey/pack/day or ~0.12 ungulate/wolf/day) compared to this study (1.08 ungulates/pack/day or 0.21 ungulate/adult wolf/day). His kill rates were based on hunting pack sizes of 4.4 wolves, which was similar to our adult wolf estimates (5.25 SD 1.50). Kill rates in this study were about 43% higher than rates of Jedrezejewski et al. (2002) even though ~ 41% of all kills were estimated through scat analysis in both studies. Kill rates reported by Jedrezejewski et al. (2002) may be lower because they were based on VHF telemetry, which is likely to miss more kill clusters than GPS-based data simply due to sampling frequency (Webb et al. 2008). Also, where two or more prey of the same species and age were killed and consumed by wolves in short succession, they were counted as only one prey if recovered from scat alone. This may have resulted in underestimates of the true number of prey killed (Jedrezejewski et al. 2002). In contrast, in using the RNP_N: RNP_A ratio and GPS located adult kills my method was less likely to produce underestimates.

Kill rates in this study are likely to be more reliable for several reasons. First, the time between the occurrence of GPS-clusters in the field and a search at the site was 7.16 days (SE = 0.27, range: 1-16 days), which was short compared to other summer studies (i.e., Metz et al. 2011: 15.6 days SE 0.4, Sand et al.

2008: 8.3 day, range: 1 -53 days, 90% percentiles: 2-24 days). This may be more important for estimating neonate kills than adults, because visible disturbances of the sites made during killing and consumption of prey are critical to finding neonate remains. Nevertheless, even for adults the potential for scavenging of prey remains increases over time, reducing kill site evidence. Second, by using 15-min GPS locations I sampled wolf movements more intensively (identifying 15,512 clusters) compared to other studies (i.e., Metz et al. 2011: two 30-min locations within 100 m, 1848 clusters; Sand et al. 2008: two 30-min locations within 200 m, 12,000 clusters).

Finally, in using scat-based estimates of kill rates of neonates, number of neonate kills increased by ~3 times over what I observed in the field. However, two types of errors may inflate kill rates using this approach: misidentification of hairs in scat analysis and wolf scavenging. Because I compiled a reference collection of neonate hairs at monthly intervals from captive, new born animals from three sources and trained individuals in hair identification that resulted in accuracy levels were $\geq$ 95% in blind tests every 3 weeks, I minimized misclassification. Finally, although I did not include known scavenging events in estimating adult kill rates, kill rate estimates were based on the assumption that the content of a scat found reflected prey killed by wolves rather than scavenged prey. Scavenging by wolves in summer is likely minimal because other predators like bears (Mathews and Porter 1988, Franzmann et al. 1980, Kunkel and Mech 1994) and cougars (Knopff et al. 2009) also kill predominately juvenile prey with low biomass and short handling times that are unlikely to provide scavenging potential for wolves. Even if scavenging occurred, I would have expected it to lower the RNP_J: RNP_A ratio, reducing the number of neonates killed.

Instead, high kill rates in this study likely reflected a switch by wolves during the prey reproductive period to small-bodied neonate deer where wolves compensate by killing a greater number of individuals to obtain the same amount of biomass as in systems where elk or moose are most available (Sand et al. 2008, Metz et al. 2011). This shift from a focus on adult prey in early May to neonates in June corresponded to an expected sudden increase in the availability of vulnerable neonates that peaked in early July, which likely represents the most vulnerable period for neonates (Nelson and Woolf 1987). Subsequent reduction in kill rates in August may have resulted from a combination of reduced availability of neonates due to mortality and increased neonate mobility and wariness. Metz et al. (2011) also reported a decline in the proportion of neonate in later summer but did not report neonate kill rates directly. In Scandinavia moose neonates were killed consistently throughout the summer, which may result from the relative difficulty of small packs to successfully kill adult moose (Sand et al. 2008, Huggard 1993).

My results also support that wolves selected for neonates of most prey species over adults during early summer, which is consistent with an increase in neonate prey in summer in a number of studies of wolf diet (Barja 2009, Fuller 1989, Peterson et al. 1984). In my estimate of neonate availability I assumed 80% of all ungulates in western-central Alberta were reproductive females (Knopff et al. 2010) and that proportion of neonates was constant across summer months.

Although these resulted in rough estimates, both assumptions would have resulted in overestimates of the true proportion of neonates in the ungulate population and therefore decreased any magnitude of selection of neonates. I found no difference in the relative selection of neonates among species across the summer, indicating young of all species were vulnerable (Ballard et al 1987, Kunkel and Pletscher 1999, Nelson and Mech 1986, Barber- Meyer et al. 2008). But there was some evidence that neonates of elk may have been relatively more detectable than deer early in the post-partum 'hiding phase', while neonate deer remained relatively more vulnerable later into the summer (Huggard 1993, Nelson and Woolf 1987). Additionally, high parental defense in moose may explain why neonate selection amongst moose was lower than other species (Huggard 1993, Mech and Peterson 2003).

Total biomass consumed in summer in this study is similar to that reported for wolves in summer in a moose-dominated system in Scandinavia moose (Sand et al. 2008: 0.16 kg/ wolf kg/ day) and to an elk-dominated system in Yellowstone (Metz. et al. 2011: ~5.7kg/adult equivalent wolf/day and remained above minimum requirements (0.09 kg/kg wolf/day, Peterson and Ciucci, 2003). Although wolves were able to exceed their energetic requirements, contrary to my prediction biomass consumption rates declined over the summer, even when I excluded data from May, which more closely represented winter predation conditions. I predicted that wolves would adjust their kill rates in order to maintain biomass requirements similar to that reported for wolves in Scandinavia (Sand et al. 2008). Two possible explanations exist for these differences between

North American studies and Scandinavia. First, it appears that wolves in Scandinavia have relatively easy access to prey: moose densities are high in Scandinavian ($1.1/km^2$) (Eriksen et al. 2009); cow moose in Scandinavia have been found to not have adapted anti- predatory behavior such as defense and habitat use (Sand et al. 2005, 2006). Therefore wolves are easily able to kill moose throughout the year thus maintaining consistent biomass consumption rates. In contrast Yellowstone's elk populations have altered their behavior and spatial distribution since the reintroduction of wolves (Launder et al. 2001, Mao et al. 2005, Kauffman et al. 2007).

Obtaining large sample sizes in large carnivore research is often difficult due their often low density, wide ranging movements, and logistical difficulties associated with capture, maintaining collars, and monitoring them (Sunquist and Sunquist 1997). Due to the intensity required to locate kills and collect scats in summer in this study it was not logistically possible to increase the sample size. Results of my study may limit my conclusions to this study area. However, the seasonal dynamics of kill rates and biomass consumption rates were consistent among packs with all packs neonates kill rates peaking and adults' rates dipping in middle summer as hypothesized. Likewise the decline in biomass consumption over the summer was consistent tend between all packs.

Conclusions

Estimating kill rates in summer remains problematic due to the short handling time of neonate ungulates, pack cohesion, and finding prey remains in the field. Kill rates especially in deer-dominated systems are likely to be underestimated from GPS cluster methods unless ancillary data from scats are used. I found neonates comprised as much as >90% of the kills at the peak of the summer. My data also support reduced pack cohesion in summer, but the social hunting behavior of wolves remains poorly quantified and requires additional research particularly in multi-prey systems.

In summer wolves appear to select for neonate prey compared to adults, which results in a high kill rate. This is likely due to the vulnerability of their relatively small body-size relative to adults (citations- from above). The impact of high kill rates on neonates on prey populations remains unclear, but it is likely to have less an effect on populations than the killing of adults because juveniles have a higher probability of dying than adults during their first year due to many causes (Barber-Meyer et al. 2008, Carstensen et al. 2006, Nelson and Mech 1986). Nonetheless, in multi-prey systems, relative body-size differences and maternal behavior among ungulate prey may play an important role in how predators structure populations. Compared to elk, moose and deer do not form as large social groups, predisposing them to wolf attacks (Huggard 1993). While moose may be formidable prey, the small body size of deer provides less ability to defend against predation. This was consistent with the high summer kill rates of neonate deer compared to larger prey in summer in other ecosystems (Sand et al. 2008, Metz et al. *in prep.*).

In central west Alberta where elk and moose densities are low (Webb 2009), if wolves had relied only on deer, the most abundant ungulate prey, they would have consumed lower biomass of prey (0.75 kg/kg/wolf) than reported for winter from other deer-dominated systems (e.g. Mech 1977; 0.1 kg/kg wolf/day, Fritts and Mech 1981; 0.09 kg/kg wolf/day), and biomass consumed would have been below the minimum energetic requirements. As such without the availability of alternative prey species wolf prey consumption may have been limiting wolves in meeting their energetic requirements. Whether wolves could have increased their kill rate of deer sufficiently in this area to meet their energetic demands in summer is unknown, but by also killing additional large prey, the wolf biomass consumption in this area exceeded their energetic requirements. The presence of an abundant, multi-species prey base likely maintains the average to high pup reproduction (5.6 ±1.4) across packs to off-set the high harvest rates of wolves reported by Webb et al. (2011: 0.34) in this area, resulting in moderate wolf densities (13.31 wolves/1000km^2) even under this high harvest rate (Webb et al. 2011).

LITERATURE CITED

Adorjan, A.S., and G.B. Kolenosky. 1969. A manual for the identification of hairs of selected Ontario mammals. Ontario Department of Lands and Forests Research Report (Wildlife) No. 90, Ontario, Canada. 63 pp.

Alberta Forestry, Lands, and Wildlife. 1991. Management plan for wolves in Alberta. Wildlife Management Planning Series No. 4. 89 pp.

Anderson, C., and F. Lindzey. 2003. Estimating cougar predation rates from GPS location clusters. Journal of Wildlife Management 67:307-316.

Ballard, W., L. Ayres, P. Krausman, D. Reed, and S. Fancy. 1997. Ecology of wolves in relation to a migratory caribou herd in northwest Alaska. Wildlife Monographs :5-47.

Ballard, W., T. Spraker, and K. Taylor. 1981. Causes of neonatal moose calf mortality in south central Alaska. Journal of Wildlife Management 45:335-342.

Barber-Meyer, S.M., L.D. Mech, and P.J. White. 2008. Elk calf survival and mortality following wolf restoration to Yellowstone National Park. Wildlife Monographs :1-30.

Barja, I. 2009. Prey and prey-age preference by the siberian wolf (*Canis lupus signatus)* in a multiple-prey ecosystem. Wildlife Biology 15:147-154.

Bender, L. C., L. A. Lomas, and J. Browning. 2007. Condition, survival, and cause-specific mortality of adult female mule deer in north-central New Mexico. Journal of Wildlife Management 71:1118-1124.

Burnham, K.P., and D.R. Anderson. 2002. Model selection and multimodel inference: A practical information-theoretic approach. Springer-Verlag, New York, New York, USA.

Carstensen, M., G.D. DelGuidice, B.A. Sampson. 2009. Survival birth characteristics and cause-specific mortality of white-tailed deer neonates. Journal of Wildlife Management. 73:175-183.

Cooley, H.S., H.S. Robinson, R.B. Wielgus, and C. S. Lambert. 2008. Cougar prey selection in a white-tailed deer and mule deer community. Journal of Wildlife Management 72:99-106.

Ciucci, P., L. Boitani, E.R. Pelliccioni, M. Rocco, and I. Guy. 1996. A comparison of scat-analysis methods to asses the diet of the wolf (*Canis lupus)*. Wildlife Biology 2:37–48.

DeMarinis, A.M., A, Asprea. 2006. Hair identification key of wild and domestic ungulates from southern Europe. Wildlife Biology. 12:305-320.

Elgmork, K. 1982. Caching behavior of brown bears (*Ursus arctos*). Journal of Mammalogy 63:607-612.

Eriksen, A., P. Wabakken, B. Zimmermann. 2009. Encountered frequencies between GPS-collared wolves (*Canis lupus*) and moose (*Alces alces*) in a Scandinavian wolf territory. Ecological Research. 24:547-557.

Floyd, T., L. Mech, and M. Nelson. 1979. Improved method of censusing deer in deciduous-coniferous forests. Journal of Wildlife Management 43:258-261.

Frair, J.L., E.H. Merrill, J.R. Allen, and M.S. Boyce. 2007. Know thy enemy: Experience affects elk translocation success in risky landscapes. Journal of Wildlife Management 71:541-554.

Franzmann, A.W., C.C. Schwartz, and R.O. Peterson. 1980. Moose calf mortality in summer on the Kenai Peninsula, Alaska. Journal of Wildlife Management 44:764-768.

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

Glowacinski, Z., and P. Profus. 1997. Potential impact of wolves (*Canis lupu)* on prey populations in eastern Poland. Biological Conservation 80:99-106.

Gunson, J. 1992. Historical and present management of wolves in Alberta. Wildlife Society Bulletin 20:330-339.

Hayes, R., A. Baer, U. Wotschikowsky, and A. Harestad. 2000. Kill rate by wolves on moose in the Yukon. Canadian Journal of Zoology-Revue Canadienne De Zoologie 78:49-59.

Hebblewhite, M. 2000. Wolf-elk predator prey dynamics in Banff National Park. Msc. thesis, University of Alberta.

Hebblewhite, M.,P. Paquet, D. Pletscher, R. Lessard, and C. Callaghan. 2003. Development and application of a ratio estimator to estimate wolf kill rates and variance in a multiple-prey system. Wildlife Society Bulletin 31:933-946.

Hebblewhite, M., E.H. Merrill, L.E. Morgantini, C. A. White, J. R. Allen, E. Bruns, L. Thurston, and T. E. Hurd. 2006. Is the migratory behavior of montane elk herds in peril? the case of Alberta's Ya Ha Tinda elk herd. Wildlife Society Bulletin 34:1280-1294.

Huggard, D. J. 1993. Prey selectivity of wolves in Banff national-park .2. age, sex, and condition of elk. Canadian Journal of Zoology-Revue Canadienne De Zoologie 71:140-147.

Husseman, J.S., D.L. Murray, G. Power, C. Mack, C.R. Wenger, and H. Quigley. 2003. Assessing differential prey selection patterns between two sympatric large carnivores. Oikos 101:591-601.

Jedrzejewski, W., K. Schmidt, J. Theuerkauf, B. Jedrzejewska, N. Selva, K. Zub, and L. Szymura. 2002. Kill rates and predation by wolves on ungulate populations in bialowieza primeval forest (Poland) RID B-6823-2009. Ecology 83:1341-1356.

Jones, C., and D. Jackson. 2009. A first record of latrine use by european hedgehogs (*Erinaceus europaeus)* (linnaeus, 1758). Mammalia 73:145-147.

Kauffman, M.J., N. Varley, D.W. Smith. 2007. Landscape heterogeneity shapes predation in a newly restored predator-prey system. Ecology Letters. 10:690:700.

Kennedy, A.J., and L.N. Carbyn. 1981. Identification of wolf prey using hair and feather remains with special reference to western Canadian national parks. Canadian Wildlife Service, Edmonton, Alberta, Canada.

Knopff, K.H., A.A. Knopff, and M.S. Boyce. 2010. Scavenging makes cougars susceptible to snaring at wolf bait stations. Journal of Wildlife Management 74:644-653.

Knopff, K.H., A.A. Knopff, M.B. Warren, and M.S. Boyce. 2009. Evaluating global positioning system telemetry techniques for estimating cougar predation parameters. Journal of Wildlife Management 73:586-597.

Kunkel, K.E., T.K. Ruth, D.H. Pletscher, and M.G. Hornocker. 1999. Winter prey selection by wolves and cougars in and near Glacier National Park, Montana. Journal of Wildlife Management 63:901–910.

Kunkel, K., and D. Pletscher. 2001. Winter hunting patterns of wolves in and near Glacier National Park, Montana. Journal of Wildlife Management 65:520-530.

Kunkel, K., and L. Mech. 1994. Wolf and bear predation on white-tailed deer fawns in northeastern Minnesota. Canadian Journal of Zoology-Revue Canadienne De Zoologie 72:1557-1565.

Latham, A. 2009. Wolf ecology and caribou primary prey-wolf spatial relationships in low productivity petland complexes in north-eastern Alberta. Ph.D. University of Alberta.

Laundre, J.W., L. Hernandez, K.B. Altendorf. 2001. Wolves, elk, and bison: reestablishing the “landscape of fear” in Yellowstone National Park, USA. Canadian Journal of Zoology- Revue Canadienne De Zoologie. 79:1401-1409

Logan, K., And L. Irwin. 1985. Mountain lion habitats in the big horn mountains, Wyoming. Wildlife Society Bulletin 13:257-262.

