# FORAGING STRATEGIES OF EASTERN WOLVES IN RELATION TO MIGRATORY PREY AND HYBRIDIZATION

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# ABSTRACT

## Foraging strategies of Eastern wolves in relation to migratory prey and hybridization

### Karen Loveless

Modeling of predator-prey dynamics in relation to changes in predator and prey densities has failed to explain most variation in kill rates or prey selection in multiple prey systems. This thesis focuses on other sources of variation in kill rates and prey use, specifically changes in costs and benefits of prey types with variation in accessibility and vulnerability to predators, as well as variation in genetic admixture of wolves (*Canis* sp.) potentially influencing predator effectiveness with different prey. Using fine scale GPS data and intensive field efforts, relative use of moose and deer by wolves was quantified, and assessed relative to changes in winter conditions affecting accessibility and vulnerability, and among hybrid classes of wolves. Predation patterns were influenced by accessibility of deer and vulnerability of moose, and changed with winter progression. Predation patterns differed among hybrid classes of wolves, suggesting further research on this question is warranted.

Keywords: eastern wolf, moose, deer, predator-prey dynamics, optimal foraging, genetic admixture, hybridization, prey selection

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And thanks to my wonderful and crazy family, it's been a long haul and I could not have done it without their love and support.

## Dedication

This thesis is dedicated to the memory of my sister, Leslie Ann Loveless, whose footsteps I followed on my early adventures into the canyons and forests of our childhoods, and who fought with all her heart and soul to stay with us. Her infectious love of life and appreciation for the big and little things will remain with me always.

## TABLE OF CONTENTS

Page

# LIST OF TABLES

APPENDIX

# LIST OF FIGURES

## LIST OF FIGURES-CONTINUED

# Foraging strategies of Eastern wolves in relation to migratory prey and hybridization

## INTRODUCTION

Animals adapt to changes in availability of resources in a variety of ways, with implications for movement patterns, diet and population dynamics. Optimal foraging theory predicts selective pressures cause animals to make foraging decisions that optimize benefits and minimize costs (Charnov 1976). However, attempts to document optimal foraging in natural predator-prey systems have produced conflicting results (Sih & Christensen 2001). Though animals may not always forage optimally, perhaps due to incomplete knowledge of available resources, limited documentation of optimal foraging could be due to the difficulty in accurately quantifying costs and benefits of exploiting various prey types (Lima et al. 2003) or changes in environmental conditions. Understanding foraging choices by animals is important for habitat and population management.

To date, large mammal predator-prey research has focused on identifying the patterns and mechanisms influencing how predators select prey, the rate at which they kill these prey, the resulting influence on population dynamics, and how systems stabilize or destabilize over time (eg Fuller and Keith 1980, Messier and Crete 1985, Dale et al. 1994, Creel and Creel 1995, O'Donoghue 1998, Hayes and Harestad 2000, Honer et al. 2002, Jedrzejewski et al. 2002, Smith et al. 2004). Mechanisms influencing predator foraging strategies may be driven by prey abundance (Holling 1959), accessibility (Hopcraft et al. 2005) and vulnerability (Quinn and Cresswell 2004). They may likewise be driven by a predator’s skill in locating and subduing prey (Sand et al. 2006, Holekamp et al. 2007, McNulty et al. 2008), density-dependent competition (Becker et al. 2009) and grouping behavior of both predators and prey (Fryxell et al. 2007). Although much attention has been paid to abundances and ratios of prey and predator, recent work has highlighted that predator-prey dynamics are likely mediated by abiotic factors as well, which can vary on large and small scales and interact with prey abundance, accessibility and vulnerability, and predator efficiency. Though there is ongoing debate on the issue (Abrams & Ginsberg 2000), the importance of prey density (Messier 1994, Hayes and Harestad 2000) and predator-prey ratios (Arditi & Ginsberg 1999, Vucetich et al. 2002, Jost et al. 2005, Schenk et al. 2005) has been established for some systems. However, predator and prey densities only partially explain observed variations in kill rates measured in natural systems (Vucetich et al. 2002, Jost et al. 2005, Becker et al. 2009). Quinn and Cresswell (2004) found that prey vulnerability was a better predictor of kill rates than prey density for sparrow hawks (*Accipiter nisus*) preying on redshanks (*Tringa tetanus)*, and long term data suggest that moose vulnerability contributes to variation in wolf population dynamics on Isle Royale (Vucetich and Peterson 2004). Hopcraft et al. (2005) found that prey accessibility was more important than abundance in explaining lion foraging success. Incorporating variation in costs and benefits of predation on different prey types due to changes in prey accessibility and vulnerability should improve our understanding of prey selection in multiple prey systems, and refine existing functional response models.

For northern ungulate-wolf systems, winter conditions mediate predator-prey relationships. Energetic demands of thermoregulation in severe temperatures (Verme

1969, Renecker 1978, Delgiudice 2002), locomotion in deep snow (Kelsall 1969, Telfer 1970, Renecker & Schwartz 1998, Peek 1998), as well as reduced availability of high quality forage (Schwartz & Renecker 1998) result in deteriorating body condition of ungulates in winter. Wolves also have increased locomotor challenges in winter; however, they may have an advantage in deep or crusted snow conditions as they are more able to travel on top of the snow due to their lower foot-loading relative to most prey (Paquet 1992, Crete and Lariviere 2003). The cost-benefit ratio of individual prey species may change as prey vulnerability and costs of locomotion for both wolves and their prey increase with snow depth.

Whereas shifts in prey habitat associations with changing winter conditions may affect accessibility for predators on a fine scale (Hebblewhite et al. 2005, Gower et al. 2008), seasonal migration of prey species can result in a larger scale decline in resource availability (Nelson and Mech 1986, Dale et al. 1994). Non-hibernating predators may respond by moving with prey (Hofer and East 1993, Frame 2005), or switching to an alternative resource (Dale et al. 1994, Danell 2006, Patterson et al. 1998). In some predator-prey systems both responses have been observed (Messier 1985, Ballard et al. 1997, Honer et al. 2005). Alternate prey availability (Messier 1985, Ballard et al. 1997) and proximity to prey wintering areas (Messier 1985) can influence whether predators switch prey or move with the principal prey species. However, low alternate prey availability has not consistently resulted in migratory foraging (Patterson and Messier 2001, Danell 2006). These contrasting results highlight the need to further examine predator response to changes in accessibility of preferred prey.

In Algonquin Provincial Park, eastern wolves (*Canis lycaon*) prey on moose (*Alces alces*), white-tailed deer (*Odocoilus virginianus*) and beaver (*Castor canadensis*). Most deer leave the park in winter (Quinn 2005). Some wolf packs follow, foraging primarily in the deer wintering areas on “migratory foraging” excursions (Forbes and Theberge 1996), while other packs remain on territory, apparently relying on moose and alternate prey such as beaver and snowshoe hare (*Lepus americanus*). Migratory foraging can be costly due to the energetic cost of travel, possible human-caused mortality (Forbes and Theberge 1995), and an increased risk of intra-specific conflict with territorial trespassing. Likewise, increased predator densities in areas of high prey density may increase intra-specific conflict as well as competition for prey (Beckett et al. 2008). However switching prey may not be a viable option if alternate prey are scarce or unmanageable. Eastern wolves are small in relation to other species of wolves, and body size is important to foraging success (Sand et al. 2006, McNulty et al. 2009). Previous research concluded that eastern wolves were “deer specialists” (Pimlott et al. 1969) and “inefficient predators of moose” (Forbes and Theberge 1996) whose use of moose is primarily scavenged winter kills (Forbes and Theberge 1992), However predation on moose does occur in this system (Theberge and Theberge 2004). Recent observations of inconsistency in off-territory foraging by Algonquin wolves (B. Patterson et al., unpublished data) raised several questions. For example, what is the extent of reliance on moose by non-migratory wolves? Can small bodied eastern wolves subsist on moose? What factors influence migratory foraging among packs?