Mech, L.D. 1966. The wolves of Isle Royale. US National Park Service Fauna Service, no.7. U.S. Government Printing Office.

Mech, L.D. 1974. The Current Techniques in Studying elusive wilderness carnivores. Trans. Int. Congr. Game Biol. 11:315-22.

Mech, L.D., and L. Boitani. 2003. Wolf social ecology. Pp. 1-34 in Wolves: behavior, ecology, and conservation (L.D. Mech, and L. Boitani, eds.). The University of Chicago Press, Chicago, Illinois, USA.

Mao, J., M. Boyce, D. Smith, F. Singer, D. Vales, J. Vore, and E. Merrill. 2005. Habitat selection by elk before and after wolf reintroduction in Yellowstone national park. Journal of Wildlife Management 69:1691-1707.

Mathews, N.E., and W.F. Porter. 1988. Black bear predation of white-tailed deer neonates in the central Adirondacks. Canadian Journal of Zoology-Revue Canadienne De Zoologie 66:1241-1242.

Mattioli, L., C. Capitani, E. Avanzinelli, I. Bertelli, A. Gazzola, and M. Apollonio. 2004. Predation by wolves (*Canis lupus*) on roe deer (*Capreolus capreolus*) in north-eastern Apennine, Italy. Journal of Zoology 264:249-258.

Mech, L. 1966. Hunting behavior of timber wolves in Minnesota. Journal of Mammalogy 47:347-&.

Mech, L.D. 1974. New profile for wolf. Natural History 83:26-31.

Mech, L.D. 1977. Wolf-pack buffer zones as prey reservoirs. Science 198(4314): 320-321.

Mech, L.D., and R.O. Peterson. 2003. Wolf-prey relations. L. D. Mech, and L. Boitani, editors. .

Merrill, E., H. Sand, B. Zimmermann, H. McPhee, N. Webb, M. Hebblewhite, P. Wabakken, and J. L. Frair. 2010. Building a mechanistic understanding of predation with GPS-based movement data. Philosophical Transactions of the Royal Society B-Biological Sciences 365:2279-2288.

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

Messier, F., and M. Crete. 1985. Moose-wolf dynamics and the natural regulation of moose populations. Oecologia 65:503-512.

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:e17332.

Metz, M.C., J.A. Vucetich, D.W. Smith, D.R. Stahler, and R.O. Peterson. 2011. Seasonal patterns of predation for grey wolves in the multi-prey system of Yellowstone National Park. (*in prep*).

Moore, T.D., L.E. Spence, and C.E. Dugnolle. 1974. Identification of the dorsal guard hairs of some mammals of Wyoming. Wyoming Game and Fish Department, Bulletin no. 14.

Nelson, M., and L. Mech. 1986. Relationship between snow depth and gray wolf predation on white-tailed deer. Journal of Wildlife Management 50:471-474.

Nelson, T. A., and A. Woolf. 1987. Mortality of white-tailed deer fawns in southern Illinois. Journal of Wildlife Management 51:326-329.

Webb, S.L., M.R. Dzialak, J.J. Wondzell, S.M. Harju, L.D. Hayden-Wing, and J.B. Winstead. 2011. Survival and cause-specific mortality of female rocky mountain elk exposed to human activity. Population Ecology 53:483-493.

Palacios, V., and L.D. Mech. 2011. Problems with studying wolf predation on small prey in summer via global positioning system collars. European Journal of Wildlife Research 57:149-156.

Peterson, R.O., and P. Ciucci. 2003. The wolf as a carnivore. Pp. 104-130 in Wolves: behavior, ecology, and conservation (L.D. Mech, and L. Boitani, eds.). The University of Chicago Press, Chicago, Illinois, USA.

Peterson, R., J. Woolington, and T. Bailey. 1984. Wolves of the Kenai peninsula, Alaska. Journal of Wildlife Management :1-52.

Reed, J.,R. Baker, W. Ballard, and B. Kelly. 2004. Differentiating Mexican gray wolf and coyote seats using DNA analysis. Wildlife Society Bulletin 32:685-692.

Reynolds, J., and N. Aebischer. 1991. Comparison and quantification of carnivore diet by fecal analysis - a critique, with recommendations, based on a study of the fox (*Vulpes-vulpes)*. Mammal Review 21:97-122.

Sand, H., B. Zimmermann, P. Wabakken, H. Andren, and H. Pedersen. 2005. Using GPS technology and GIS cluster analyses to estimate kill rates in wolf-ungulate ecosystems. Wildlife Society Bulletin 33:914-925.

Sand, H., P. Wabakken, B. Zimmermann, O. Johansson, H. C. Pedersen, and O. Liberg. 2008. Summer kill rates and predation pattern in a wolf-moose system: Can we rely on winter estimates? Oecologia 156:53-64.

Sand, H., C. Wikenros, P. Wabakken, and O. Liberg. 2006. Effects of hunting group size, snow depth and age on the success of wolves hunting moose. Animal Behaviour 72:781-789.

Seal, U., and L. Mech. 1983. Blood indicators of seasonal metabolic patterns in captive adult gray wolves. Journal of Wildlife Management 47:704-715.

Smith, D., T. Drummer, K. Murphy, D. Guernsey, and S. Evans. 2004. Winter prey selection and estimation of wolf kill rates in Yellowstone national park, 1995-2000. Journal of Wildlife Management 68:153-166.

Stahler, D., D. Smith, and D. Guernsey. 2006. Foraging and feeding ecology of the gray wolf *(Canis lupus*): Lessons from Yellowstone national park, Wyoming, USA. Journal of Nutrition 136:1923S-1926S.

Stelfox B. J., editor. 1993. Hoofed Mammals of Alberta. Lone Pine Publishing, Edmonton, Alberta, Canada.

Tambling, C. J., E. Z. Cameron, J. T. Du Toit, and W. M. Getz. 2010. Methods for locating African lion kills using global positioning system movement data. Journal of Wildlife Management 74:549-556.

Testa, J., E. Becker, and G. Lee. 2000. Temporal patterns in the survival of twin and single moose (*Alces alces*) calves in south-central Alaska. Journal of Mammalogy 81:162-168.

Weaver, J. 1993. Refining the equation for interpreting prey occurrence in gray wolf scats. Journal of Wildlife Management 57:534-538.

Webb, N. F., M. Hebblewhite, and E. H. Merrill. 2008. Statistical methods for identifying wolf kill sites using global positioning system locations. Journal of Wildlife Management 72:798-807.

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

Webb, S.L., M.R. Dzialak, J.J. Wondzell, S.M. Harju, L. D. Hayden-Wing, and J. B. Winstead. 2011. Survival and cause-specific mortality of female rocky mountain elk exposed to human activity. Population Ecology 53:483-493.

White, P., and R. Garrott. 2005. Yellowstone's ungulates after wolves - expectations, realizations, and predictions. Biological Conservation 125:141-152.

Zimmermann, B., P. Wabakken, H. Sand, H.C. Pedersen, and O. Liberg. 2007. Wolf movement patterns: A key to estimation of kill rate? Journal of Wildlife Management 71:1177-1182.

Table 2.1. Ungulate and wolf masses (kg) used in converting scats to relative mass of prey and in estimating prey biomass consumed (kg ungulate/ kg wolf/day) of wolves in west central Alberta, Canada. Masses of prey reported as edible mass (kg) assuming wolves consumed 65% of prey mass >100kg, 75% of prey 20-100kg, and 90% of prey <20kg: (Hayes et al. 2000, Jedrzejewski et al. 2002, Sand et al. 2008). Mean birth dates of species: deer and elk - 1 June (Kunkel and Mech 1994, Carstensen et al. 2006, Barber- Meyer et al. 2008); moose - 26 May (Tesst 2002, Feldhamer 2003); horse - 21 May (Coleman 2010) and wolf - 1 May.

	Species				
	Deer	Elk	Moose	Horse	Wolf
Adult male	71[a]	208[a]	286[a]	273[b]	45[d]
Adult female	52[a]	150[a]	272[a]	273[b]	36[d]
Yearling	41[f]	117[f]	214[f]	213[f]	--
Unknown	55[c]	158[c]	257[c]	253[c]	33[e]
<u>Neonate</u>					
15 Aug – 31 Aug	15[f]	49[f]	83[f]	80[f]	18[g]
31 July – 14 Aug	13[f]	38[f]	71[f]	70[f]	15[g]
15 July – 30 July	11[f]	34[f]	62[f]	60[f]	12[g]
30 June – 14 July	9[f]	24[f]	47[f]	45[f]	8[g]
15 June – 29 June	5[f]	17[f]	39[f]	38[f]	6[g]
31 May – 14 June	3[f]	11[f]	26[f]	25[f]	4[g]
15 May – 30 May	--	--	14[f]	14[f]	3[g]
1 May – 14 May	--	--	--	--	1.5[g]

[a] Lancia and Hodgdon (1984); Renecker and Hudson (1993); Bubenik (1998).

[b] Adult estimate from Salter and Hudson (1982); neonate mass assumed to be similar to domestic horse (Coleman 2010). Government of Alberta.

[c] Mean adult/yearling mass used in estimates of biomass consumed where differences in sexes or between yearlings and adults could not be determined. Also live weight equivalents were used for non-neonates in scat analysis.

[d] Mean summer wolf mass obtained from weights of wolves at time of capture during this study (females=5, males = 3 males) and from packs in a previous study within the same area (Webb 2008: female = 8, male = 5).

[e] Mean mass of adults and yearlings of both sexes in this study (n= 21) that was used for all non-pup pack members excluding alpha pair.

[f] Neonate mass predicted from mean mass estimate of Stelfox (1993): daily growth of deer: 0.21, elk: 0.85 and moose 1.01 kg/day) and horse estimates of 1.01 kg/day (Coleman 2010) and von Bertalanffy growth curve: $M(t) = A[1 - 1/3e^{-K(t-I)}]^3$, where $M(t)$ = mass (kg) at age t, A = maximum mass of either adult male or adult female, $K = 0.0049$, and $I = 80$ days. Estimate reported reflects mean mass at midpoint of each 15-day period.

[g] Derived from: $y = 22.91 / (1 + \exp(-(x-74.70)/ 25.36))$, (n= 13, $r^2 = 0.96$) where y is body mass and x is number of days since birth, 1 May (Mech 1970, Nathan Webb unpublished data).

Table 2.2. Mean proportion and standard deviation (SD) in each prey category of 20 hairs from wolf scats (n=364) collected in summer within and across home ranges of 4 wolf packs in west-central Alberta in 2008-2009. Scats were assigned to a tracking session of which the mid-date is shown

		Blackstone					Clearwater				Jock lake			Kootenay Plains					
		27 Apr	11 May	29 Jun	17 Jul	10 Aug	26 May	13 Jun	24 Jul	7 Aug	26 May	12 Jun	25 Jul	22 May	21 Jun	21 Jul	11-Aug	22-Aug	Mean
Deer																			
Adult	Mean	0.56	0.39	0.06	0.13	0.19	0.30	0.18	0.09	0.21	0.30	0.23	0.14	0.70	0.40	0.4	0.48	0.32	0.30
	SD	0.43	0.45	0.17	0.34	0.36	0.44	0.39	0.30	0.37	0.46	0.41	0.32	0.37	0.47	0.4	0.45	0.43	0.17
Neonate	Mean	0.00	0.06	0.57	0.71	0.30	0.16	0.24	0.32	0.15	0.17	0.22	0.63	0.06	0.49	0.6	0.35	0.20	0.31
	SD	0.00	0.24	0.45	0.44	0.45	0.37	0.42	0.45	0.34	0.35	0.41	0.44	0.22	0.50	0.4	0.46	0.41	0.22
Elk																			
Adult	Mean	0.23	0.24	0.05	0.00	0.08	0.00	0.06	0.18	0.00	0.18	0.21	0.00	0.05	0.00	0.0	0.00	0.00	0.08
	SD	0.42	0.42	0.22	0.00	0.24	0.00	0.24	0.40	0.00	0.37	0.39	0.00	0.20	0.00	0.0	0.00	0.00	0.09
Neonate	Mean	0.00	0.00	0.00	0.08	0.14	0.00	0.14	0.13	0.05	0.18	0.13	0.10	0.00	0.03	0.0	0.00	0.00	0.06
	SD	0.00	0.00	0.00	0.27	0.36	0.00	0.34	0.30	0.21	0.38	0.32	0.30	0.00	0.18	0.0	0.00	0.00	0.07
Moose																			
Adult	Mean	0.06	0.09	0.08	0.00	0.16	0.25	0.13	0.09	0.14	0.00	0.04	0.00	0.00	0.03	0.0	0.00	0.00	0.06
	SD	0.21	0.29	0.26	0.00	0.36	0.42	0.33	0.30	0.33	0.00	0.21	0.00	0.00	0.16	0.0	0.98	0.00	0.07
Neonate	Mean	0.00	0.03	0.14	0.00	0.00	0.00	0.00	0.09	0.08	0.00	0.00	0.00	0.00	0.00	0.0	0.00	0.39	0.04
	SD	0.00	0.18	0.33	0.00	0.00	0.00	0.00	0.30	0.23	0.00	0.00	0.00	0.00	0.00	0.0	0.00	0.50	0.10
Horse	Mean	0.00	0.03	0.00	0.00	0.00	0.17	0.09	0.00	0.15	0.08	0.00	0.05	0.00	0.00	0.0	0.00	0.00	0.03
	SD	0.00	0.14	0.00	0.00	0.00	0.38	0.27	0.20	0.35	0.25	0.00	0.20	0.00	0.00	0.0	0.00	0.00	0.06
Other[a]	Mean	0.06	0.05	0.11	0.05	0.04	0.01	0.053	0.039	0.03	0.09	0.05	0.08	0.06	0.05	0.0	0.07	0.06	0.04
	SD	0.214	0.31	0.211	0.214	0.20	0.213	0.12	0.15	0.36	0.219	0.29	0.127	0.19	0.018	0.0	0.31	0.12	0.06
Total		28	28	36	35	27	28	33	11	20	30	22	27	29	29	27	28	15	

[a] Other includes prey such as beaver (0.8%), snow shoe hair (0.9%) squirrel (1.3 %) and unknown (1%)

Table 2.3.Deer biomass (kg) consumed by 4 packs based on scats, and estimated number of neonates killed (K_N)/tracking session. Biomass estimates (derived from scats) of adult (SB_A) and neonate deer (SB_N) were dividing by estimated prey weights (Table 2.1) to obtain a relative number of adults (RNP_A) and neonates (RNP_N). The estimated number of neonates killed through scat analysis (K_N) were calculated as the product of GPS located adult kills (K_{AU}) adjusting for kill attendance (93% large, 73% for small bodied prey Metz et al. 2011) (KA), and the ratio of the relative number of neonates: adult ($RNP_{N:}RNP_A$). Total number of adult (K_A) and neonate killed (K_N) were converted to adult (B_A) and neonate biomass (B_N) using edible biomass weights of prey (Table 2.1). The proportion of neonate prey killed (P_{NK}) and proportion of neonate biomass (P_{NB}) is also reported, as is the number of neonate kills located using GPS (K_{NUGPS}). Wolf scats (n=364) were collected during the same tracking periods (n=17) that GPS-collared wolves were monitored in west-central Alberta in 2008 and 2009

	Blackstone				Clearwater					Jock lake				Kootenay Plains			
	27 Apr	11 May	29 Jun	17 Jul	10 Aug	26 May	13 Jun	24 Jul	7 Aug	26 May	12 Jun	25 Jul	22 May	21 Jun	21 Jul	11 Aug	22 Aug
SB_A	17.1	12.28	6.54	5.12	5.54	9.19	6.14	1.02	4.66	9.91	5.52	4.6	23.07	19.13	11.46	18.53	4.91
SB_N	0	0.91	10.88	19.1	5.33	2.27	3.93	1.97	2	2.48	2.49	9.97	0.84	7.17	9.26	6.74	1.98
RNP_A	0.24	0.17	0.09	0.08	0.08	0.13	0.09	0.01	0.06	0.25	0.08	0.09	0.32	0.31	0.19	0.25	0.07
RNP_N	0	0.25	1.62	1.18	0.23	0.62	0.82	0.1	0.1	0.6	0.43	0.6	0.23	1.07	0.6	0.32	0.07
RNP_N: RNP_A	0	1.49	18.09	14.75	2.85	4.76	9.11	10	1.66	2.4	5.37	6.66	0.71	3.45	3.15	1.28	1.00
K_{NUGPS}	0	0	11	14	2	1	1	3	2	0	3	9.1	0	6	2	4	1
K_N	0	9.59	24.66	20.2	3.93	13.06	20.55	4.11	2.74	9.86	7.35	8.5	4.91	23.64	17.31	8.76	2.74
K_{AU}	7	4	1	1	1	2	0	0	0	3	1	2	5	5	4	5	2
K_A	9.59	6.85	1.37	1.37	1.37	2.74	0	0	0	4.11	1.37	1.37	6.85	6.85	5.48	6.85	2.74
B_A	525	375	75	75	75	150	0	0	0	225	75	75	375	375	300	375	150
B_N	0	30	85	159	52	42	73	32	25	46	32	130	13	148	192	126	42
P_{KN}	0	0.58	0.95	0.93	0.75	0.83	1	1	1	0.71	0.83	0.86	0.41	0.77	0.76	0.55	0.5
P_{BN}	0	0.07	0.53	0.68	0.41	0.22	1	1	1	0.17	0.3	0.63	0.03	0.28	0.39	0.25	0.22
P_{BN}	0	0.07	0.53	0.68	0.41	0.22	1	1	1	0.17	0.3	0.63	0.03	0.28	0.39	0.25	0.22

Table 2.4. Elk biomass (kg) consumed by 4 packs based on scats, and estimated number of neonates killed (K_N)/tracking session. Biomass estimates (derived from scats) of adult (SB_A) and neonate deer (SB_N) were dividing by estimated prey weights (Table 2.1) to obtain a relative number of adults (RNP_A) and neonates (RNP_N). The estimated number of neonates killed through scat analysis (K_N) were calculated as the product of GPS located adult kills (K_{AU}) adjusting for kill attendance (93% large, 73% for small bodied prey Metz et al. 2011) (KA) and the ratio of the relative number of neonates: adult ($RNP_{N:}RNP_A$). Total number of adult (K_A) and neonate killed (K_N) were converted to adult (B_A) and neonate biomass (B_N) using edible biomass weights of prey (Table 2.1). The proportion of neonate prey killed (P_{NK}) and proportion of neonate biomass (P_{NB}) is also reported, as is the number of neonate kills located using GPS (K_{NUGPS}). Wolf scats (n=364) were collected during the same tracking periods (n=17) that GPS-collared wolves were monitored in west-central Alberta in 2008 and 2009. N/A indicates it was not possible to calculate RNP_N :RNP_A because no adult hair was found in scat; where no RNP_N :RNP_A, K_N was calculated using the mean ratio of all other tracking sessions

	Blackstone					Clearwater				Jock lake			Kootenay Plains				
	27 Apr	11 May	29 Jun	17 Jul	10 Aug	26 May	13 Jun	24 Jul	7 Aug	26 May	12 Jun	25 Jul	22 May	21 Jun	21 Jul	11 Aug	22 Aug
SB_A	16.44	17.99	4.77	0	5.18	0	8.69	4.77	0	13.94	11.68	0	3.81	0	0	0	0
SB_N	0	0	0	2.4	4.22	0	3.01	1.19	0.98	3.26	1.79	2.41	0	0.64	0	0	0
RNP_A	0.07	0.07	0.02	0	0.03	0	0.36	0.02	0	0.06	0.05	0	0.02	0	0	0	0
RNP_N	0	0	0	0.05	0.07	0	0.12	0.02	0.01	0.2	0.11	0.05	0	0.03	0	0	0
RNP_N :RNP_A	0	0	0	N/A	2.33	N/A	3.33	1.00	N/A	3.33	2.2	N/A	0	N/A	N/A	N/A	N/A
K_{NUGPS}	0	0	0	1	2	0	0	0	0	1	2	1	0	0	0	0	0
K_N	0	0	0	2.52	2.52	0	3.6	1.08	0	3.6	4.11	2.74	0	1.37	0	0	0
K_{AU}	0	0	0	1	1	0	1	1	0	1	0	0	0	0	0	0	0
K_A	0	0	0	1.08	1.08	0	1.08	1.08	0	1.08	0	0	0	0	0	0	0
B_A	0	0	0	170	170	0	170	170	0	170	0	0	0	0	0	0	0
B_N	0	0	0	103	103	0	77	46	0	44	61	111	0	27	0	0	0
P_{KN}	0	0	0	0.70	0.70	0	0.77	0.5	0	0.77	1	1	0	1	0	0	0
P_{BN}	0	0	0	0.38	0.38	0	0.31	0.21	0	0.21	1	1	0	1	0	0	0

Table 2.5. Moose biomass (kg) consumed by 4 packs based on scats, and estimated number of neonates killed (K_N)/tracking session. Biomass estimates (derived from scats) of adult (SB_A) and neonate deer (SB_N) were dividing by estimated prey weights (Table 2.1) to obtain a relative number of adults (RNP_A) and neonates (RNP_N). The estimated number of neonates killed through scat analysis (K_N) were calculated as the product of GPS located adult kills (K_{AU}) adjusting for kill attendance (93% large, 73% for small bodied prey Metz et al. 2011) (KA) and the ratio of the relative number of neonates: adult ($RNP_{N:}RNP_A$). Total number of adult (K_A) and neonate killed (K_N) were converted to adult (B_A) and neonate biomass (B_N) using edible biomass weights of prey (Table 2.1). The proportion of neonate prey killed (P_{NK}) and proportion of neonate biomass (P_{NB}) is also reported, as is the number of neonate kills located using GPS (K_{NUGPS}). Wolf scats (n=364) were collected during the same tracking periods (n=17) that GPS-collared wolves were monitored in west-central Alberta in 2008 and 2009. N/A indicates it was not possible to calculate RNP_N :RNP_A because no adult hair was found in scat; where no RNP_N :RNP_A, K_N was calculated using the mean ratio of all other tracking sessions

	Blackstone					Clearwater				Jock lake			Kootenay Plains				
Date	27 Apr	11 May	29 Jun	17 Jul	10 Aug	26 May	13 Jun	24 Jul	7 Aug	26 May	12 Jun	25 Jul	22 May	21 Jun	21 Jul	11 Aug	22 Aug
SB_A	5.95	10.46	0	0.00	15.87	26.83	0	0	11	0	4.32	0	0	0	0	0	0
SB_N	0	0	4.33	0	0	8.23	3.47	1.19	2.39	0	0.65	0	0	0	0	0	3.1
RNP_A	0.02	0.03	0	0.00	0.04	0.07	0	0	0.03	0	0.01	0	0	0	0	0	0
RNP_N	0	0	0.09	0	0	0.07	0.07	0.01	0.03	0	0.02	0	0	0	0	0	0.07
RNP_N:RNP_A	0	0	N/A	N/A	N/A	1.00	N/A	N/A	1.00	N/A	2.00	N/A	N/A	N/A	N/A	N/A	N/A
K_{NUGPS}	0	0	3	0	0	0	1	2	1	1	1	0	0	0	0	0	1
K_N	0	0	3.81	0	0	1.37	1.37	2.74	1.37	1.37	2.74	0	0	0	0	0	1.37
K_{AU}	2	1	0	0	1	1	0	0	1	0	1	0	0	0	0	0	0
K_A	2.15	1.08	0	0	1.08	1.08	0	0	1.08	0	1.08	0	0	0	0	0	0
B_A	554	277	0	0	277	554	0	0	277	0	277	0	0	0	0	0	0
B_N	0	0	196	0	0	16	57	124	84	16	114	0	0	0	0	0	95
P_{KN}	0	0	1	0	0	0.55	1	1	0.56	1	0.71	0	0	0	0	0	1
P_{BN}	0	0	1	0	0	0.028	1	1	0.23	1	0.29	0	0	0	0	0	1

Table 2.6. Models predicting neonate (KR_N) and adult (KR_A) kill rates (ungulates killed/adult wolf /day) as a function of Julian date (x) showing the coefficient of determination (r^2), the small sample size corrected Akaike Information Criterion (AICc) value, AICc differences (Δ_i,) from the best model and Akaike weight (W_i) for each model.

Model Structure	Model type	r^2	AICc	Δ_i	W_i
Neonate					
$KR_N = ax^2 + bx + c$	Quadratic	0.44	-43.52	0.00	>0.99
$KR_N = ax/(b+x)$	Hyperbola	0.00	-32.31	11.20	<0.01
$KR_N = ax + b$	Linear	0.01	-30.91	12.61	<0.01
Adult					
$KR_A = ax^2 + bx + c$	Quadratic	0.59	-83.50	0.00	0.75
$KR_A = ae(-bx)$	Exponential	0.55	-81.10	2.39	0.23
$KR_A = ax + b$	Linear	0.48	-76.78	6.71	<0.05

Table 2.7. Models predicting neonate (BCR_N) and adult (BCR_A) biomass consumption rates (Kg ungulate/ metabolic-rate-adult equivalent kg wolf/day) as a function of Julian date (x) showing the r^2, the small sample size corrected Akaike Information Criterion (AICc) value, AICc differences Δ_i, and Akaike weight (W_i) for each model.

Model Structure	Model Type	r^2	AICc	Δ_i	W_i
Neonate					
$BCR_N = ax^2 + bx + c$	Quadratic	0.28	-77.56	0.00	0.48
$BCR_N = ax + b$	Linear	0.25	-77.61	4.57	0.49
$BCR_N = ax/(b+x)$	Hyperbola	0.22	-71.22	4.89	0.02
Adult					
$BCR_A = ae(-bx)$	Exponential	0.87	-49.04	0	0.55
$BCR_A = ax^2 + bx + c$	Quadratic	0.54	-47.55	1.48	0.26
$BCR_A = ax + b$	Linear	0.54	-46.89	2.14	0.18

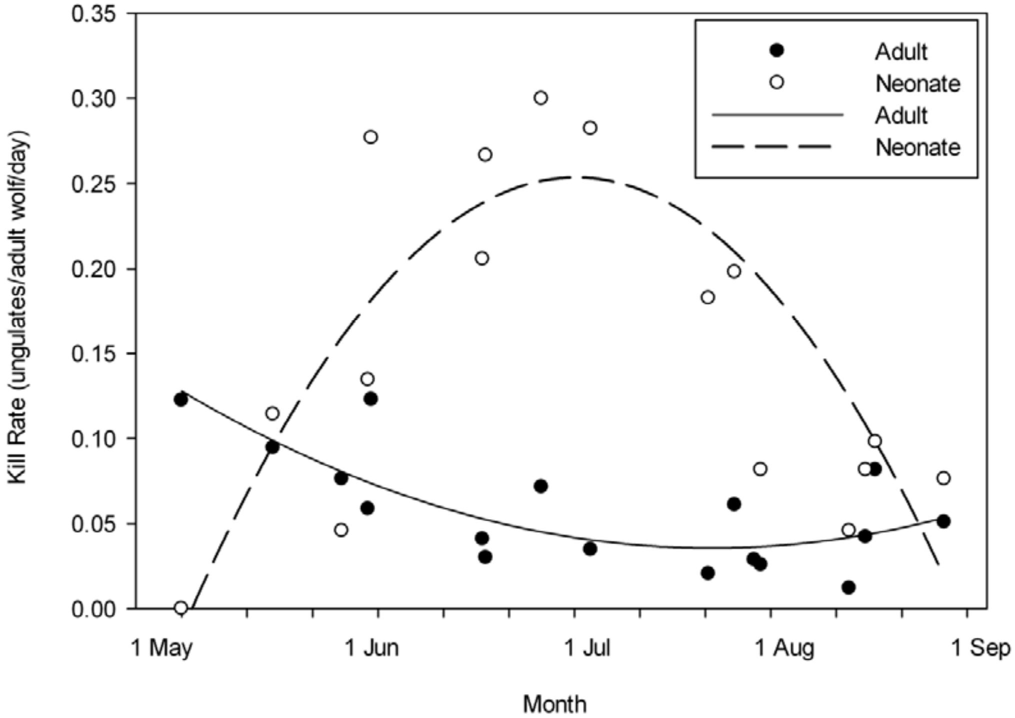


Figure 2.1. Relationship between neonate and adult kill rates (ungulate killed/adult wolf /day) time during the summer for 4 wolf packs in west-central Alberta, Canada. Kill rates were determined for 17 tracking sessions (mean length 15 days, SD= 2.63). Neonate kill rate: $Y = -0.00007x^2 + 0.0094x - 0.0679$, $r^2 = 0.44$; Adult kill rate: $Y = 0.0000143x^2 - 0.0025x + 0.1444$, $r^2 = 0.59$

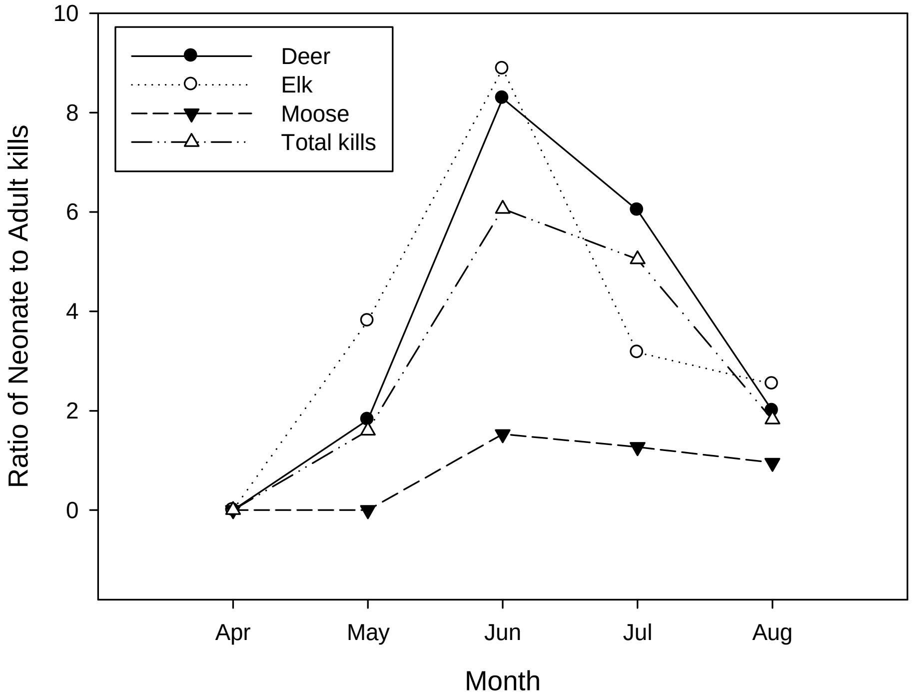


Figure 2.2. Mean ratio of neonates killed per adult killed by 4 wolves during summer by prey species and for total ungulate kills in west-central Alberta, Canada. Graph based on data presented in Tables 2.3 - 2.5. Horse is not included because sample size of horse neonate kills was too small (*n* = 2).