Though environment and learning are important in terms of what prey are available and the ability of an animal to exploit resources, there is also evidence that genetics influence foraging behavior due to variable preferences across genotypes (Riechert 2005), as well as differences in predator ability due to morphological variation (McNulty et al. 2009). Small variations in physiology or behavior could influence how efficient an animal is at exploiting a resource, and therefore which resource will be most beneficial for an animal to select. Though research is scant, there is evidence of genetically influenced foraging in social, behaviorally plastic animals. For example, hooded crows (*Corvus corone cornix*) and carrion crows (*Corvus c. corone*) have distinct foraging habitat preferences, with hybrids selecting intermediate habitat (Saino 1992). In a morphological study in an eastern wolf hybrid zone in southern Ontario, coyote-like phenotypes used small bodied prey (snowshoe hare, muskrat, ground-hog), whereas wolf-like phenotypes preferred deer (Sears et al 2003). Though there is evidence of landscape (Manel et al. 2003, Geffen et al. 2004), behavioral (Kingston and Gwilliam 2007), and ecological factors (Carmichael et al. 2001, Pilot et al. 2006, Musiani et al. 2007) exerting significant influence over patterns of gene-flow, differences in resource selection due to genetic variability within populations has received little attention. Investigating genotype-specific resource selection is important not only for managing admixed populations, but for gaining theoretical insight into the aspects of ecology that may be influenced by genetic variation.

Recent genetic research has concluded that *C. lycaon* is a distinct species of wolf, most closely related to the red wolf (*C. rufus*, Wilson et al. 2000). The range of eastern wolves is thought to be limited to central Ontario and western Quebec, and there is evidence of historic hybridization with both gray wolves (*Canis lupus)* and coyotes (*Canis latrans)*. The extent and mechanisms of hybridization are still being investigated, however, it is apparent that long-standing hybridization exists throughout Ontario and the Great Lakes region, with a *C. lupus* x *C. lycaon* hybrid dominating central and northern Ontario and the Great Lakes, a *C. latrans* x *C. lycaon* hybrid (eastern coyote) dominating southern Ontario, and the Algonquin area representing the core of the purest remaining *C. lycaon* population (Wilson et al. 2009, Fig. 1). Given that there is variation in foraging strategies of Algonquin wolves, and hybridization with *C. lupus* and *C. latrans* in Algonquin, the potential influence of hybridization on foraging behavior is important to consider. If there is a genetic predisposition for prey preference, or if body size is a determining factor in prey utilization, then hybridization may have implications for current and future predator-prey relations in Ontario.

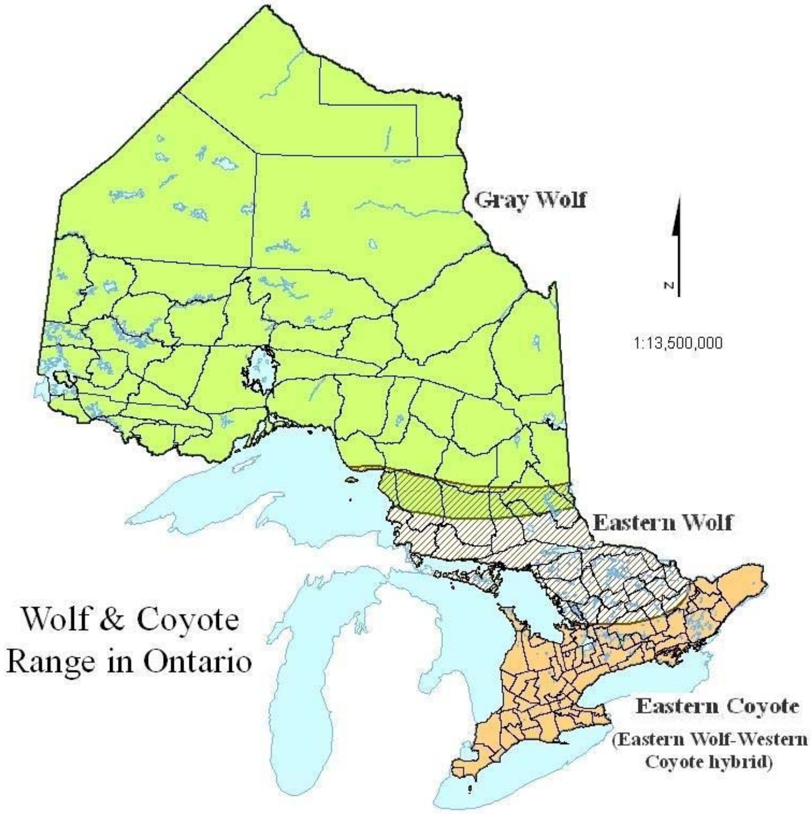


Figure 1. Range of eastern wolf (*C. lycaon*) compared to populations dominated by Gray wolf (*C. lupus*) and eastern coyote (*C. latrans*) in Ontario, based on Kolenosky and Stanfield (1975).

Methods for measuring prey use have been inconsistent across studies, with predation rates (per prey), kill rates (per predator) or handling time (days per kill) commonly used but with varied definitions (Hebblewhite 2003). Estimation of biomass available for consumption by wolves from measured kill rates is a widely used approach (Kolenosky 1972, Fuller and Keith 1980, Fuller 1989, Creel and Creel 1995, Creel 1997, Hayes et al. 2000, Vucetich et al. 2004, Hebblewhite et al. 2003); however, it involves many potential sources of error including estimating biomass of prey (which can vary greatly by sex and age class), number of wolves feeding on each carcass, proportion of biomass that is edible, proportion of carcass utilized by specific individuals or packs, and loss of biomass to intra- and inter-specific scavengers, especially ravens (*Corvus corax*). Additionally, if relating biomass consumed to energy requirements or expenditure of wolves, there is additional error involved in estimating metabolic rates, costs of locomotion in relation to movement rates and snow depth, and conversion of biomass to Kjoules (Creel & Creel 1995, Creel 1997, Vucetich et al. 2004). Despite these many sources of error, kill rates remain an important currency for examining predator-prey relationships and animal energetics. Handling time is often used in conjunction with or alternatively to kill rates, where days per kill are used to estimate predation rates. These calculations are less informative in that they do not address the precise energetic gain derived per kill, but are used for considering wolves gross kill rates (e.g., deer/day/wolf), impact on prey populations (#prey/winter), and the relative importance of various prey species to wolf sustenance. Though work has been done to standardize methodology and increase accuracy in studies of kill rates, error and bias in each of these methods has not been examined.

Apparent variation in prey use among wolf packs, and the naturally occurring spatial and temporal variability of prey distribution and vulnerability with respect to winter progression in Algonquin Provincial Park provided an opportunity to examine the influence of changing prey accessibility and vulnerability on kill rates and prey selection by wolves in this multi-prey system. Additionally, hybridization within the study population provided an opportunity to examine the influence of genetic admixture on patterns of prey use. We employed a fine-scale continuous monitoring study design to develop a precise measure of prey utilization. We then compared methods of measuring prey use and examined how differences among methods may influence analysis of kill rates and prey selection. Objectives of the study were to:

1) Examine predator responses to variation in accessibility and vulnerability of prey types
2) Investigate influence of hybridization on prey selection
3) Refine analytical methods for measuring kill rates and relative prey use.

## METHODS

### Study area

The study was centered in Algonquin Provincial Park (45 N, 78 W) in south central Ontario, at the boundary of Boreal and the St. Lawrence Forest regions (Rowe 1972). A longitudinal divide in topography separated the study area into two distinct forest types. The western portion consisted of rocky upland forest consisting of a mix of tolerant hardwood and mixed conifer/hardwood forests dominated by sugar maple (*Acer saccharum*), American beech (*Fagus grandifolia*), yellow birch (*Betula alleghaniensis*) with eastern hemlock (*Tsuga canadensis*) and balsam fir (*Abies balsamea*). The eastern portion was rolling to flat terrain dominated by white pine (*Pinus strobes*), red pine (*P. resinosa*) and jack pine (*P. banksiana*) interspersed with poorly drained areas dominated by tamarack (*Larix laricina*), eastern white cedar (*Thuja occidentalis*) and black spruce (*Picea mariana*). Lakes and streams were abundant throughout the study area, with extensive bogs and ponds in low-lying areas. Elevation ranged to 580m on the west side, and between 180-380m in the eastern portion (Strickland 1993).

## Field data collection

We captured wolves using modified foothold traps, neck snares, and aerial netgunning as described in Patterson et al. (2004). Wolves were fitted with Lotek VHF or GPS 4400 radiocollars, and blood, hair samples and body measurements were taken during handling. Packs were monitored from the air weekly or as weather permitted, and from the ground when possible. GPS data were downloaded bi-weekly from each GPS collar, or as conditions allowed.

GPS data were imported into GIS using ARCview 3.2, and potential kill sites were identified as “clusters” of GPS points representing a location where one or more collared wolves spent 3 or more hours within a 100 meter radius. GPS collars were programmed to take locations every 90 minutes for most of the study period; however, there were some periods of intensive monitoring where fixes were obtained every 30 minutes to investigate effects of fix interval on estimation of kill rates. For sets of consecutive GPS fixes within a 100m cluster, we calculated the time spent at the cluster by allocating half of the fix interval (45 minutes) for the first and last fixes present, and 90 minutes for all other consecutive fixes present at the cluster. Though individuals within wolf packs may not always travel together, kills are normally fed upon by all pack members (Mech 1970, Peterson et al. 1998). In cases where multiple GPS collars were deployed within the same pack (n = 2), we did not find differences in clusters identified using data for either collar, until one of the animals dispersed from the pack. Therefore we assumed that the movement patterns of the GPS collared wolf were representative of the pack for the purposes of identifying kill sites. GPS error may have affected identification of possible kill sites when GPS fix acquisition attempts failed. Fix success for GPS collars in this study were fairly consistent, with an average collar fix success rate of 81% (+/- 2.3% SE).

Cluster sites were investigated from the ground as quickly as possible, depending on weather conditions and accessibility (see results). Field crews thoroughly searched a 100 m radius around the cluster center for signs of kills, beds, and tracks. Clusters that could not be adequately searched due to snowfall or accessibility were investigated in spring after snowmelt. Any remains of a kill or wolf activity were documented. Prey species were identified, and prey sex and age class (juvenile, yearling, adult, old adult) were recorded if sufficient remains were present. Incisors were collected for aging by cementum annuli (Mattsons Lab, MT) to investigate age structured predation patterns.

Pack sizes were estimated through aerial and ground tracking throughout the winter. When visual observations from the air were not possible, tracks of wolves were backtracked until the number of wolves travelling together could be estimated from the number of tracks. Additional pack counts were obtained by ground tracking and searching recently used cluster sites.

## Data Preparation and Analysis

### Prey use

Prey use was calculated based on estimates of biomass consumed, and handling time measured at a coarse and fine scale for each respective prey species. Past estimates of handling time have typically used days per kill as the most precise measurable unit of time (eg., Fuller and Keith 1980, Fuller 1989, Messier and Crete 1995, Hayes et al. 2000, Hebblewhite et al. 2005). More recently however, fine-scale GPS data have allowed handling time to be measured more precisely as hours spent at each kill site.

For biomass consumed, we categorized each prey item by species, sex and age class. Biomass available per kill was estimated using the average weights for moose (bull = 492 kg, cow = 461 kg, calf = 160 kg; Quinn and Aho 1989), and deer in this region (buck = 105 kg, doe = 69 kg, fawn = 45 kg; Kolenosky 1972). Individuals of unknown sex or age for either species were estimated as the average of adult female and juvenile. Edible biomass was estimated at 80% and 90% for adult and fawn deer respectively following Kolenosky (1972) and 65% and 80% for adult and calf moose (Hayes et al. 2000). Scavenging by ravens is an important factor affecting biomass available to wolves and varies by pack size (Promberger 1992, Kazcenskya et al. 2003, Vucetich et al. 2004). Rates of raven scavenging were estimated using data from Promberger (1992, cited in Hayes et al. 2000) and Kazcenskya et al. (2003) by interpolating categorical estimates of scavenging rates to a continuous linear function (rate = 0.73 – 0.06*pack size) because categories for pack sizes in those studies were inconsistent with pack sizes in our study. Estimates of biomass available from all kills per pack were then divided by the number of wolves in each pack to estimate kg/wolf.

The sum of biomass available (total and by prey species for each pack) was divided by the number of days each pack was monitored during the study period, to estimate kg/wolf/day. For comparison with other studies, kg prey/kg wolf/day was also calculated by estimating average winter wolf weights from this study (28 kg), multiplied by the number of wolves in each pack. For proportion of prey in diet, biomass of moose or deer was divided by total biomass available to the pack for estimates of proportion moose (BMMS) or deer (BMDR) available to the pack. Estimated biomass available for kills known to have been used by 2 packs was reduced by half for each pack (n=4). If a carcass was not fully utilized biomass estimates were adjusted according to observations of remains (range 0.25 – 0.75, n=6).

Fine scale handling time was calculated by multiplying the GPS fix-rate with the number of GPS locations within 100m of a kill, until a subsequent kill was made. Revisits to kill sites after a subsequent kill was made were calculated separately (see data analysis). In some instances wolves carried portions of kills to other locations to consume, so we included any time spent at kill associated resting sites where evidence of prey consumption was found. Total time spent at deer and moose kill sites were each divided by total time spent at all ungulate kill sites for proportion deer (OKDR) and proportion moose (OKMS) for each pack.

For coarse-scale handling time, days to next kill were also calculated for comparison with day 0 representing the day a kill was made and including all days until the subsequent kill (Hayes et al. 2000). Proportional use of deer (HTDR) and moose (HTMS) for handling time days was calculated as the sum of deer or moose handling time divided by the total days the pack was monitored.

### Territory delineation

To quantify prey availability within each territory it was necessary to define territory boundaries for each pack. Extra-territorial excursions by wolf packs to forage on deer on their wintering grounds and migration travel routes complicated territory definitions. In order to avoid overestimating defended resources, GPS data used for defining the territory boundaries were restricted to summer months (May 1 – October 31), when deer migration and aggregation were not influencing wolf movement patterns. Fixed kernel density estimates were calculated using Home Range Tool (Rogers et al. 2007) in Arcmap 9.2, using 90% isopleths to represent defended territories (Borger et al. 2006). Data was sub-sampled to 12-hour fixes for consistency, and a proportional reference bandwidth smoothing method was used (Mills et al. 2006) in order to obtain territory boundaries represented by a single minimum polygon.

For packs with insufficient summer GPS data, we supplemented GPS points with locations obtained from VHF collared individuals during telemetry flights or ground tracking. Two packs had a low number of summer locations (n = 64 and 90) and were supplemented with VHF locations (n=22 and 20). Two other packs had no summer GPS data and territories were estimated entirely from VHF locations (n=22 and 20). The remaining 9 packs had over 100 locations for territory calculations (range 136 – 307 locations).