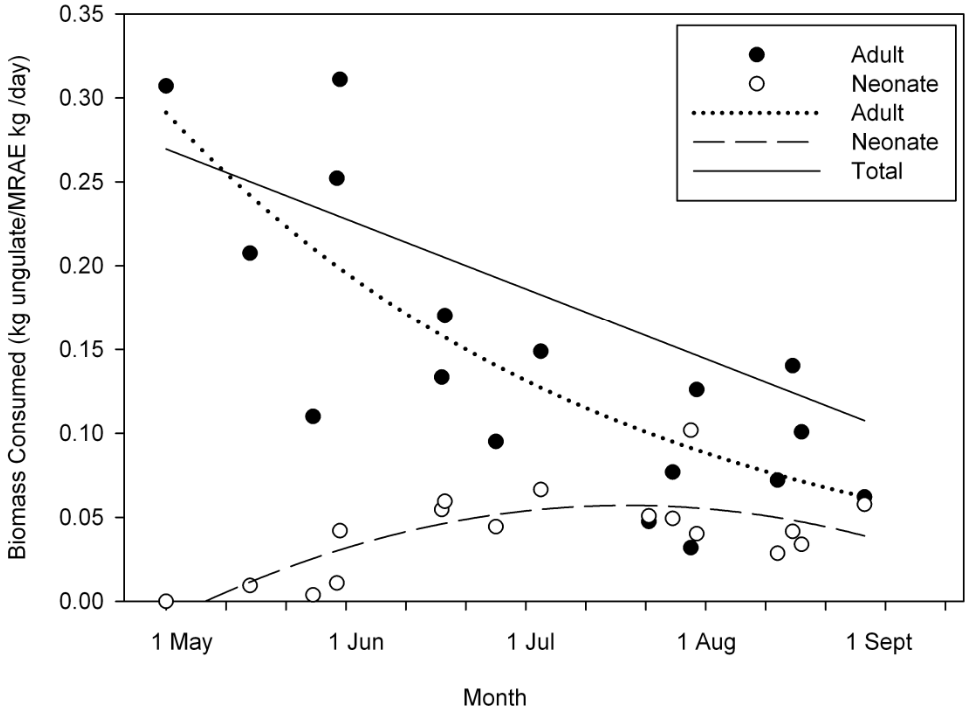


Figure 2.3. Relationship between neonate and adult biomass consumed (kg ungulate killed or scavenged/kg wolf/ day) and time during the summer for 4 wolf pack in west-central Alberta, Canada. Biomass consumed was determined for 17 tracking sessions (mean length 15 days, SD 2.63) and reflects edible biomass consumed. Prey weights and wolf weights were adjusted for growth of both neonate prey and wolf pup development. Neonate: $Y=0.000012x^2+0.002x-0.026$ $r^2= 0.28$; adult: $Y=0.320\exp(-0.013x.)$, $r^2= 0.87$, where x = Julian day. Total biomass consumption rate is also shown. $Y=0.0279+-0.001x$, $r^2=0.46$

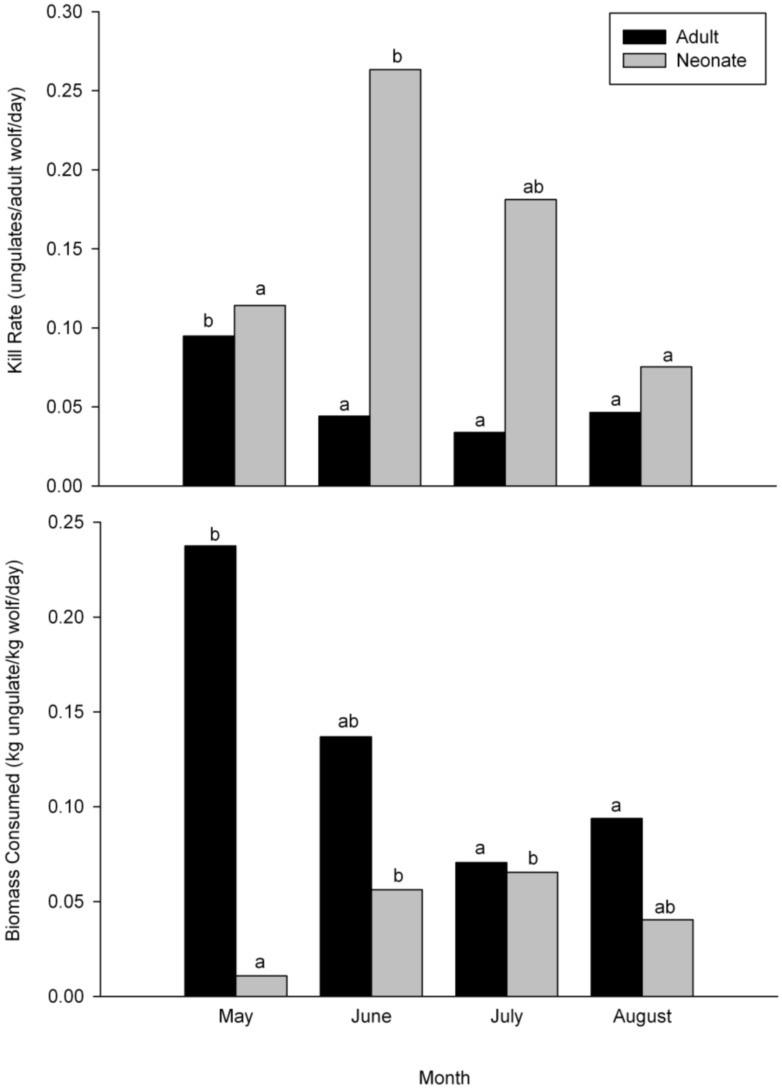


Figure 2.4. Monthly mean kill rate (number of ungulates/pack/day) and biomass consumed (kg ungulate/kg wolf/day) of neonate and adults for 4 wolf packs in summer 2008 and 2009 in west central Alberta, Canada. Kill rates of adults and neonate significantly differed among months ($F_{3,13} = 5.83$., $P = 0.01$; $F_{3,13} = 5.33$, $P = 0.01$, respectively). Monthly mean biomass consumed for adult and neonate prey also differed significantly ($F_{3,13} = 8.28$, $P < 0.01$ and $F_{3,13} = 5.07$, $P = 0.01$ respectively). Different letters indicate significant differences between months within age classes using Bonferroni post hoc analysis

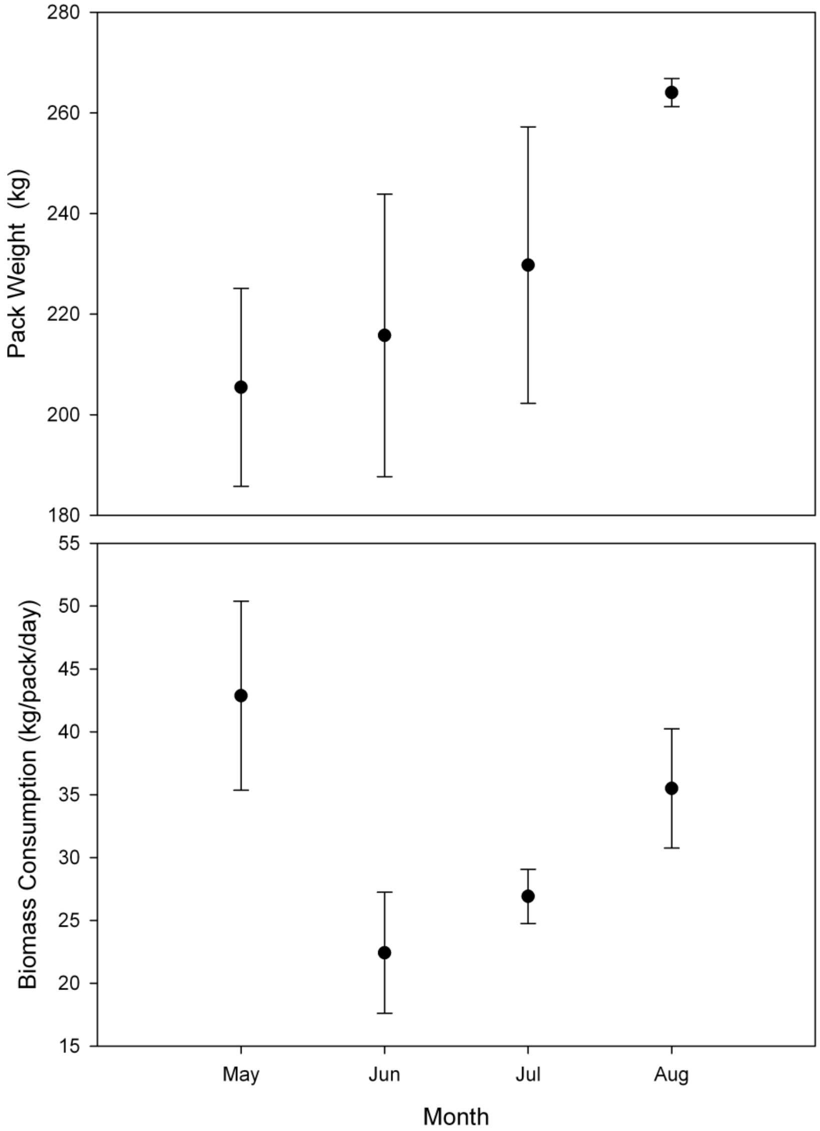


Figure 2.5. Monthly mean total wolf pack weights and standard errors. Wolf mass was obtained from weights of wolves at time of capture during this study (females=5, males = 3 males) and from packs in a previous study within the same area (Webb 2008: female = 8, male = 5). Monthly mean pack biomass consumption rates and standard errors.

CHAPTER 3

SUMMER AND WINTER KILL RATES, BIOMASS CONSUMPTION, AND PREY SELECTION OF WOLVES IN WEST-CENTRAL ALBERTA

The importance of large carnivores in structuring communities has received considerable attention with the recognition that both direct and indirect effects may play significant roles (Schmitz and Suttle 2001, Wilmers et al. 2003, Beschta and Ripple 2007, Hebblewhite 2005). Until recently most studies quantifying direct effects of wolf (C*anis lupus*) predation in northern environments have focused on quantifying kill rates in winter because snow facilitates tracking and finding kills. Recent advances in GPS-technology in radio-collars now permit quantification of wolf kill rates in both winter (Sand et al. 2005, Zimmermann et al. 2007) and summer (Sand et al. 2008, Metz et al. 2011, Chapter 2). Nonetheless, there remains a poor understanding of how wolf kill rates change seasonally because quantification of kill rates of wolves in single-prey dominated systems have produced variable results about their relative importance (Jedrezjewski et al. 2002, Metz et al. 2011, *in prep*.). A better understanding of these dynamics may enhance the management of wolves and their prey populations.

Until recently it was assumed that summer kill rates were lower than in winter resulting in lower biomass consumption, which was reflected in poorer condition and reduced weight of wolves in summer (Seal and Mech 1983, Stahler et al. 2006, White and Garrott 2005, Laundré 2008). Results from studies in Yellowstone National Park where elk (*Cervus canadensis*) comprise >90% of the annual wolf diet, support this hypothesis and show a 35% lower biomass consumption rates in summer than winter (Metz et al. 2011, *in prep.*). In contrast, Sand et al. (2008) in Scandinavia found wolf summer biomass consumption rates in a moose (*Alces alces*) dominated system were comparable to winter (Sand et al. 2005). However, in both studies kill rates were higher in summer than in winter, which was due primarily to killing of neonates of the same species. In one of the few studies to address seasonal variation of wolf kill rates in a multi-prey system, Jedrzejewski et al. (2002) found that while kill rates of adult red deer (*Cervus elaphus*) decreased in summer, kill rates of neonate wild boar (*Sus scrofa*) increased in summer resulting in total seasonal biomass consumed being similar across seasons. The lack of consistency in studies of seasonal kill rates of wolves across systems suggests further study is needed because of the important role that top-down effects of wolves play on prey dynamics in ungulate communities (Hebblewhite 2005, Ripple and Beschta 2004).

Two key factors influencing kill rates and composition are prey density (Pimlott 1967, Messier 1994, Fuller 1989) and body size (Carbyn et al. 1995, Kunkel and Mech 1994). In temperate environments where snow is a major environmental constraint in winter, ungulate prey typically become more concentrated in low snow areas (Nelson and Mech 1981, Huggard 1993, Kauffman et al. 2007) making them more predictable and detectable in space, which potentially increases overall encounter rates of wide-ranging predators like wolves (Huggard 1993). Further, the relative vulnerability of large-bodied individuals may change when in poor body condition and/or pregnant (Metz et al. 2011, DelGiudice et al. 1991, Knopff et al. 2009). In contrast, during summer there is an influx of neonates post-birth pulse. If wolves are generalist-opportunistic predators (Becker et al. 2008, Mattioli et al. 2011), diet should reflect the most accessible prey. Selection for small-bodied neonates in summer is well documented (Nelson and Mech 1986, Fuller 1989, Barber-Meyer et al. 2008, Sand et al. 2008), which despite initial low detection post-partum (Nelson and Woolf 1987), has been attributed to their relatively high vulnerability (Peterson and Ciucci 2003, Huggard 1993). There also is a dynamic shift in the distribution of prey size during summer due to rapid growth of neonates that may influence prey selection and kill rates (Barber-Meyer et al. 2008, Knopff et al. 2010). In single ungulate-dominated systems, this dynamic involves a shift in the relative predation on young vs. adults of the same species, but in multi-prey systems it may involve a more complex switching among species as well.

In Chapter 2 I found summer kill rates in west-central Alberta to be 1.5-2.5 times higher than reported in other systems in summer (Metz et al. *in prep*., Sand et al. 2008), while estimates of biomass consumption were comparable to these studies. I attributed this to high kill rates of an abundance of small-bodied prey (i.e. deer). In this Chapter, I compare species/age-specific kill rates and prey selection of ungulates by wolves in summer to those in winter with three objectives. First, I determine whether winter and summer kill rates and biomass consumption are similar. I predicted that wolf kill rates (ungulates/adult wolf/day) would be lower in winter, but total biomass consumed (kg ungulate/metabolic-rate-equivalent adult kg wolf/day) would be higher because more adult and large-bodied species of prey would be killed in winter than in summer. As a result, I also predicted that weights of adult wolves captured in winter from across the study area would be higher than in summer.

Second, I determined whether the magnitude of selection for the four major ungulate species differed between seasons. Because neonate deer are likely to be most vulnerable due to small body size of both the neonate and the defending adult, I expected that wolves selected more strongly for deer in summer than in winter compared to other species. In contrast, because factors other than body size, such as snow depth, are likely to play a prominent role in wolf predation in winter, I expected selection for deer relative to other species to be more similar in winter. For the other three prey species I expected similar selection patterns between summer and winter. Finally, I derived annual kill rates of ungulate prey in the study area for use in modeling future predator-prey dynamics in this area

STUDY AREA

The study area includes 20,000 km^2 in the eastern slopes of the Rocky Mountains of central Alberta about 200 km southwest of Edmonton, Alberta (52^o 27’N, 115^o 45’W). The area is comprised of crown lands under the jurisdiction of the provincial government as well as a small portion of Jasper National Park (Fig. 3.1). Elevation ranges from 900 m in the eastern foothills to 3,600 m in the steep mountains in the western portion of the study area. Conifer forests dominate the landscape (48.4%) including large stands of lodge pole pine (*Pinus contorta*) and white spruce (*Picea glauca*) interspersed with mixed conifer-deciduous (7.3%) of aspen (*Populus tremulodies*), open grassland (18.9%), and clearcuts (5.0%). The high elevations in the western portion of the study area consist of subalpine meadows (7.4%), bare rock and permanent ice or snow (13.0%). Extensive forest harvesting and oil and gas development together with associated seismic exploration lines and roads occur throughout the majority of the provincial lands except for high elevation areas in the western mountainous region.

Historically, wolves along the east slopes of the Rocky Mountains of Alberta were subject to government sponsored bounties, government paid hunters and trappers, liberal hunting and trapping seasons, and intensive poisoning campaigns that resulted in a decline in wolf numbers during the 1900's to 1920's with recovery during the late 1960's and the 1970's (Gunson 1992, Alberta Forestry Lands, and Wildlife 1991). In 2003-2008, wolf density was estimated at 22.3 wolves/1000 km^2 in the foothills to 9.68 wolves/1000 km^2 in the mountainous west portion of the study area (Webb 2009:197). Currently wolves are managed as a furbearer and big-game animal on provincial lands and are subject to a 6-month trapping season (October-March) with no harvest quotas, and a 10-month hunting season from August to May or June, depending on location.

Webb et al. (2011) reported annual harvest rates of wolves in this area of 0.34, which appeared sustainable because the harvest was comprised mostly (71%) of pre-reproductive aged wolves. Wolves are protected from harvest when in Jasper National Park.

Major ungulate prey for wolves in this area include elk (*Cervus elaphus*), moose (*Alces alces*), white-tailed deer (*Odocoileus virginianus*), mule deer (*O. hemionus*), and feral horses (*Equus caballus*), which were present throughout the study area. Bighorn sheep (*Ovis canadensis*) were present only in isolated areas. Domestic livestock (primarily cattle) were available in summer but limited to the Clearwater wolf pack's home range only. Other carnivores including bobcat (*Lynx rufus*), lynx (*L. canadensis*), cougar (puma concolor), coyote (*Canis latrans*), wolverine (*Gulo gulo*), black bear (*Ursus americanus*) and grizzly bear (*U. arctos*) were present as potential prey and/or competitors for wolves.

METHODS

Wolf Capture, Radio-collaring and Monitoring

Comparisons of winter and summer kill rates and prey selection were based on data from four GPS-collared wolves in four different packs during winter of 2005-2006 and seven GPS-collared wolves in four packs in summer of 2008-2009. Wolves were captured using either a modified foothold trap during the summer (2005, *n*= 2; 2008 *n*=1 wolf) or by helicopter netgunning during the winters of 2004-2005 (*n*= 2) and 2008- 2009 (*n*= 3). Captured wolves were physically restrained using a noose pole and/or 'Y-stick and collared. All capture and handling procedures followed University of Alberta Animal Care Protocols No. 391305, 353112 (winter 2005-2006); and 411601 (summers 2008-2009). All wolves were collared with remote-downloadable GPS collars (Lotek 4400S, Lotek Engineering, Newmarket, ON).