## Prey availability

### *Moose density*

Moose aerial inventories are conducted within and around the study area by Algonquin Provincial Park and Ministry of Natural Resources every 2 – 3 years. Surveys are done by helicopter transect between January and March, using tracks in snow to locate and record moose within 2.5 x 10 km plots throughout the park, using either a stratified or random stratified design, in accordance with Ontario Ministry of Natural Resources standards for moose population monitoring (Bisset and McLaren 1999). Kriging is a technique for interpolating spatial data, using a semivariogram to model autocorrelation within the dataset then applying this model to estimate values at unsampled locations (Clark 1979, Fortin and Dale 2005). The Geospatial Analyst extension in Arcmap 9.2 was used to krige survey data from Algonquin Park and the surrounding wildlife management units collected 2001-2006. In 2001 and 2006 surveys were truncated due to weather, resulting in some areas of the study area not surveyed. However the 2003 survey was complete. In order to address the error and variation between survey years while still incorporating all data, I supplemented partial survey data from 2001 and 2006 with 2003 data, then kriged 2001-2003 and 2003-2006 separately. Kriged layers were averaged into one predictive map, composed of $100m^2$ cells with values of estimated moose density across the study area, which corresponded well to observations of moose distribution in Algonquin (B. Steinberg, personal communication). Wolf pack territories were overlaid onto the grid of moose distribution to calculate spatial statistics of moose density for each wolf territory (Fig. 2). Mean moose density per territory was used to represent moose availability for each pack (Table 1).

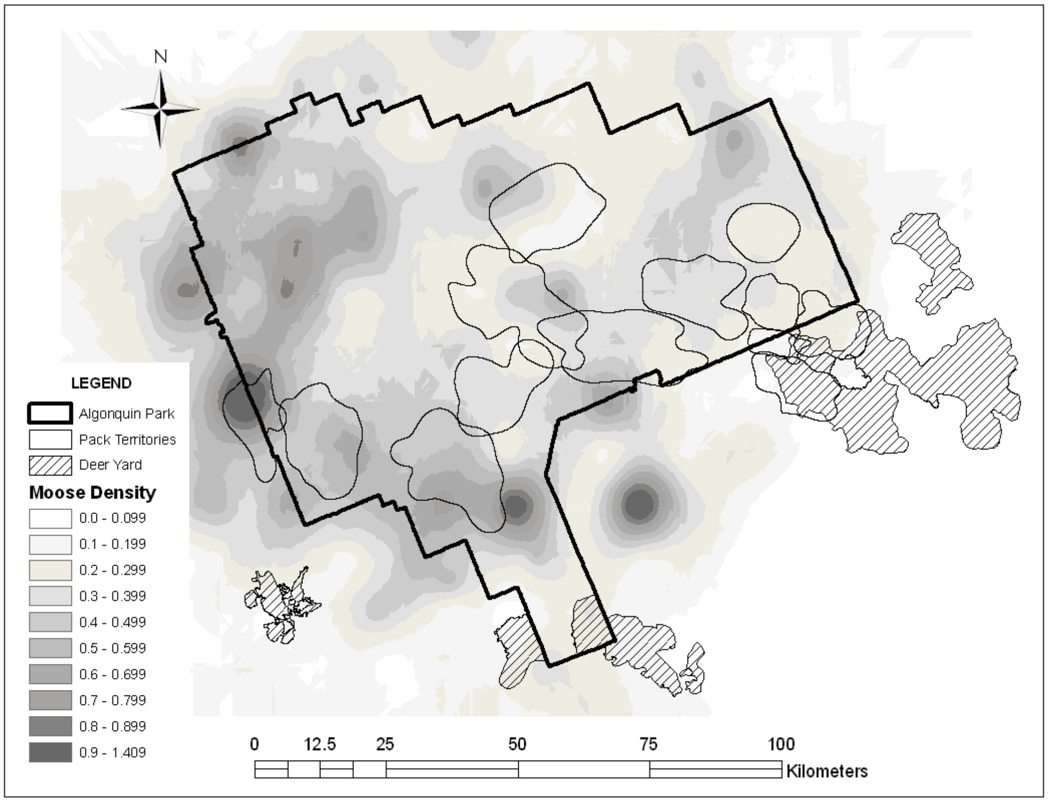


Figure 2. Algonquin Park, Ontario, including territories of wolf packs with predation data collected for 2006-2007, moose density kriged from aerial surveys conducted in 2001, 2003 and 2006, and deer wintering areas ("yards").

Table 1. Moose density within wolf territories in Algonquin Park, Ontario, kriged from 2001-2006 aerial surveys. Mean values were used to represent moose density for each pack territory.

| PACK | Territory size (km$^2$) | Min | Max | Range | Mean | Std Dev |
|---|---|---|---|---|---|---|
| Achray | 110 | 0.148 | 0.450 | 0.302 | 0.247 | 0.071 |
| BigCrow | 270 | 0.056 | 0.816 | 0.760 | 0.272 | 0.166 |
| BuckHill | 136 | 0.019 | 0.162 | 0.143 | 0.077 | 0.027 |
| Jocko | 212 | 0.208 | 0.464 | 0.256 | 0.380 | 0.052 |
| Lafluer | 49 | 0.044 | 0.280 | 0.237 | 0.101 | 0.047 |
| Louisa | 305 | 0.215 | 1.375 | 1.160 | 0.602 | 0.218 |
| Mckaskil | 330 | 0.116 | 0.735 | 0.619 | 0.366 | 0.123 |
| Pine | 86 | 0.096 | 0.445 | 0.349 | 0.321 | 0.095 |
| Potter | 239 | 0.374 | 0.871 | 0.497 | 0.466 | 0.063 |
| Radiant | 255 | 0.048 | 0.884 | 0.837 | 0.346 | 0.204 |
| Rain | 135 | 0.335 | 1.366 | 1.031 | 0.912 | 0.308 |
| Stevenson | 131 | 0.101 | 0.424 | 0.323 | 0.289 | 0.085 |
| Sunday | 212 | 0.049 | 0.527 | 0.478 | 0.333 | 0.124 |

### *Deer Distribution*

Maps of deer wintering areas within the study area are maintained by the Pembroke office of the Ontario Ministry of Natural Resources. These maps were created and are updated periodically by conducting aerial surveys and hand drawing boundaries of deer yards, and secondary wintering areas used in mild winters. The deer yard boundaries corresponded well to field observations of deer distribution in the winter of 05-06, as deer tracks were only encountered twice outside the deer yard during all winter tracking. The winter of 2006-07 was unusually mild, affecting the timing of deer migration and overall distribution. To quantify the temporal-spatial distribution of deer in winter 2006-07, track surveys were conducted throughout the study area from mid-January (onset of snow), through mid-March. Field crews recorded GPS track logs as they traversed off road, and marked a waypoint on their GPS for every set of fresh deer tracks encountered. Deer tracks partially obscured by rain or snow were not recorded. Tracks were recorded as having been made by 1, 2, 3 or 4+ individuals. Deer densities per transect were calculated by dividing total number of tracks per linear kilometer surveyed, then dividing by the number of days since rain or snowfall (day of precipitation = 1) for tracks per km per day For areas of high deer density, the inability to distinguish groups greater than four resulted in underestimation of density; however, precise densities were not necessary for determining the timing and boundaries of deer aggregation. Results of deer transects (Appendix I) were used to delineate deer yarding areas in winter 2007. Relative accessibility of deer for each pack was defined as the distance to the boundary of the deer yard, averaged over the wolf pack territory.

## Winter Progression

To investigate shifts in prey use with winter progression, winters were divided into four periods based on shifts in conditions known to influence ungulate distribution and vulnerability. Based on literature reviews of winter severity indices and ungulate/wolf winter ecology the following criteria were considered important:

Autumn deer migration to winter yards: Deer migration in areas with persistent snow cover such as Algonquin is likely to be obligate (Nelson & Mech 1986, Sabine et al. 2002, Fieberg et al. 2008) and peaks in late fall or early winter, with the majority of deer aggregated within yards once snow reaches limiting levels (Kelsall 1969, Sabine et al. 2002, OMNR 2007).

Snow depth: Hunting success of wolves increases with snow depths that hinder prey movement (Huggard 1983, Nelson & Mech 1986, Delgiudice 1998, Delgiudice et al. 2002). Deer are hindered by snow beginning at depths of 25-35cm (Kelsall 1969, Telfer 1970, OMNR 2007). Moose may shift habitat use with snow depths as shallow as 30cm (Peek 1998), and are hindered in their movements by snow depths 60-70cm (Telfer 1970, Renecker & Schwartz 1998, Peek 1998).

Snow quality: Hard crusts on top of snow occur after thaw-refreeze events or rain in winter, and create an additional hindrance to ungulates while facilitating travel for wolves (Verme 1969, Mech and Peterson 2003, Lundmark & Ball 2008).

Severe temperatures: Sustained temperatures <-17.8°c (0°f) create critical thermoregulatory demands for deer (Verme 1969, Delgiudice 2002), and temperatures <-20°c cause increased metabolic rates in moose calves when standing, requiring an energetic compromise in order to forage (Renecker 1978).

Based on above criteria winter was divided into 4 periods, with dates for each period varying by year depending on the progression of conditions specific to each winter:

1. Fall: November 1 until snow accumulation begins. Light snow and freeze/thaw cycles, deer migration in progress.
2. Early winter: Snow accumulation begins; most deer concentrated in yards, moose may begin shifting habitat use.
3. Mid-Winter: Deep snow, cold temperatures, snow crusts; deer limited to yards, moose locomotion may be hindered, behavioral adaptations for thermoregulation.
4. Late Winter: Thaw/refreeze cycles, snow melt, snow depth <30cm.

### Genetic admixture

DNA was extracted primarily from blood samples taken during capture, and several additional genetic profiles were obtained from hair or scat. Extraction and profiling of individuals was described in Rutledge et al. (submitted). To identify genetic introgression from the regions surrounding the Algonquin study area, wolves sampled from northeast Ontario, Quebec, and Frontenac Axis were included as outgroups in the admixture analysis. Because of historic hybridization throughout Ontario and the Great Lakes region, individuals of pure *C. lupus, C. latrans* or *C. lycaon* ancestry are rare or possibly non-existent (Wilson et al. 2009). Though gray wolves and coyotes throughout the region share genetic material with *C. lycaon*, Northeast Ontario and Quebec populations are *C. lupus x C. lycaon* hybrids, whereas Frontenac Axis animals are *C. latrans x C. lycaon* hybrids (Grewal et al 2004, Wilson et al. 2009), with distinct differences in morphology among the outgroups and Algonquin animals (Kolenosky and

Standfield 1975). For simplicity, we refer to outgroups as *C. lupus* and *C. latrans*, and Algonquin type wolves as *C. lycaon*, while acknowledging that admixture occurs in all three groups.

Admixture analysis was performed by L. Rutledge, PhD candidate, using a Bayesian approach in STRUCTURE 2.1 (Pritchard et al. 2000; Falush et al. 2003) to assign probability of population origin of each individual without *a priori* population assignments, and were visually corroborated using factorial correspondence analysis (FCA) using GENETIX v 4.0.5 (Belkhir et al 2004). All adult wolves sampled during the 5 year wolf demographic study (B. Patterson et al., unpublished data) were included in the analysis, as well as one pup per pack if fewer than 2 adults from that pack were sampled.

Thresholds for identifying non-admixed individuals are commonly set to 0.9 likelihood of population membership, with values falling below 0.9 indicative of admixture (Vaha & Primmer 2006). In populations known to be highly hybridized, in which there may no longer be individuals of "pure" origin, a threshold of 0.8 has been used for a wider definition of the parental types, and more conservative definition of hybrid animals (Pierpaoli et al. 2003, Adams et al. 2007). To minimize the subjectivity in our analysis, we considered admixture as a continuous variable, using raw values of likelihood of membership in each outgroup to represent admixture. Admixture influence may operate on a pack or individual level, therefore we calculated admixture by pack using two approaches:

1) Pack-average: average likelihood values across sampled pack members
2) Pack-maximum: the highest likelihood score among sampled pack members.

For the purposes of summarizing trends by admixed packs, we categorized packs as admixed with a threshold of 0.8. Accordingly, individuals with less than 0.8 likelihood of membership in the *C. lycaon* population were categorized as "admixed" then assigned to a category of either *lupus*-admixed or *latrans*-admixed, depending on which of these populations showed >0.2 likelihood of membership. Packs were then categorized as "*C. lycaon*", "admixed-*lupus*" or "admixed-*latrans*" accordingly:

<u>Pack Average:</u> Only those packs with a pack average less than 0.8 likelihood of membership in *C. lycaon* and greater than 0.2 likelihood membership in an outgroup would be considered admixed.

<u>Pack Maximum:</u> A pack with any member <0.8 likelihood of membership in *C. lycaon*, and >0.2 likelihood of membership in an out-group was categorized as an admixed pack.

## Data Analysis

Population level patterns of prey use and differences among measures of prey use were tested for significance using one-way ANOVA or t-tests. Comparisons between distribution of ages in the moose population and predated moose were done using Kolmogorov-Smirnov test (K-S test). Chi-square tests were used to compare predation on moose by age category. Multiple linear regression was used to test for significant effects of moose density, distance to deer aggregation, pack size and *C. latrans* and *C. lupus* admixture on prey use, represented by time spent on deer kills as proportion of time spent on all ungulate kills (OKDR). Global models for full winter and for each winter period were tested separately. Independent variables were tested for linearity before inclusion in each model, and variables that did not improve model $R^2$ values ≥3% were dropped from each model (Quinn and Keough 2002). Multicollinearity was examined with tolerance tests for all independent variables used in each model, and was defined as any relationship with a tolerance score < 0.1 (Quinn and Keough 2002). ANOVA table results were included with regression output in order to report proportion of variation explained by each variable (Table 6). ANCOVA was used to examine the effects of winter progression on full winter prey use, with winter period included as a discrete independent variable in addition to above listed continuous variables.

## RESULTS

### Field data collection

Predation data was collected on 13 packs for portions of 16 pack-winters (2006, n=11; 2007, n=5), including 87 wolves over 1669 days. Monitoring of packs was continuous throughout winter, or from collar deployment to collar failure or wolf mortality. Continuous days monitored ranged from 43–171 (Table 2). A total of 1572 locations where wolves spent 3 or more hours were identified and considered “clusters”. Of these, 1482 (94.2%) were investigated with prey remains being discovered at 374 clusters: 243 deer, 106 moose and 25 alternate prey (beaver (17), snowshoe hare (4), and 1 each grouse, muskrat, raccoon, wolf). The remains of many individual prey items were spread out over more than one cluster, so the numbers presented above do not reflect actual kill rates. Although some clusters were not searched due to inaccessibility or field constraints, >90% of clusters were located and searched for each pack. The proportion of clusters with remains was 25.1% for 2006, 25.4% for 2007, and 25.2% overall. The proportion of clusters with remains was higher for clusters searched in winter versus those searched in spring after snowmelt, however the difference was minimal in 2006 (winter 28.8%, spring 27.4%) compared to 2007 (winter 25.8%, spring 20.3%), and these differences likely reflected changes in field methods that prioritized winter searches of likely moose kills and clusters on frozen water bodies in winter 2007.