In winters 2005-2006 GPS-collared wolves were monitored between 1 December – 31 March. GPS-collars were programmed to take locations at 1-hr intervals with remote down loads every 1-2 weeks during telemetry flights. In summer the GPS-collared wolves were alternately monitored such that they were relocated at 15-min intervals for two weeks per month followed by two weeks of 2-hr interval locations. Data were downloaded at the end of each tracking session from the ground. This schedule was selected to obtain the highest frequency of relocations for detecting kills given the restraints of battery life while still sampling each wolf from June – August. GPS location fix success rates were similar in winter (mean 82%, SD=4.08, range: 79- 88%) and summer (90% ±5.0, 85-97%), indicating minimal habitat- induced GPS bias (Frair et al. 2004). Positional error was not evaluated in this study, but previous trails using Lotek 4400S GPS collars in an adjacent area reported 95% of locations fell within 114 m of the true position (Hebblewhite et al. 2006).

Seasonal Wolf Mass

Wolf mass was measured during live captures within Clearwater County, Alberta (Fig. 3.1) between 2003-2009 and included wolves from 19 packs. Weights were measured using a suspended spring scale (Slater 235-6S) in the field. Wolves were sexed and categorized as adults or yearling based on tooth wear and gum line recession (Gipson et al. 2000). I tested for seasonal weight differences of adult males and females using a t-test.

Seasonal Kill Rates

Winter kill rates of adults and juveniles were estimated in several steps. First, clusters of GPS collar locations along a wolf path were identified using a Space-Time Permuation Scan Statistic (STPSS) as described in Webb et al. (2008). Second, of the identified clusters, a random set of clusters of each collared wolf were visited in the field (74% +17, range: 54-100%) and searched for prey remains. Clusters were classified as a kill site where there was evidence of an animal being killed by a wolf, which included remains of the hide, bones, hair, and/or rumen and the age of the remains were estimated to match the date when wolves were at the kill (Webb et al. 2008). Third, to account for non-visited clusters I divided the number of each species located at visited clusters by the proportion of total clusters visited in a tracking session to predict species-specific kills for un-visited clusters. In addition, because Webb et al. (2008) reported that STPSS missed 17% ± 37 of small-bodied ungulate prey (i.e., deer) but missed none of the kills of large-bodied prey using a 1-hour GPS location interval (Webb et al. 2008), I divided the winter deer kill rate of each pack by 0.83 to correct for deer kills missed by the cluster scan technique. For non-visited kills I assigned age class of prey assuming equal ratio of species-specific adult: juveniles as identified from field visited kills. Finally, because Metz et al. (2011) reported that probability of attendance of a wolf at a kill site in winter was 0.95±0.01, I assumed high pack cohesion in winter and made no further adjustments. Daily species and age-specific kill rates for each collared wolf and tracking session in winter were estimated by dividing the adjusted numbers of kills located during field visitation of clusters by the number of days in a tracking session.

Summer kill rates were estimated as described in Chapter 2. Briefly, I identified location clusters as any set of ≥ 2 15-min GPS locations within 200 m along a wolf path and visited every cluster to determine whether it was a kill site based on searching for evidence of kill remains. I then used the ratio of the relative number of neonates (RNP_N) to relative number of adults (RNP_A) determined from scat analysis to estimate kill rates of neonate prey following a modified version of the approach presented by Mattioli et al. (2004). I calculated daily species-specific kill rates for each adult wolf by dividing the number of kills by the number of sampling days within each tracking session. Because Metz et al. (2011) found low pack attendance in summer, which was consistent with the limited data from this study, summer kill rates were corrected differently for large prey (adult elk, moose, horse: 0.93) and small prey (deer, all neonates: 0.73) (see Chapter 2 for details).

For both winter and summer, I expressed kill rates on a per adult wolf basis where adults included adult and yearlings because it was not possible to distinguish between age classes and both age groups have the potential to contribute to the killing of prey within a pack (Mech 1995). In winter, I used a monthly estimate of the pack size due to wolf removal by trapping and hunting, while in summer I assumed a constant number of adults in the pack assuming emigration most likely compensated for dispersal (Webb 2009). Monthly pack sizes from December - March in 2005 and 2006 were estimated based on a combination of ground-based snow-tracking sessions and aerial telemetry once every 2 weeks. Field counts of pack size were supplemented further with information from collared wolves that dispersed and known harvested wolves.

Prey Biomass Composition

I estimated daily species-specific biomass consumption rates using the metric kg ungulate/ kg adult wolf/day in winter, and ungulate/metabolic-rate-adult equivalent-kg/day in summer, (which accounts for pups mass) by multiplying the number prey items by species and age-specific prey mass. For winter I used a fixed, edible prey mass for adult prey (Table 2.1) and juvenile (young of year: deer = 29 kg, elk 81 kg, moose 147 kg and horse 148 kg). In summer I used the same fixed weights for yearling/adult prey (Table 2.1). For neonates of a species, however, I used variable weights across tracking seasons to account for seasonal growth (Table 2.1). For both seasons I assumed wolves consumed only a portion of the biomass of prey killed: 65% of the mass of large-bodied (> 100 kg, adult moose, elk, horse), 75% of medium-bodied (20-100 kg, adult deer or neonate elk, moose, horse), and 90% of small-bodied prey (< 20 kg, neonate deer) (Glowacinski and Profus 1997, Hayes et al. 2000, Jedrzejewski et al. 2002, Sand et al. 2008).

To express biomass consumption based on metabolic requirements, I divided the prey biomass consumed by the estimated weight of a wolf pack. In winter I used fixed masses over the winter for the alpha pair of wolves (43 kg each) and a mean winter mass (36 kg) of adults, yearlings and pups captured in winter in the study area between 2003 and 2006 (see above). Because pups were aged 8-11 months old by winter, they were considered comparable to yearlings. In summer I used the weighted average of the adult pair and non-alpha adults/yearlings body masses based on wolves captured in summer (see above). Body mass of pup was based on the growth rate curve presented in Appendix I and described in detail in Chapter 2. I compared biomass consumed on a per kg wolf basis in winter to biomass consumed in summer on an metabolic- rate-adult equivalent per kg of wolf to account for differences in adult and pup metabolic rates (see Chapter 2 for details).

Statistical Analyses of Kill Rates and Biomass Consumption

I evaluated differences in seasonal kill rates and biomass consumption on total, species-specific, and adult kill rates and biomass consumption rates using a generalized linear model (GEE, STATA v.10.0, StataCorp, College Station, TX), blocking by pack and using repeated estimates from each pack from tracking sessions in each season (winter: $n = 11$, summer: $n = 12$). For all statistical analysis I assumed a significant difference at $\alpha = 0.10$.

Prey Selection

To compare differences in selection by wolves between seasons, I calculated a selection ratio (Manly et al. 2002) for each prey species by pack as the percent a prey species comprised of the total prey killed by a pack divided by the percent of the available ungulate prey within the home range of the respective pack. Number of prey killed was based on kills determined across the seasons as described above. To determine relative prey availability, I counted pellet groups in 10 1-km × 2-m transects within each wolf pack's 95% minimum convex polygon (MCP) home range such that 3.2±1.28 % of each home range in winter and in summer 2.4±0.92 % was sampled.

Locations of pellet count transects were selected to ensure coverage of the study area while avoiding water bodies that prevented travel on foot. Pellet counts were conducted after snow melt from 5 May to 15 June in 2005 and 2006 to reflect winter prey availability and from 15 August to 10 September in 2008 and 2009 to reflect summer ungulates (Huggard 1993). Pellets groups were recorded within each 100-m segment by species (deer, elk, moose or horse) and recorded as either aged (decaying), old (dry /crusted), or new, (moist/oily); only new pellet groups were included in the count. To adjust for possible underestimates of pellet group counts due to detection bias along a transect (Lehmkuhl et al. 1994, Theuerkauf et al. 2008), a species-specific correction factor was determined by regressing the initial count of the last 100-m segment of each transect on a more intensive recount by two observers and applied to each 100-m segment count (Webb 2008).

I also adjusted counts for differences in defecation rates among ungulate species by calibrating deer, elk and feral horse pellet counts against moose defection rates. I used a defecation rate of 14 (10-14) pellet groups/day for moose (Joyle and Richard 1986, Timmerman 1974, Persson et al. 2000, Ronnegard et al. 2008) 26 (20-35) pellet groups/day for elk (Collin and Urness 1981, Gregory et al. 2009), 22 (15-35) pellets/day for deer (Collins and Urness 1981, Sawyer et al. 1990, Knopff et al 2010), and 9.7 (7-12) pellets/day for horse (Tyler 1972).

Statistical Analysis of Selection Indices

I present selection ratios by pack for each prey species for summer and winter. Following Manly (1993) I divided the proportion of each prey species killed by a pack in a given season by the proportion that each species comprised of the total available within that packs home-range for that season. Composition of wolf kills were estimated from wolf kill data for both summer and winter using the kill data as described above. Confidence intervals were calculated for mean selection indices following Manly et al. (2002). I used a Kruskal-Wallis rank test to test for variation between seasons in species-specific selection indices.

Because defecation rates can be highly variable, with reports of both increased defecation with higher forage quality and intake rate in summer (Rogers 1958, Neff 1968, Collins and Urness 1981), I assessed the effect of varying defecation rates on estimates of relative abundance and consequently wolf selection indices. I varied defecation rates to the extreme for each species within the ranges identified in the literature (as above). Percentage change of selection indices were: 15% deer, 12% elk, 8% moose with no change for horse. These changes were not great enough to alter the conclusion of species specific selection.

RESULTS

Wolves were monitored for an average of 264 wolf days (70±12.5 days/collared wolf, $n = 4$) in winter (1 December - 31 March) and 188 wolf days (50±6.5 days/collared wolf, $n = 4$) in summer (1 June to 26 August). Winter monitoring consisted of 11 sessions (24±8.7 days/ session, range:11-31), while summer tracking consisted of 12 tracking sessions (16±4.4 days/session, range: 9-20). Winter pack sizes including all age classes averaged 4.75±1.84 (range 3-8). In summer wolf pack sizes including pups averaged 8.78+1.15 (range: 7-10) and excluding pups averaged 5.25±1.5 (range: 3-6).

Wolf Weights

Wolf weights measured at the time of capture in winter averaged 47.2±6.4 kg for males (n=23) and 39.1±2.5 kg for females (n= 12), while yearling males in winter were 40.3±8.7 kg (n= 3) and yearly females were 36.3±4.0 kg (n=3). In summer measured weights of male adults (n=5) were 44.7±1.78 kg and female adults (n=8) were 36.2+2.53kg. Yearling males (n=3) averaged 29±3.6 kg and females (n=4) were 23.2+4.2kg. Adult wolf weights were lower in summer than winter for both male (t_{26} = -1.28, P= 0.10), and female wolves (t_{18} = -1.94, P = 0.03).

Kill Composition and Rates

In winter, GPS cluster searches detected a total of 58 kills (14.5±2.64/collared wolf of all age and sex classes). This figure was increased to 95 kills (24±3.4/collared wolf) due to non-detection. Composition of known kills was comprised of 69% deer, 21% elk, 7% moose, 3% horse after correction for missed deer clusters. Of the 95 ungulates killed, 7 were juvenile kills (4 deer and 3 elk). In summer a total of 38 adult kills (9.5±1.2/collared wolf) were located at GPS-clusters, which resulted in an estimated 45 adult kills (80% deer, 8% elk, 10% moose, 2% horse) due to corrections for pack cohesion. Based on this estimate a total of 215 neonates kills were estimated through scat analysis, which were comprised of 82% deer, 10% elk, 7% moose, 1% horse.

Across all packs winter total kill rates averaged 0.08±0.024 ungulates/adult wolf/day (range: 0.05 - 0.08), which was 2.5 times lower ($P<0.001$) than the summer total kill rates of 0.21± 0.05 ungulate/adult wolf/day (range: 0.06 - 0.37, Table 3.1). Kill rates of neonates were higher in summer compared to winter ($P<0.01$) while adult kill rates were lower in summer than winter ($P<0.01$). Average species-specific kill rates of adult prey did not differ between seasons; however, kill rates of total (adult plus neonate) deer ($P<0.001$) and total moose ($P<0.02$) were both higher in summer than winter.

Winter kill rates in this study were 62% lower ($P=0.01$) than the rate estimated for summer. Using the above kill rates during summer (1 June – 31 August) and winter (1 Sept-31 May), annual kill rates were 0.10±0.05. If only winter kill rates had been used to estimate annual kill rates, this would have resulted in a 29% underestimate of annual kill rates.

Biomass Consumption

Winter biomass consumption rates averaged 7.93±4.08 kg/adult wolf/day (range: 4.42-13.68) or 0.19±0.08 kg/kg wolf/day (range: 0.11-0.34); in summer biomass consumption averaged 4.22±0.36 kg/adult equivalent wolf/day (range: 2.96- 5.61) or 0.118±0.01 kg/metabolic-rate-adult equivalent kg/day (range: 0.08-0.18) across packs (Table 3.2). Adult prey biomass across all species combined was significantly lower in summer ($P< 0.01$) than winter, whereas neonate biomass of all ungulate prey species combined was higher in summer than all juveniles combined in winter ($P<0.01$). Average total prey biomass consumed in winter (kg/kg wolf/day) was higher ($P = 0.02$) than in summer (kg/metabolic-rate-adult equivalent kg/day). Total species-specific biomass consumption rates did not differ for any species across seasons. Biomass consumption rates (winter: kg/kg wolf/day, summer: kg/metabolic-rate-adult equivalent kg/day) were positively correlated with kill rates (ungulates/adult wolf/day) in winter ($r = 0.77$) but not summer ($r = 0.01$) (Fig. 3.2).

Estimated winter biomass consumption rates from this study were 65% higher ($P=0.02$) than the rates estimated for summer. Using winter biomass estimates for summer would have resulted in an 11% overestimates of annual biomass consumption rates of wolves.

Wolf Selection

Based on confidence intervals of selection ratios (Table 3.3), wolf selected only for deer in summer, and avoided moose and horse. In winter there was no selection for any species and only moose was avoided. Within species, the magnitude of selection did not differ between winter and summer (Kruskal-Wallis $X^2=0.75$, $df = 1$, $P= 0.38$ deer; $X^2=0.08$, $df = 1$, $P= 0.77$ elk; $X^2=0.01$, $df = 1$, $P= 0.80$ moose; $X^2=0.083$, $df = 1$, $P= 0.77$).

DISCUSSION

Both summer and winter biomass consumption of ungulate prey in this study fell within the range of consumption rates reported for wolves in other areas. Winter biomass consumption of 0.19 kg/kg wolf/day was higher than estimates from deer-dominated systems (0.09±0.02 kg/kg wolf/day), and more similar to elk (0.18±0.01) and moose-dominated systems (0.19±0.05 (Peterson and Ciucci 2003), which may reflect the diverse ungulate prey base in this area. In summer, biomass consumption rates (0.12±0.01 kg/metabolic-rate-adult equivalent kg/day or 4.22±0.36 kg/adult equivalent wolf/day) were similar to other studies in single-ungulate dominated systems (Sand et al. 2008: 0.16 kg/ wolf kg/ day, Metz. et al. 2011: ~5.7 kg/adult equivalent wolf/day) (see Chapter 2 for more detailed comparison of summer kill rates).

As predicted, the total kill rates of ungulates in summer were higher (2.5x) than in winter, but biomass consumption by wolves in winter was higher (1.6x) than in summer. The differences between seasons were unlikely to result from methodological inconsistencies. For example, although potential kill site clusters were identified using 1-hr interval GPS locations in winter compared to15-min intervals in summer, Webb et al. (2008) reported that using the STPSS technique 95% of kills were detected using 1-hr relocations. Also, longer prey handling times in winter due to larger prey size increases the likelihood of detecting prey despite less frequent sampling. Webb et al. (2008) also reported that the STPSS technique identified only 77% of small-bodied prey like deer, but 100% of large-bodied prey like elk and moose. By dividing the deer kill rates in winter by 0.83, I corrected for this potential underestimate of deer. Finally, Metz et al. (2011) reported lower probability of attendance (PA) of wolves at kill sites in summer than winter in Yellowstone National Park. I accounted for this difference in summer by adjusting summer kill rates using the PA reported by Metz et al.