Table 2. Data collected on Algonquin wolf packs during winters 2006-2007. Columns below each year represent winter periods, with "x" indicating data collected during that period: F = fall, EW=early winter, MW=mid-winter, LW=late winter.

| Pack | Days Tracked 2006 | Days Tracked 2007 | 2006 | | | | 2007 | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | F | EW | MW | LW | F | EW | MW | LW |
| Radiant | 171 | - | x | x | x | x | - | - | - | - |
| Rain | 171 | - | x | x | x | x | - | - | - | - |
| Stevenson | 84 | - | x | x | - | - | - | - | - | - |
| Sunday | 100 | - | x | x | - | - | - | - | - | - |
| Achray | 83 | - | - | x | x | x | - | - | - | - |
| Mckaskil | 83 | - | - | x | x | x | - | - | - | - |
| Lafluer | 43 | - | - | x | x | - | - | - | - | - |
| Louisa | 51 | - | - | - | x | x | - | - | - | - |
| Pine | 82 | 170 | - | x | x | x | x | x | x | x |
| Buckhill | 51 | 94 | - | x | x | x | x | x | - | - |
| Potter | 51 | 95 | - | - | x | x | - | x | x | x |
| BigCrow | - | 170 | - | - | - | - | x | x | x | x |
| Jocko | - | 170 | - | - | - | - | x | x | x | x |

## Measures of Prey Use

### Biomass

Prey consumed during 16 pack-winters included 88 moose and 194 deer, at an overall rate of 0.0006 moose/wolf/day, 0.0013 deer/wolf/day, and 0.0018 kills/wolf/day. Estimates of biomass consumption ranged from 1.47–7.45 kg/day/wolf, or 0.052-0.266 kg meat/kg wolf/day. With the exception of one deer-reliant pack that may have had a high proportion of its kills shared with other packs in the deer yard, estimated biomass consumption was positively correlated with proportion of moose in diet (r=0.47, p<0.01) (but see discussion regarding methodological bias). Average biomass consumed was slightly higher in 2007 than 2006 (4.04 vs 2.93 kg/wolf/day) but the difference was not significant (F=0.96, df= 1, 14, p=0.35), and overall proportion of moose in diet was higher in 2006 (64%) than 2007 (47%), however this difference was not significant (F=1.42, df= 1, 14, p=0.25). In both 2006 and 2007, biomass consumption (kg/wolf/day) varied between winter periods (F=4.5, df= 3, 42, p<0.01), increasing progressively from fall through mid-winter, and decreasing in late winter, with a more dramatic decrease in 2007. Kills/day/wolf increased progressively from fall through mid-winter, and dropped sharply in late winter, due to a decrease in the rate of deer kills. Moose biomass consumed, and moose/day/wolf increased from fall through mid-winter, and leveled off between mid- and late-winter. Proportion of biomass of moose vs deer in wolves diet for all packs combined increased progressively through the winter in both years (range 0.30–0.89), however on the individual pack level the pattern of biomass consumption and proportion of prey in diet was variable through winter (see prey use section below).

### Handling Time

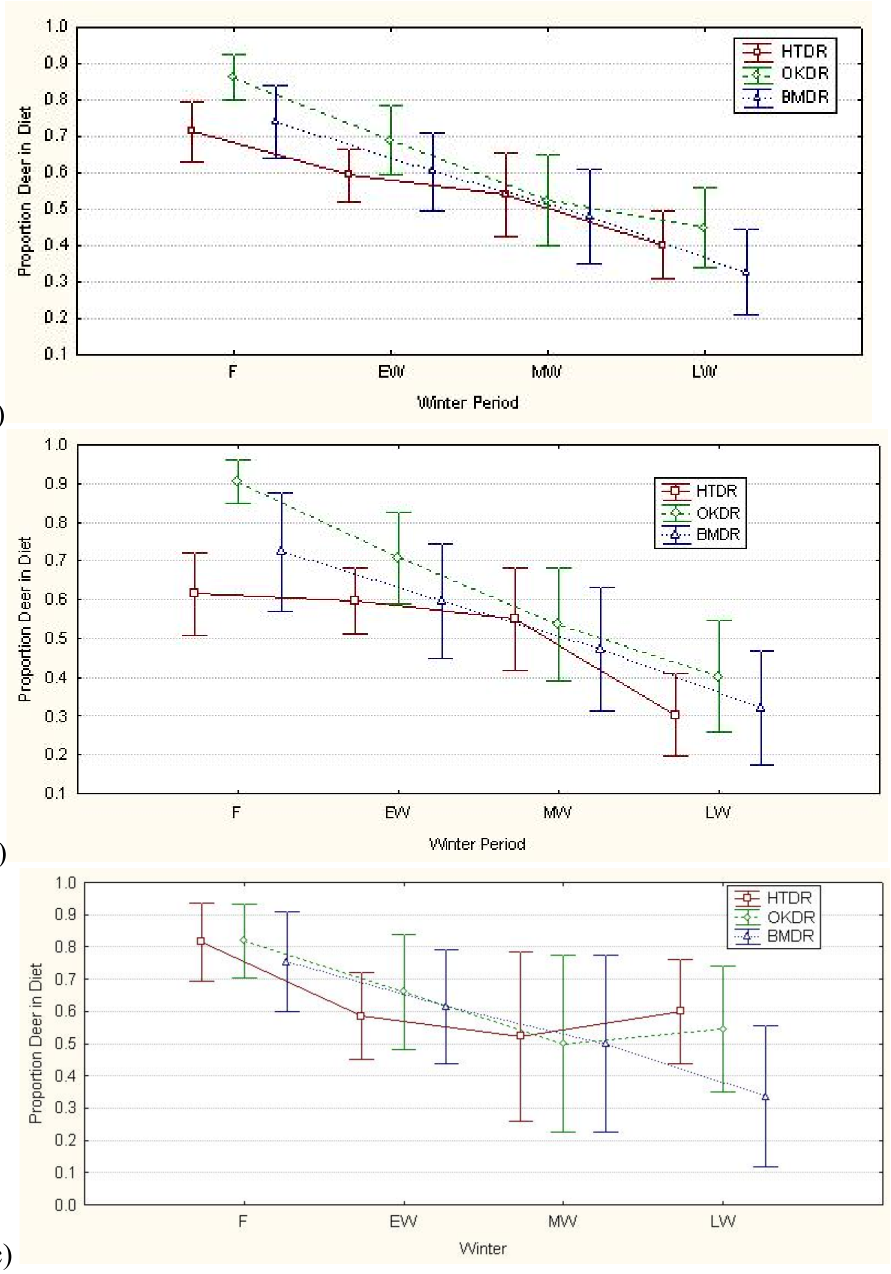
*Time on kill:* The ratio of time spent on deer vs moose for all packs combined decreased progressively through winter, with an overall increased reliance on moose with winter progression, however variability among packs was high (range 0.00–1.00 proportion deer in diet), with significant differences among winter periods (F=6.6, df= 3, 42, p=0.01). There was no significant difference between years in overall proportion of deer vs moose, nor relative use of prey between the corresponding winter periods of each year. The winters of 2006 and 2007 showed some variation in patterns of prey use, and though these differences were not significant they are worth noting. In 2006 the proportion of deer in diet progressively decreased with each winter period (Fig. 3b). In 2007, use of deer decreased from fall through mid-winter, but increased in late winter (Fig. 3c).

*Days to next kill:* The pattern of prey use measured as days per kill differed between 2006 and 2007. In 2006, reliance on deer from fall through mid-winter was consistent (~60%), then dropped to 30% in late winter. In 2007, use of deer decreased gradually from fall through mid-winter, then increased slightly in late winter (Fig. 3b-c).

Comparison of Methods:

At the population level, there were no significant differences between proportions of deer vs moose in diet as measured by biomass or time on kill, however the biomass measure of deer use was consistently less than the time on kill measure (Fig. 3a). Estimates of deer use from handling time days were lower than time on kill estimates in fall 2006 (t=-2.3, df=6, p=0.06, Fig. 3b). The biomass measure did not reflect an increase in deer use in late winter 2007, as did both handling time measures (Fig. 3c). Though statistical testing of variation between methods was not possible on the pack level, in some cases estimates of prey use by pack varied widely among prey use measures, with biomass tending to estimate higher reliance on moose, and handling time days varying less predictably (Fig 4). Within the 46 periods for which prey use was estimated (among 16 pack-winters) differences in estimates of prey use among the three methods ranged from 0.00–0.81, with differences >0.1 in 37% (n=17) of HTDR vs OKDR (range 0.00–0.81), 48% (n=22) of HTDR vs BMDR (range 0.00–0.81), and 28% (n=13) of OKDR vs BMDR (range 0.00–0.50). In most cases HTDR estimated lower proportion of deer in diet than OKDR, but patterns of divergence with BMDR were inconsistent. BMDR tended to estimate lower proportion of deer in diet than OKDR (Fig 5a-d).

For analysis of proportional prey use by pack, we chose to use time at kill (OKDR), as it was the most precise measure of actual utilization of prey (see discussion).


(3a)

(3b)

(3c)

Figure 3a-c. Comparison of measures of prey use for wolf packs in Algonquin Park, Ontario for (a) 2006-07, (b) 2006, (c) 2007 by winter period. HTDR=deer kill days as proportion of all days tracked, OKDR = hours on deer kills as proportion of hours on all kills, BMDR = biomass deer as proportion of biomass of all kills. F=Fall, EW=early winter, MW=mid-winter, LW=late winter

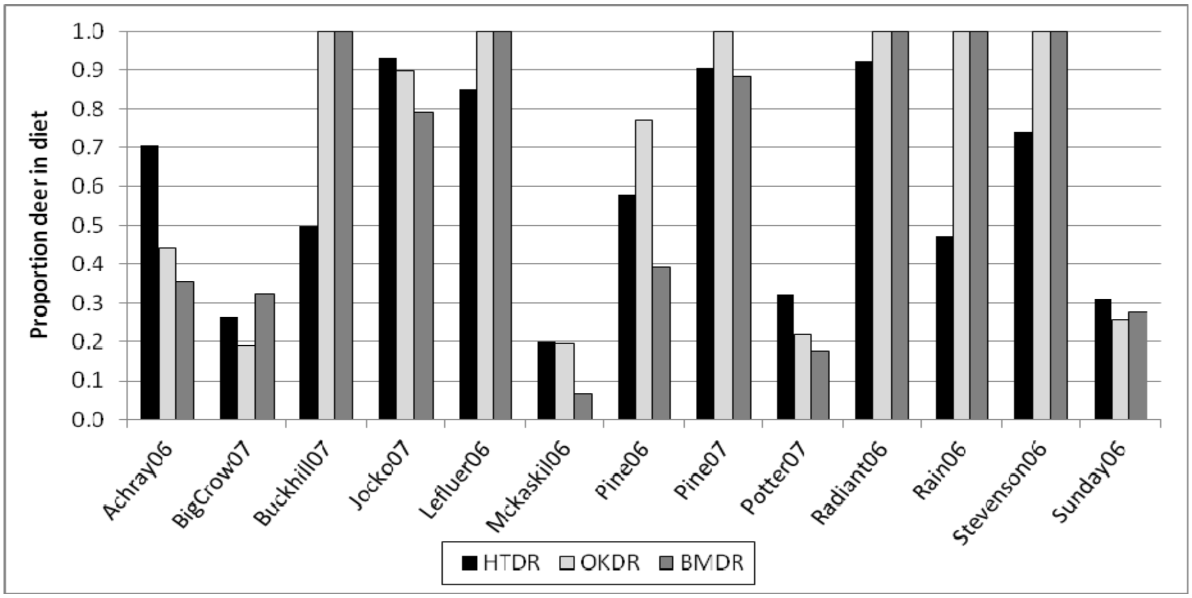


Figure 4. Variation in estimates of full winter prey use by wolf packs in Algonquin Park, Ontario, 2006-2007: Importance of deer in diet as measured by HTDR (days spent on deer kills as proportion of days tracked), OKDR (hours spent on deer kills as proportion of hours spent on all kills) and BMDR (Biomass of deer kills as proportion of biomass all kills).

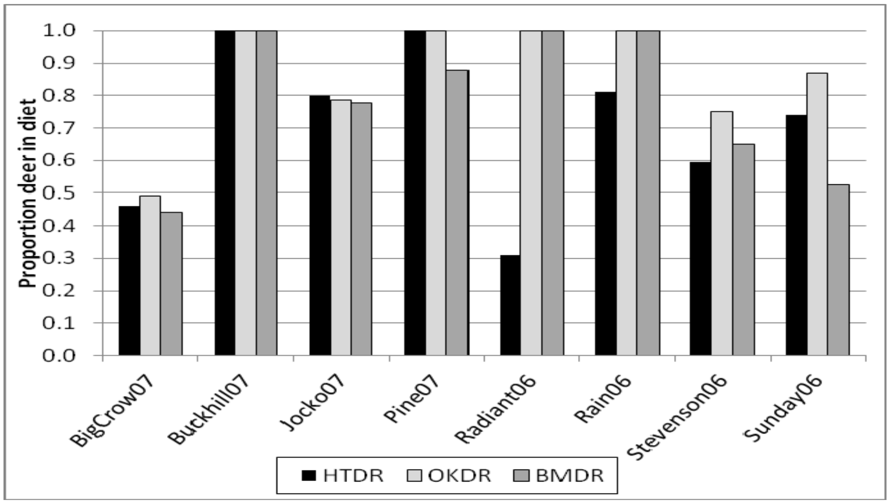


Figure 5a. Fall Prey use estimates.

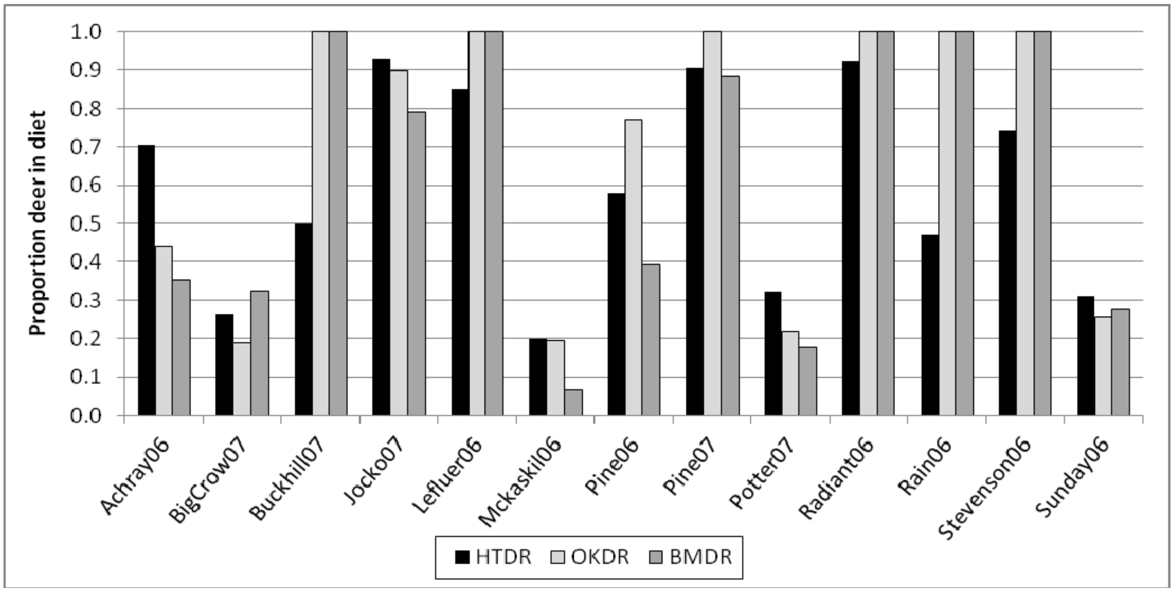


Figure 5b. Early winter prey use estimates.