(2011) because data on PA from my study was limited. In winter I did not adjust kill rates because Metz et al. (2011) identified PA was ~100% at kills, and this included 49% elk calves for wolf packs of similar sizes (Yellowstone: 5-8 wolves; this study: 3-8 wolves). Because elk calves in winter have roughly similar mass to adult deer (~100 vs 90 kg, Barber-Meyer et al. 2008, Table 2.1), PA was likely close to 100% because small-bodied juvenile deer comprised only <5% of prey killed in winter.

Higher kill rates by wolves in summer than winter found in this study are consistent with findings from other systems even when wolves preyed largely on single ungulate species. For example, in Yellowstone, Metz et al. (2011) reported summer kill rates of elk were 1.7 times higher than in winter, while Sand et al. (2008) reported kills rates of moose by wolves in Scandinavia were 1.9-2.2 times higher in summer than winter. The higher summer kill rates reported by Sand et al. (2008) included neonate kills that were detected at single wolf relocations and small pack sizes (mean=5.0) and. In Yellowstone pack sizes averaged >15 wolves and Metz et al. (*in prep.*) did not include neonates found at single relocations. In my study where kills of neonates were included and comprised 62% of the prey killed, there was a 2.5 times increase in kill rates of prey in summer from winter. Despite the substantial increase in kill rates, prey biomass consumed by wolves in west-central Alberta in summer was 40% lower than in winter, largely due to wolves selecting for neonates (Chapter 2) and neonate weights being only ~ 5-25% of adult animals killed in winter (Chapter 2: Table 2.1).

Overall deer remained the primary prey killed by wolves in both summer (82±7 %) and winter (69±26%) in this multi-prey system, likely because deer were the most abundant species based on our pellet counts. One exception was the apparent shift toward predation on elk in winter (Table 3.3). This shift was related to individual variation among packs that was not controlled for in my design because collar failures did not allow me to compare the same packs during summer and winter. The wolf pack whose home range included the Ya-Ha-Tinda Ranch (Table 3.3, winter pack 3) was unique in that there were 3-6 times as many elk in this pack's home-ranges, and elk were the primary prey species in this area (Hebblewhite 2005). When I excluded data from the Ya-Ha-Tinda wolf pack, deer comprised 83% of the winter diet, which was similar to summer. Thus, contrary to my prediction, there was little evidence that wolves broadened the diversity of their diet in winter when larger prey might be more vulnerable due to body condition.

Instead, the major shift was between killing neonate and adults of the same species. As generalists, wolf diets are likely to reflect prey availability (Becker et al. 2008). However, in west-central Alberta deer are both the most abundant, particularly during the summer due to their high fecundity rates, and the most vulnerable based on body size (Huggard 1993). Further, while moose have small social groups, they have been reported to have particularly aggressive behavior (Huggard 1993, Peterson and Ciucci 2003), while elk form larger social groups than moose and deer, which can reduce predation risk (Hebblewhite and Merrill *in press*). Thus, this may contribute to the lack of selection for elk and avoidance of moose in summer. Because feral horses were relatively rare, an estimate of their selection is not sufficiently sampled, although their avoidance is consistent with reduced vulnerability due to large-body size and aggressive behavior .

Wolf Weights and Biomass Consumption

Wolf weights reported for summer and winter were within the range of 12 studies from north-western North America (Fuller 1989, Adams et al. 2008). Winter wolf weights in this study were taken in December or March for animals captured with helicopter net-gunning with an almost equal number of animals weighed within sexes in each of these months. In contrast, wolf weights in summer were taken during foothold trapping in May-August with a mean date of 17 July for females and 29 June for males. Because weights of male wolves were measured earlier in summer on average than females, this could explain the lack of a significant reduction in male weights compared to winter, even though there was a decline in summer weights of males.

Lower wolf weights in summer compared to winter has been the basis for expecting lower kill rates in summer than winter (Messier 1994). Indeed, lower wolf weights have been linked to declining white-tailed deer densities in Superior National Forest, Minnesota (Van Ballenberghe and Mech 1975) and low moose densities in Southwestern Quebec (Messier 1987). In my study female and males wolves were ~3 kg lighter in summer. No female wolves captured were lactating so it is unlikely that declines in female weight resulted from changes in pregnancy status. Because kill rates were higher in summer than winter, weight loss in summer was instead related to reduced biomass consumption and/or higher energy expenditures in summer than to reduced kill rates per se.

Lower biomass consumption by wolves in summer reflected both the shift in the age structure of prey consumed and the growing demands of pups over the summer. Despite lower consumption rates, consumption remained above the 0.09 kg/kg wolf/day needed to meet field metabolic rates (Peterson and Ciucci 2003). However, during the reproductive period wolves also are tied to the den sites for feeding pups. More widely distributed prey in summer and reduced prey size could require more frequent hunting bouts that necessitates returning to the den site more often, and this would increase distances traveled, energy expenditures, and weight loss in summer. But large variation in daily movements of different pack members is likely, particularly in summer when some wolves may be involved in pup rearing (Mech 1999). I did not quantify movement rates of wolves between seasons, but assessment of GPS movement data could provide information required to evaluate these concepts. Research has also reported that up to 37 kg/day can be removed from a moose carcass in winter by scavenging ravens (Peterson and Ciucci 2003). Due to small prey sizes and short handling times, food loss to scavengers is less likely to be important in this study area. Ultimately seasonal dynamics in food consumption rates by wolves may constrain pup survival and influence wolf dispersal and pack sizes and remains a topic that merits further research.

The small sample size of this study (*n*= 4) is similar to other summer kill rate studies (Metz et al. *in prep*. *n* = 6, and Sand et al. 2008, *n*= 6), which result from the high intensity of monitoring required to locate kills in summer. Despite the low power associated with the limited number of packs I studied, I found differences in summer and winter total kill rates and total biomass consumption rates. Where differences were not detected, (i.e., species–specific kill rates and prey selection) this may have resulted from variation among packs. Many factors have been identified as affecting prey selection and kill rates of wolves including pack size (Huggard 1993, Hayes et al. 2000), prey availability (Kunkel and Pletscher 2001), and the special distribution of prey (Kauffmann et al. 2007). In this study an example of the variation in wolf selection was clearly identified by the Ya-Ha-Tinda pack, which strongly selected for elk compared to all other packs. This is likely a result of the 3-6 times higher abundance of elk compared to other packs monitored. Due to such variation across packs and differences in the packs monitored in summer and winter, caution must be taken when making generalizations to the population level. Indeed increased sample size would increase the power of our findings.

Conclusions and Implications

Comparison of winter and summer predation has shown that predator-prey interactions are seasonally dynamic, but the implications of these dynamics are less well understood (Oksanen et al. 2001). In the multi-prey system of west-central Alberta wolves exhibited selection of neonates in summer, particularly for small-bodied deer, which resulted in high kill rates but lower biomass consumption relative to requirements compared to in winter. Variation in prey selection existed among packs with one pack killing more elk rather than deer in winter due to their high abundance. Wolves in this study were less food limited in winter than summer largely because more large-bodied, adult prey were killed and packs sizes did not substantially increase due either to dispersal or harvest (Webb 2009). Because studies have now consistently shown that summer kill rates are 1.7-2.5x higher in summer than winter (Metz et al. *in prep*., Sand et al. 2008, this study), past extrapolations of winter kill rates across the year are likely underestimates of the impact of wolves on prey populations (Kolenosky 1972, Mech 1971).

However, seasonal predation by wolves also targets different age classes, with vulnerable neonates often comprising the major component of the diet in summer and adults in winter. The importance of this seasonal shift in predation on age classes to predator-prey dynamics is unknown. Neonate survival in ungulates typically has high among-year variation and low population elasticity whereas adult survival shows the lowest temporal variation and highest elasticity, regardless of whether the temporal variation is environmental or density dependent (Gaillard et al. 1998; 2000). During summer if predation is shifted toward neonates it may provide a temporal refuge for adult prey, particularly in species with high fecundity rates, and population growth rate in this case may not be as influenced by predation as when adult prey remain a major component of the diet of predators year-round.

Further, where predation-related mortality of neonates in summer is compensatory or density-dependent processes operate after summer predation (Boyce et al. 1999), such as increased winter survival of fewer juveniles, predation may not reduce recruitment. However, targeted predation by wolves on neonates in summer may dampen a prey population's capacity to increase during favorable environmental conditions or at low densities. The strength of both density dependence (Crete 1999, Wang et al. 2009) and climatic influences (Hebblewhite 2005) have been reported to be lower in the presence of large carnivores like wolves than when absent. In a multi-prey system the relative fecundity, body size, and maternal aggression among species may play an important roles in these dynamics.

LITERATURE CITED

Alberta Forestry, Lands, and Wildlife. 1991. Management plan for wolves in Alberta. Wildlife Management Planning Series No. 4. 89 pp.

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 :1-25.

Barber-Meyer, S.M., L.D. Mech, and P.J. White. 2008. Elk calf survival and mortality following wolf restoration to Yellowstone National Park. Wildlife Monographs:1-30.

Becker, M.S. 2008. Applying predator-prey theory to evaluate large mammal dynamics: wolf predation in a newly-established multiple-prey system. Thesis, Montana State University, Bozeman, Montana, USA.

Beschta, R.L., and W.J. Ripple. 2007. Wolves, elk, and aspen in the winter range of jasper national park, Canada. Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere 37:1873-1885.

Carbyn, L.N., S.H. Fritts, D.R. Seip. 1995. Ecology and conservation of wolves in a changing world. Canadian Circumpolar Institute, Edmonton, Alberta.

Collins, W.B., and P.J. Urness. 1981. Habitat preferences of mule-deer as rated by pellet-group distributions. Journal of Wildlife Management 45:969-972.

DelGiudice, G., L. Mech, and U. Seal. 1991. Gray wolf density and its association with weights and hematology of pups from 1970 to 1988. Journal of Wildlife Diseases 27:630-636.

Frair, J.L., S.E. Nielsen, E.H. Merrill, S.R. Lele, M.S. Boyce, R.H. M. Munro, G.B. Stenhouse, and H.L. Beyer. 2004. Removing GPS collar bias in habitat selection studies. Journal of Applied Ecology 41:201–212.

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

Gaillard, J., M. Festa-Bianchet, N. Yoccoz, A. Loison, and C. Toigo. 2000. Temporal variation in fitness components and population dynamics of large herbivores RID A-1493-2008. Annual Review of Ecology and Systematics 31:367-393.

Gaillard, J., M. Festa-Bianchet, and N.G. Yoccoz. Population dynamics of large herbivores: variable recruitment with constant adult survival. TREE. 13:58-63.

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.

Glowacinski, Z., and P. Profus. 1997. Potential impact of wolves *(Canis lupus)* on prey populations in eastern Poland. Biological Conservation 80:99-106.

Gregory, A. J., M. A. Lung, T. M. Gehring, and B. J. Swanson. 2009. The importance of sex and spatial scale when evaluating sexual segregation by elk in Yellowstone. Journal of Mammalogy 90:971-979.

Gunson, J. 1992. Historical and present management of wolves in Alberta. Wildlife Society Bulletin 20:330-339.

Hayes, R., A. Baer, U. Wotschikowsky, and A. Harestad. 2000. Kill rate by wolves on moose in the Yukon. Canadian Journal of Zoology-Revue Canadienne De Zoologie 78:49-59.

Hebblewhite, M. 2005. Predation by wolves interacts with the north pacific oscillation (NPO) on a western north American elk population. Journal of Animal Ecology 74:226-233.

Hebblewhite, M., E.H. Merrill, L. E. Morgantini, C. A. White, J. R. Allen, E. Bruns, L. Thurston, and T. E. Hurd. 2006. Is the migratory behavior of montane elk herds in peril? the case of Alberta's Ya Ha Tinda elk herd. Wildlife Society Bulletin 34:1280-1294.

Huggard, D. J. 1993. Prey selectivity of wolves in Banff National-Park .2. age, sex, and condition of elk. Canadian Journal of Zoology-Revue Canadienne De Zoologie 71:140-147.

Jedrzejewski, W., B. Jedrzejewska, H. Okarma, K. Schmidt, K. Zub, and M. Musiani. 2000. Prey selection and predation by wolves in Bialowieza Primeval Forest, Poland. Journal of Mammalogy 81:197-212.

Jedrzejewski, W., K. Schmidt, J. Theuerkauf, B. Jedrzejewska, N. Selva, K. Zub, and L. Szymura. 2002. Kill rates and predation by wolves on ungulate populations in Bialowieza Primeval Forest (Poland) RID B-6823-2009. Ecology 83:1341-1356.

Joyal, R., and J.G. Ricard. 1986. Winter defecation output and bedding frequency of wild, free-ranging moose. Journal of Wildlife Management 50:34–736.

Kauffman, M.J., N. Varley, D.W. Smith. 2007. Landscape heterogeneity shapes predation in a newly restored predator-prey system. Ecology Letters. 10:690:700.

Knopff, K.H., A.A. Knopff, and M.S. Boyce. 2010. Scavenging makes cougars susceptible to snaring at wolf bait stations. Journal of Wildlife Management 74:644-653.

Knopff, K.H., A.A. Knopff, M.B. Warren, and M.S. Boyce. 2009. Evaluating global positioning system telemetry techniques for estimating cougar predation parameters. Journal of Wildlife Management 73:586-597.

Kolenosky, G.B. 1972. Wolf predation on wintering deer in east-central Ontario. Journal of Wildlife Management 36: 357-369

Kunkel, K., and D. Pletscher. 2001. Winter hunting patterns of wolves in and near Glacier National Park, Montana. Journal of Wildlife Management 65:520-530.

Kunkel, K.E., and L.D. Mech. 1994. Wolf and bear predation on white-tailed deer fawns in northeastern Minnesota. Canadian Journal of Zoology-Revue Canadienne De Zoologie 72:1557-1565.

Laundre, J. W. 2008. Summer predation rates on ungulate prey by a large keystone predator: How many ungulates does a large predator kill? Journal of Zoology 275:341-348.

Lehmkuhl, J.F., C.A. Hansen, and K. Sloan. 1994. Elk pellet-group decomposition and detectability in coastal forests of Washington. Journal of Wildlife Management 58:664-669.

Manly, B. 1993. A review of computer intensive multivariate methods in ecology. G. R. Patil CR, editor. Volume 6. Elsevier Science Publ B V, Amsterdam; Sara Burgerhartstraat 25, Po Box 211, 1000 Ae Amsterdam, Netherlands.

Manly, B.F.J., L.L. McDonald, D.L. Thomas, T.L. McDonald, and W.P. Erickson. 2002. Resource selection by animals: statistical design and analysis for field studies.

Mattioli, L., C. Capitani, E. Avanzinelli, I. Bertelli, A. Gazzola, and M. Apollonio. 2004. Predation by wolves (*Canis lupus*) on roe deer (*capreolus capreolus*) in north-eastern Apennine, Italy. Journal of Zoology 264:249-258.

Mattioli, L., C. Capitani, A. Gazzola, M. Scandura, and M. Apollonio. 2011. Prey selection and dietary response by wolves in a high-density multi-species ungulate community. European Journal of Wildlife Research 57:909-922.

Mech, L.D., L.D. Frenzel, Jr., and P.D. Karns. 1971. The effect of snow conditions on the ability of wolves to capture deer. Pp. 51-59 in Ecological studies of the timber wolf in Minnesota (L.D. Mech, and L.D. Frenzel, Jr., eds.). USDA Forest Service Research Paper NC-52. North Central Forest Experiment Station, St. Paul, Minnesota, USA.

Mech, L. 1995. A ten-year history of the demography and productivity of an arctic wolf pack. Arctic 48:329-332.

Mech, L. 1999. Alpha status, dominance, and division of labor in wolf packs. Canadian Journal of Zoology, 77:1196-1203.

Messier, F. 1987. Physical condition and blood physiology of wolves in relation to moose density. Canadian Journal of Zoology-Revue Canadienne De Zoologie 65:91-95.

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:e17332.

Metz, M.C., J.A. Vucetich, D.W. Smith, D.R. Stahler, and R.O. Peterson. 2011. Seasonal patterns of predation for grey wolves in the multi-prey system of Yellowstone National Park. (*in prep).*

Neff, D. J. 1968. Pellet-group count technique for big game trend census and distribution - a review. Journal of Wildlife Management 32:597-&.

Nelson, M., and L. Mech. 1981. Deer social-organization and wolf predation in northeastern Minnesota. Wildlife Monographs :1-53.

Nelson, M., and L. Mech. Relationship between snow depth and gray wolf predation on white-tailed deer. Journal of Wildlife Management 50:471-474.

Nelson, T.A., and A. Woolf. 1987. Mortality of white-tailed deer fawns in southern Illinois. Journal of Wildlife Management 51:326-329.

Oksanen, T., L. Oksanen, and M. Schneider. 2001. Regulation cycles and stability in northern carnivore-herbivore systems: back to first principles. Conference: Oikos seminar on costs and grains of recent progress in ecology. Hallnas, Sweden. Oikos. 94:101-117.

Persson, I.L., K. Danell, and R. Bergstrom. 2000. Disturbance by large herbivores in boreal forests with special reference to moose. Annales Zologici Fennici 37:254 263.

Peterson, R.O., and P. Ciucci. 2003. The wolf as a carnivore. Pp. 104-130 in Wolves: behavior, ecology, and conservation (L.D. Mech, and L. Boitani, eds.). The University of Chicago Press, Chicago, Illinois, USA.

Pimlott, D.H. 1967. Wolf predation and ungulate populations. American Zoologist 7:267-&.

Ripple, W., and R. Beschta. 2004. Wolves and the ecology of fear: Can predation risk structure ecosystems? Bioscience 54:755-766.

Rogers, G., O. Julander, and W. Robinette. 1958. Pellet-group counts for deer census and range-use index. Jour Wildlife Management 22:193-199.

Ronnegard, L., H. Sand, H. Andren, J. Mansson, and A. Pehrson. 2008. Evaluation of four methods used to estimate population density of moose (*Alces alces).* Wildlife Biology 14:358-371.

Sand, H., B. Zimmermann, P. Wabakken, H. Andren, and H. Pedersen. 2005. Using GPS technology and GIS cluster analyses to estimate kill rates in wolf-ungulate ecosystems. Wildlife Society Bulletin 33:914-925.

Sand, H., P. Wabakken, B. Zimmermann, O. Johansson, H.C. Pedersen, and O. Liberg. 2008. Summer kill rates and predation pattern in a wolf-moose system: Can we rely on winter estimates? Oecologia 156:53-64.

Sawyer, T.G., R.L. Marchinton, and W. Maclentz. 1990. Defecation rates of female white-tailed deer in Georgia. Wildlife Society Bulletin 18:16-18.

Schmitz, O., and K. Suttle. 2001. Effects of top predator species on direct and indirect interactions in a food web. Ecology 82:2072-2081.

Seal, U., and L. Mech. 1983. Blood indicators of seasonal metabolic patterns in captive adult gray wolves. Journal of Wildlife Management 47:704-715.

Stahler, D., D. Smith, and D. Guernsey. 2006. Foraging and feeding ecology of the gray wolf (*Canis lupus*): Lessons from Yellowstone National Park, Wyoming, USA. Journal of Nutrition 136:1923S-1926S.

Theuerkauf, J., and S. Rouys. 2008. Habitat selection by ungulates in relation to predation risk by wolves and humans in the Bialowieza Forest, Poland. Forest Ecology and Management 256:1325-1332.

Timmerman, H.R. 1974. Moose inventory methods: a review. Naturaliste Canadienne. 101:615-629.

Tyler, S. J. 1972. The behavior and social organization of the New Forest ponies. Animal Behavior Monographs 5:85–196.

Vanballenberghe, V., and L. Mech. 1975. Weights, growth, and survival of timber wolf pups in Minnesota. Journal of Mammalogy 56:44-63.

Webb, N.F., M. Hebblewhite, and E.H. Merrill. 2008. Statistical methods for identifying wolf kill sites using global positioning system locations. Journal of Wildlife Management 72:798-807.

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

Webb, S.L., M.R. Dzialak, J.J. Wondzell, S.M. Harju, L.D. Hayden-Wing, and J.B. Winstead. 2011. Survival and cause-specific mortality of female rocky mountain elk exposed to human activity. Population Ecology 53:483-493.

White, P., and R. Garrott. 2005. Yellowstone's ungulates after wolves - expectations, realizations, and predictions. Biological Conservation 125:141-152.

Wilmers, C., R. Crabtree, D. Smith, K. Murphy, and W. Getz. 2003. Trophic facilitation by introduced top predators: Grey wolf subsidies to scavengers in Yellowstone National Park. Journal of Animal Ecology 72:909-916.

Zimmermann, B., P. Wabakken, H. Sand, H.C. Pedersen, and O. Liberg. 2007. Wolf movement patterns: A key to estimation of kill rate? Journal of Wildlife Management 71:1177-1182.

Table 3.1. Kill rate of wolves (ungulates/adult wolf/day) of four wolf packs from 1 December-31 March, 2005-2006 (winter) and four packs from 1 May-26 August, 2008-2009 (summer) of adult and neonate ungulate prey in west-central Alberta, Canada. Pack total reflects kill rate by entire pack regardless of size.

	Summer						Winter					
	Ungulates/adult wolf/day						Ungulates/adult wolf/day					
	Adult		Neonate[1]		Total		Adult		Juvenile[2]		Total	
Prey type	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Deer	0.026	0.028	0.135	0.031	0.162	0.047	0.052	0.026	0.002	0.003	0.054	0.025
Elk	0.004	0.004	0.025	0.023	0.028	0.022	0.014	0.027	0.002	0.005	0.017	0.033
Moose	0.002	0.002	0.015	0.007	0.018	0.009	0.004	0.006	0.000	0.000	0.004	0.006
Horse	0.000	0.000	0.005	0.006	0.005	0.007	0.003	0.009	0.000	0.000	0.003	0.009
Total	0.032	0.024	0.181	0.047	0.211	0.053	0.074	0.023	0.005	0.006	0.079	0.024
Pack total	0.174	0.019	0.908	0.169	1.081	0.288	0.325	0.046	0.021	0.015	0.346	0.038

[1] 1-90 days old

[2] 180-300 days old

Table 3.2. Biomass consumption rates (kg ungulate/ kg wolf /day) of four packs from 1 December-31 March, 2005-2006 (Winter) and biomass consumption rates (kg ungulate/ metabolic-rate-adult equivalent kg/day) of four wolf packs from 1 May-26 August, 2008-2009 (summer) by wolves in west- central Alberta, Canada. Pack total is consumption rates (kg ungulate/pack/day) by a pack regardless of size.

	Summer						Winter					
	Adult		Neonate[1]		Total		Adult		Juvenile[2]		Total	
Prey type	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Deer	0.032	0.036	0.025	0.011	0.058	0.046	0.067	0.034	0.002	0.004	0.070	0.033
Elk	0.014	0.016	0.016	0.014	0.030	0.019	0.063	0.111	0.008	0.018	0.071	0.129
Moose	0.012	0.014	0.015	0.006	0.028	0.021	0.033	0.045	0.000	0.000	0.033	0.0453
Horse	0.000	0.000	0.002	0.005	0.002	0.005	0.020	0.064	0.000	0.000	0.020	0.064
Total	0.059	0.023	0.059	0.020	0.118	0.012	0.184	0.101	0.011	0.017	0.195	0.071
Pack total	14.31	7.552	12.548	0.711	26.89	7.603	29.153	3.347	1.521	1.765	30.674	5.086

[1] 1-90 days old

[2] 180-300 days old

Table 3.3. Selection ratio[1] by pack, mean and confidence limits (CI) for deer, elk, moose and feral horses by wolves in four packs in winter 2006 (1 December-31 March) and four packs in summer 2008-2009 (1 May-26 August) in west-central Alberta, Canada.

	Summer				Winter			
	Species							
Pack	Deer	Elk	Moose	Horse	Deer	Elk	Moose	Horse
1	1.68	0.68	0.73	0.20	0.89	1.25	0.77	5.94
2	1.22	0.71	0.55	0.00	1.30	0.00	0.49	0.00
3	1.10	1.16	0.77	0.29	0.70	2.13	0.00	0.00
4	1.34	0.06	0.74	0.00	1.39	0.31	0.79	0.00
Mean	1.33	0.65	0.70	0.12	1.07	0.92	0.51	1.49
Upper CI	1.58	1.09	0.8	0.26	1.39	1.87	0.87	4.4
Lower CI	1.08	0.21	0.6	-0.02	0.75	-0.03	0.15	-1.42
Selection	+	0	-	-	0	0	-	0

[1] Selection index based on the selection ratio of Manly et al. (1993: page 46)

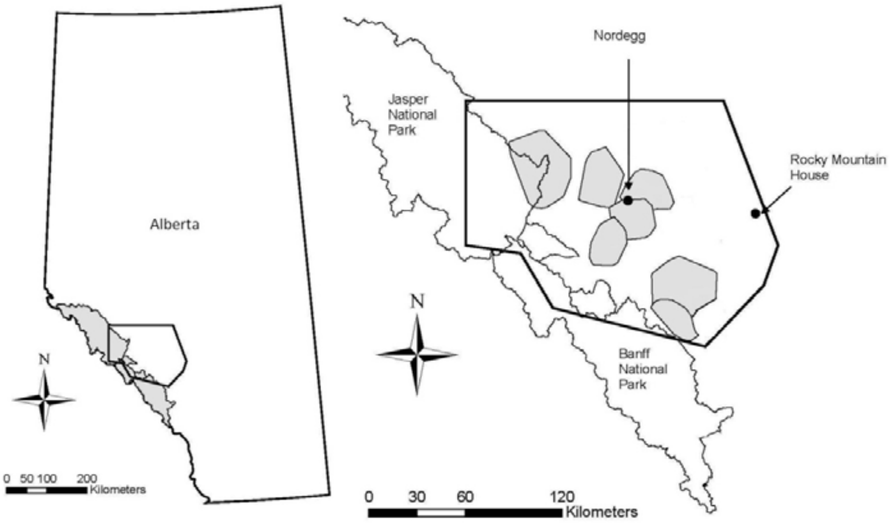


Figure 3.1. Location of the study area and wolf pack home ranges in west-central Alberta, Canada.

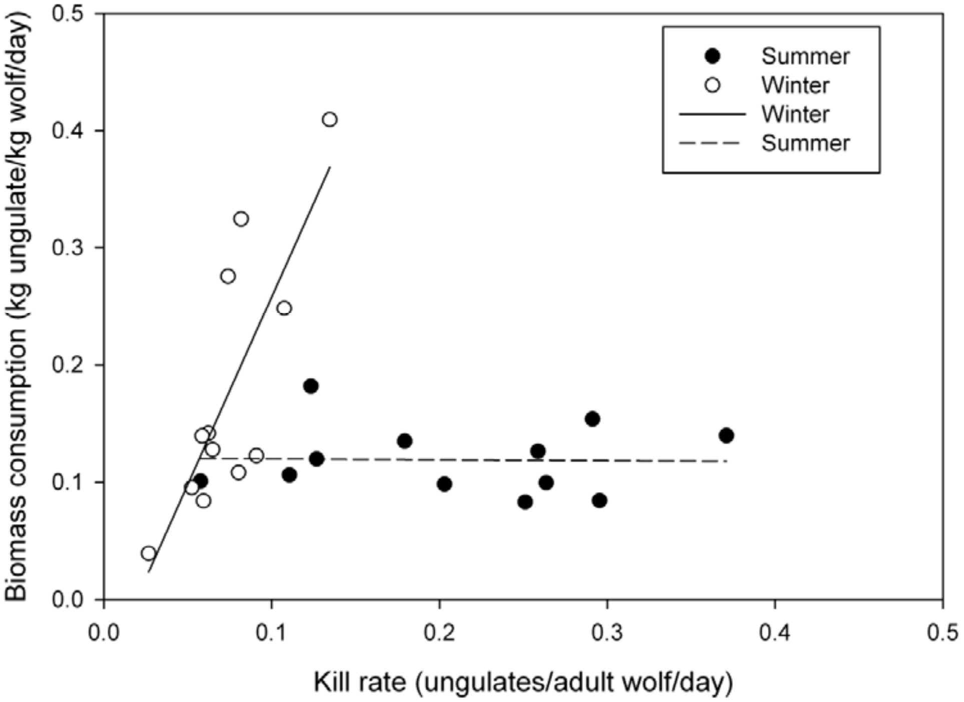


Figure 3.2. Relationship between daily biomass consumed (winter; kg ungulate/kg wolf/day, summer; kg ungulate/metabolic-rate-equivalent adult kg /day) and kill rate (ungulates/adult wolf/day) of wolves in western-central Alberta, Canada for summer *n* = 12 (black dots) and winter *n*=11 (white dots). Correlation for winter (r = 0.77) and summer (r = 0.00)

CHAPTER 4

SUMMARY

In this thesis I present a new approach to monitoring wolves and estimating wolf kill rates. I explored intra- and inter-seasonal variations in kill rates of wolves in a multi-prey ungulate population. In Chapter 1, I used a combination of high intensity GPS tracking of wolves to locate wolf-killed, adult prey and auxiliary scat analysis to estimate neonate prey killed, which were expected to be underestimated if relying on GPS techniques alone (Palacios and Mech 2011). I found that wolves selected for neonate prey of all species with deer comprising the greatest proportion of both adult and neonate prey killed. Consequently, kill rates were among the highest (~1.5-2.5 times) reported in the limited literature on summer wolf predation (Sand et al. 2008, Metz et al. 2011. *in prep.,* Jedrezejewski et al. 2002). A low contribution of adult prey, rapid growth weight of pups, and a decline in kill rates of neonate prey in later summer resulted in a decline in biomass consumption rates over the summer.

Building on my findings from Chapter 1, in Chapter 2 I compared summer kill rates to winter kill rates of wolves from the same study area (Webb 2008), and determined the relative abundance of prey species within each wolf pack's home-range for both winter and summer to identify differences in prey selection between seasons. I concluded that deer remained the abundant ungulate prey species killed and provided the greatest biomass in the diet of wolves in both seasons. While kill rates of ungulates were lower in winter than summer, wolves were less food limited in winter than summer and this was reflected in their seasonal body masses. Higher food consumption in winter was related to reduced pack size in winter, likely resulting from high wolf harvest rates (Webb et al. 2011), combined with an increase in the proportion of adult prey killed by the remaining pack. Seasonal differences in kill rates between summer and winter may lead to significant underestimates of annual kill rates when based on winter information only, that in this study area were estimated to be ~ 29%.

Wolf Management Implications

In this study I identified several aspects of wolf-prey interactions that augment information provided from previous research on wolf ecology in west-central Alberta (Hebblewhite et al. 2006, Frair et al. 2007, Webb et al. 2008, 2011, Robinson et al. 2010). Previous research by Webb (2008) provided information only on winter kill rates. By quantifying summer kill rates from the same area, I was able to show how kill rates changed seasonally and the implications for both the ungulate prey and the wolves. I also now have provided estimates of annual kill rates, which will help managers make more informed decisions on the future of wolves and ungulate populations in this area.

In west-central Alberta multi-prey system, concerns have arisen over the declining elk populations within the past decades while at the same time white-tailed deer density has increased (J. Allen, Alberta Government Regional Biologist *personal communication*). It has been suggested that the increase in white-tailed deer is a result of warmer winters, increased forage from abundant clearcutting, and possibly greater resilience to predation pressure than alternate prey species (Wishart 1984; Côté et al. 2004; Charest 2005; Latham et al. 2011). These are all factors that are likely to be occurring in many of North American wolf ranges. Earlier studies that focused in the Ya-Ha-Tinda identified wolves as a major predator of elk in the montane areas (Hebblewhite et al. 2006), but both Webb (2008) and this study found that for most wolf packs in the foothills across the Clearwater County elk are secondary to deer in their importance to wolves. High wolf densities (13.31 wolves/1000 km^2) supported by deer may be having an adverse impact on elk as has been proposed for caribou (*Rangifer tarandus caribou*) in other parts of Alberta (Latham et al. 2011). In the montane environments of the Rocky Mountains, winter prey typically become concentrated in low snow areas (Nelson and Mech 1981, Huggard 1993, Kunkel and Pletcher 2001) that reduces spatial-separation between prey species and may result in a case of apparent competition (Holt 1977). The extent to which wolves may limit elk population relies on many factors. Data presented here suggests predation on elk may not be sufficiently high to support the wolf populations, but further demographic modeling may show it to be sufficient to have an important additive effect to that of other predators (e.g. cougars and bears) in the area. At present, human harvest on elk in this area is restricted and no legal harvest occurs on females. If concerns of elk declines are substantiated in population monitoring and deteriorating habitat conditions are ruled out, then future research should focus on how current management influences the suit of predators in this area.

Finally, relatively high wolf harvest rates predominately of pre-reproductive wolves-have been identified as a probable cause of reduced pack sizes in winter compared to summer (Webb et al. 2011). The resulting smaller packs in winter (~5 wolves/pack) that obtain higher (~2 times) biomass consumption rates than wolves in summer appear adequate to support the moderately high reproductive rates reported in this area (Webb et al. 2011). Although biomass consumption declines over the summer, it also remains above the reported requirements of 0.09 kg/kg wolf/day (Peterson and Ciucci 2003), indicating that food limitations do not severely limit pup survival and population grow of wolves in this area (Webb et al. 2011).

From a broader prospective, wolves are rapidly re-colonizing their historical ranges across North America. To effectively manage these predator – prey systems depends on reliable estimates of kill rate, prey composition, the implication for prey populations and knowledge of the ecological factors causing these to vary. Kill rate data of wolves in summer is currently lacking from many areas inhabited by wolves and it is now clear there are important seasonal dynamics. I provide a potential approach to combine GPS cluster methods to estimate kill rates with scat analysis, but intensive field studies are required. What is clear is that due the controversies surrounding wolf management, reliable information is critical for wildlife managers to make informed decisions before initiating predator management actions (Smith et al. 2006, Barber-Meyer et al. 2008).

LITERATURE CITED

Barber-Meyer, S. M., L. D. Mech, and P. J. White. 2008. Elk calf survival and mortality following wolf restoration to Yellowstone National Park. Wildlife Monographs :1-30.

Charest, J. 2005. Canada and the US: Change and continuity. International Journal 60:321-328

Cote, S., T. Rooney, J. Tremblay, C. Dussault, and D. Waller. 2004. Ecological impacts of deer overabundance RID A-5410-2008. Annual Review of Ecology Evolution and Systematics 35:113-147.

Frair, J. L. 2005. Survival and movement behavior of resident and translocated wapiti (*Cervus elaphus*): Implications for their management in west-central Alberta, Canada. Thesis, University of Alberta, Edmonton, Alberta, Canada.

Frair, J.L., E.H. Merrill, J.R. Allen. 2007. Know thy enemy: experience affects elk translocation success in risky landscapes. Journal of Wildlife Management. 71:541-554.

Holt, R. 1977. Predation, apparent competition, and structure of prey communities. Theoretical Population Biology 12:197-229

Hebblewhite, M., E.H. Merrill, L.E. Morgantini, C. A. White, J. R. Allen, E. Bruns, L. Thurston, and T. E. Hurd. 2006. Is the migratory behavior of montane elk herds in peril? the case of Alberta's Ya Ha Tinda elk herd. Wildlife Society Bulletin 34:1280-1294.

Huggard, D. J. 1993. Prey selectivity of wolves in Banff National-Park .2. age, sex, and condition of elk. Canadian Journal of Zoology-Revue Canadienne De Zoologie 71:140-147.

Huggard, D.J. 1993. Prey selectivity of wolves in Banff National Park .1. prey species. Canadian Journal of Zoology-Revue Canadienne De Zoologie 71:130-139.

Kunkel, K., and D. Pletscher. 2001. Winter hunting patterns of wolves in and near Glacier National Park, Montana. Journal of Wildlife Management 65:520-530.

Latham, A.D., M.C. Latham,N.A. McCutchen, S. Boutin. 2011. Invading white-tailed deer change wolf-caribou dynamics in north-eastern Alberta. Journal of Wildlife Management. 75:204-212.

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:e17332.

Metz, M.C., J.A. Vucetich, D.W. Smith, D.R. Stahler, and R.O. Peterson. 2011. Seasonal patterns of predation for grey wolves in the multi-prey system of Yellowstone National Park *(in prep).*

Nelson, M., And L. Mech. 1981. Deer social-organization and wolf predation in northeastern Minnesota. Wildlife Monographs :1-53

Palacios, V., and L.D. Mech. 2011. Problems with studying wolf predation on small prey in summer via global positioning system collars. European Journal of Wildlife Research 57:149-156.

Peterson, R.O., and P. Ciucci. 2003. The wolf as a carnivore. Pp. 104-130 in Wolves: behavior, ecology, and conservation (L.D. Mech, and L. Boitani, eds.). The University of Chicago Press, Chicago, Illinois, USA.

Robinson, B.G., M. Hebblewhite, E.H. Marrill. 2010. Are migrant and resident elk (*Cervus elaphus*) exposed to similar forage and predation risk on their sympatric winter range? Oecologia. 164: 265-275.

Sand, H., P. Wabakken, B. Zimmermann, O. Johansson, H.C. Pedersen, and O. Liberg. 2008. Summer kill rates and predation pattern in a wolf-moose system: Can we rely on winter estimates? Oecologia 156:53-64.

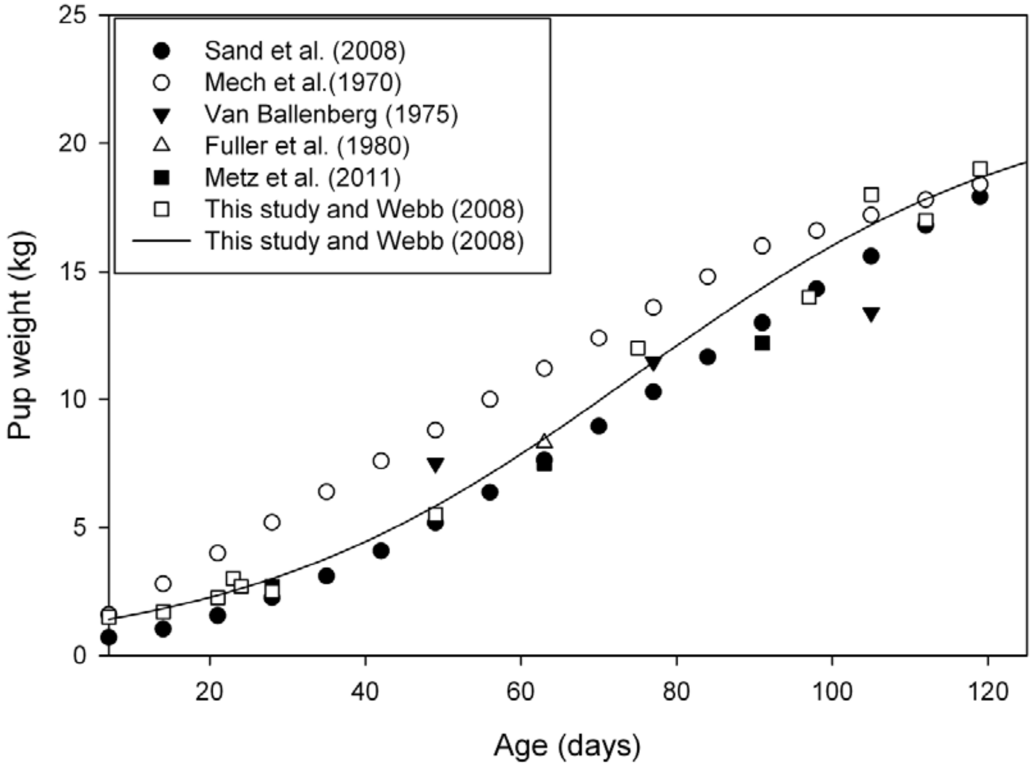
Smith, D.W., Stahler, D.R., And Guernsey, D.S. 2006. Yellowstone Wolf Project: Annual Report, 2005. National Park Service, Yellowstone Center For Resources, Yellowstone National Park, Wyoming.

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

Webb, S.L., M.R. Dzialak, J.J. Wondzell, S.M. Harju, L.D. Hayden-Wing, and J.B. Winstead. 2011. Survival and cause-specific mortality of female rocky mountain elk exposed to human activity. Population Ecology 53:483-493.

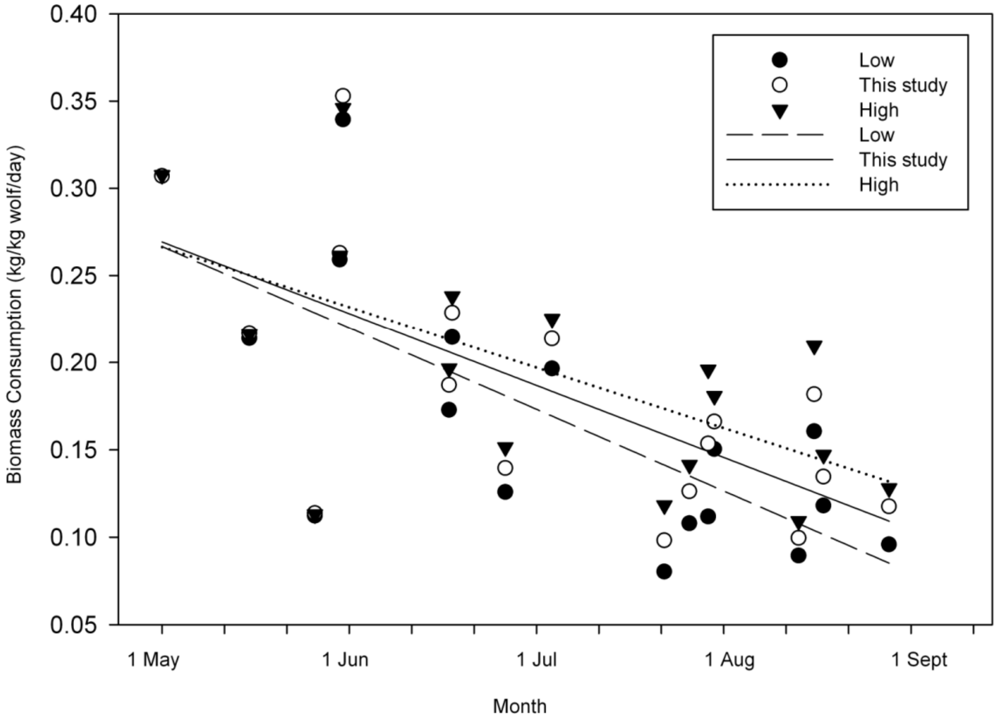
Wishart, W.D. 1984. Western Canada. Pp. 475-486 in White-tailed deer: ecology and management (L.K. Halls, ed.). Wildlife Management Institute. Stackpole Books, Harrisburg, Pennsylvania, USA.

APPENDIX I



Appendix I. Polynomial sigmoidal growth curves fitted to pup weights from this study and data from Webb (2008) data. Other studies pup weights and growth curves also shown to show close approximation. Sand et al. (2008) growth curve estimates from captive wolves (n=7) and n= 320 weighing estimates. Mech et al. (1970) is a growth curve estimated from captive wolves, Van Ballenberg (1974) n=3, Fuller et al. (1980) n=1 and Metz et al. (2011) n= 3 are all recorded weights of wild pups during captures

APPENDIX II



Appendix II. A comparison of biomass consumption trends over the summer (starting at May 1) using three scenarios of combined growth rates of neonate prey and pup survival rates. low estimates used von Bertalanffy growth curve: $M(t) = A[1 - 1/3e^{-K(t-I)}]^3$, where $M(t)$ = mass (kg) at age t, A = maximum mass of either adult male or adult female, K = 0.0049, and I = 80 days, provides low growth rate estimates compared to the literature and was combined with a comparatively high pup survival rates (0.9, Alaska) from the literature. High estimates were based on Stelfox (1993) ungulate growth curve estimates which were amongst the highest found in the literature and were combined with pup survival rates of 0.5, which is amongst the lowest in the literature excluding diseased populations survival rates. Mean is the mean value between the two scenarios and the rates used in this study. All survival rates are based on summer survival (1 May - 1 October). Although prey weights and pup survival rates are significantly different all three scenarios show a similar decreasing tend in biomass consumption rates of wolves over the summer. However, biomass consumption estimates between the 3 scenarios become increasingly different towards later summer with a difference of ~ 0.05kg/kg wolf/day by 1 September.

APPENDIX III

Appendix III. Wolf weights; Season, date of measurement, sex, estimated age, weight (kg) and location of capture of wolves from west-central Alberta, 2003-2009.

Season	Date	Sex	Estimated Age	Weight (kg)	Location
Winter	1/8/2005	Female	Adult	36.36	Ya Ha Tinda
Winter	3/1/2006	Female	Adult	32.73	McGregor Lake
Winter	1/29/2005	Female	Adult	38.64	Brazeau Slopes
Winter	1/29/2005	Female	Adult	38.64	Prairie Creek
Winter	12/23/2005	Female	Adult	40.91	Brazeau Flats
Winter	1/12/2006	Female	Adult	40.91	Camp 15 Rd
Winter	3/12/2006	Female	Adult	40.00	Radial Lk
Winter	12/18/2004	Female	Adult	37.27	Radial Lk
Winter	2/10/2006	Female	Adult	38.64	Trout Creek
Winter	12/5/2003	Female	Adult	39.55	Radial Lake
Winter	12/6/2003	Female	Adult	37.27	Brazeau
Winter	12/27/2005	Female	Adult	42.27	Trout Creek
Winter	3/3/2006	Male	Adult	44.09	Bar 75 Ranch
Winter	1/9/2004	Male	Adult	41.82	McGregor Lak
Winter	2/18/2006	Male	Adult	41.82	Radial Lake
Winter	12/13/2004	Male	Adult	59.09	Prairie Creek
Winter	12/25/2004	Male	Adult	47.73	Nordegg River
Winter	1/7/2005	Male	Adult	48.18	Radial Lake
Winter	1/4/2005	Male	Adult	55.00	Brazeau
Winter	12/20/2005	Male	Adult	63.64	Ya Ha Tinda
Winter	12/21/2005	Male	Adult	43.18	Brazeau
Winter	2/12/2005	Male	Adult	41.82	Jock Lake
Winter	1/23/2005	Male	Adult	44.09	Radial lake
Winter	3/13/2006	Male	Adult	50.00	Radial lake
Winter	2/12/2005	Male	Adult	43.18	Trout creek
Winter	1/29/2005	Male	Adult	43.18	Jock lake
Winter	1/28/2006	Male	Adult	45.45	Williams Crk
Winter	1/7/2004	Male	Adult	40.91	Onion Lake
Winter	12/30/2003	Male	Adult	54.55	Nordegg river
Winter	3/16/2006	Male	Adult	39.09	Brazeau
Winter	3/12/2004	Male	Adult	40.00	Colt Creek
Winter	1/22/2005	Male	Adult	41.82	Trout Creek

Season	Date	Sex	Estimated Age	Weight (kg)	Location
Winter	1/12/2006	Male	Adult	50.00	Radial Lake
Winter	3/26/2004	Male	Adult	43.18	Jock Lake
Winter	12/27/2003	Male	Adult	50.00	Colt Creek
Winter	12/8/2005	Female	Yearling	32.00	Ranch
Winter	12/12/2005	Female	Yearling	37.00	Wildhorse
Winter	12/6/2006	Female	Yearling	40.00	Colt Creek
Winter	12/7/2005	Male	Yearling	34.00	Trout Creek
Winter	12/7/2005	Male	Yearling	36.00	Jock Lake
Winter	12/8/2005	Male	Yearling	50.00	Ram Falls
Summer	5/21/2004	Female	Adult	39.09	Nordegg River
Summer	7/16/2004	Female	Adult	37.27	Williams Crk
Summer	7/23/2004	Female	Adult	35.91	Jock Lake
Summer	8/20/2004	Female	Adult	36.82	Shundra Creek
Summer	8/20/2004	Female	Adult	37.73	Chungo Crk
Summer	7/9/2005	Female	Adult	34.09	Colt Creek
Summer	5/31/2009	Female	Adult	34.09	Prairie Creek
Summer	6/4/2008	Female	Adult	37.73	Ranch Pack
Summer	5/31/2004	Male	Adult	44.55	Blackstone
Summer	7/13/2004	Male	Adult	40.45	McGregor Lak
Summer	8/20/2005	Male	Adult	46.36	Blackstone
Summer	6/12/2008	Male	Adult	41.82	Radial lake
Summer	6/17/2008	Male	Adult	40.91	Jock Lake
Summer	8/6/2003	Female	Yearling	28.00	Prairie Creek
Summer	8/20/2003	Female	Yearling	25.00	Radial Lake
Summer	8/23/2008	Female	Yearling	22.00	Brazeau Flats
Summer	7/20/2008	Female	Yearling	18.00	Brazeau Flats
Summer	6/11/2008	Male	Yearling	33.00	Nordegg River
Summer	5/21/2004	Male	Yearling	26.00	Nordegg River
Summer	8/20/2008	Male	Yearling	28.00	Blackstone