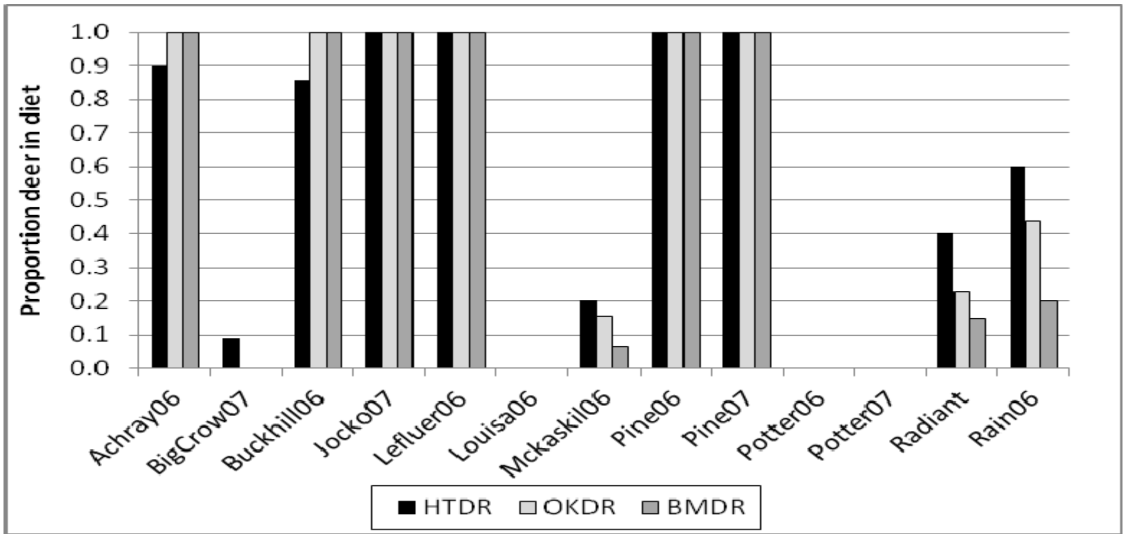


Figure 5c. Mid-winter prey use estimates.

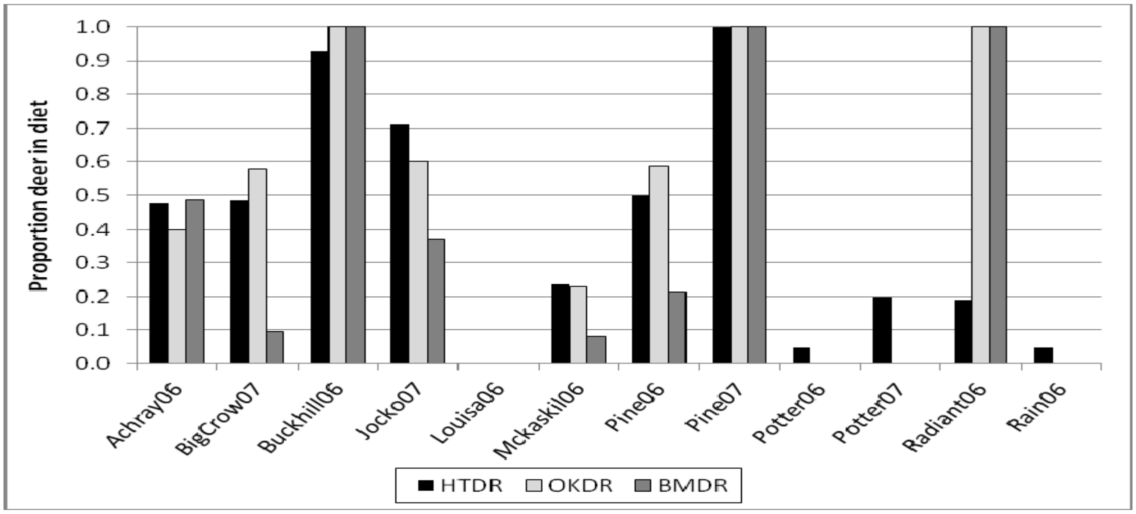


Figure 5d. Late-Winter prey use estimates.

Figure 5a-d. Variation in estimates of prey use in (a) Fall, (b) Early Winter, (c) Mid-Winter and (d) Late Winter by wolf packs in Algonquin Park 2006-2007; importance of deer in diet as measured by HTDR (days spent on deer kills as proportion of days tracked), OKDR (hours spent on deer kills as proportion of hours spent on all kills) and BMDR (Biomass of deer kills as proportion of biomass all kills).

## Prey Demographics

Of the 77 moose consumed by wolves in this study, 18 were identified as calves, and 7 as yearlings. Incisors were collected from 52 adults for aging. To increase our sample size, we included an additional 11 tooth samples collected from wolf-killed moose in Algonquin 2003-2005. For comparative purposes, the demographic structure of the Algonquin moose population was assessed in two ways: the mid-winter cow:calf ratio of 20:100 was taken from the 2006 moose aerial inventory (B. Steinberg, 2006), and adult population age structure was estimated using ages derived from cementum annuli counts in lateral incisors extracted from moose (n=46) during capture for a concurrent moose demographic study (D. Murray et al.., unpublished data). Moose were captured during winters of 2006 (n=35) and 2007 (n=11), and estimated ages of moose captured in 2007 were adjusted to their 2006 age to correct for year effects. The age distribution of wolf-killed/probable wolf-killed moose differed significantly from that of the population (k-s=0.284, p=0.006, Fig 6.). To examine selection by age class, moose were categorized by age following Fuller and Keith (1980) into juvenile (0-1 years), young adult (2-5years), mature adult (6-10 years), and old (≥11 years) age classes. Wolves selected moose age classes out of proportion to the population ($\chi^2$=32.5, df=3, p=0.003), with greater proportions of mature, old and juveniles among wolf-killed moose. The age distribution of captured moose showed a low number of yearlings and 2-year olds, which could have been due to low recruitment in recent years, or capture bias. To correct for this, all 1 and 2 year old moose were censored from both the captured and wolf-killed datasets, and the comparisons were repeated with similar results (k-s=0.357, p<0.001; $\chi^2$=15.18, df=3, p=0.002). The moose demographic study was limited to the west side of Algonquin where the moose were not subject to harvest, whereas this study also included the east side of Algonquin where First Nations harvest moose each autumn. Patterns of selection by wolves appeared to be influenced by the age structure of the standing population; the distribution of age classes likely differed between eastern and western

Algonquin due to harvest by humans. Wolves killed a higher proportion of calves and young adult moose in the harvested portion of the study area, and higher proportion of mature moose in non-harvested areas ($\chi^2$ = 7.02, df=3, p=0.07, Table 3, Fig. 7). This trend of age-specific predation occurred most notably during late winter (Fig. 8), and was most distinct in the more severe winter of 2006.

Few deer incisors were collected for aging, as wolves tended to completely consume or remove mandibles from deer kill sites. Of 194 deer identified, 108 were classified as adult or juvenile; of these 38 (35%) were classified as fawns, and 70 (65%) were classified as adults with incisors collected from 20 of these for aging (Table 4). The ages of these 20 animals were 1 (5%) yearling, 12 (60%) adult (2-5yo) and 7 (40%) old adult (>5yo). With small sample size and no data on the current population age structure, we cannot determine age-specific patterns of selection by wolves on deer in this study.

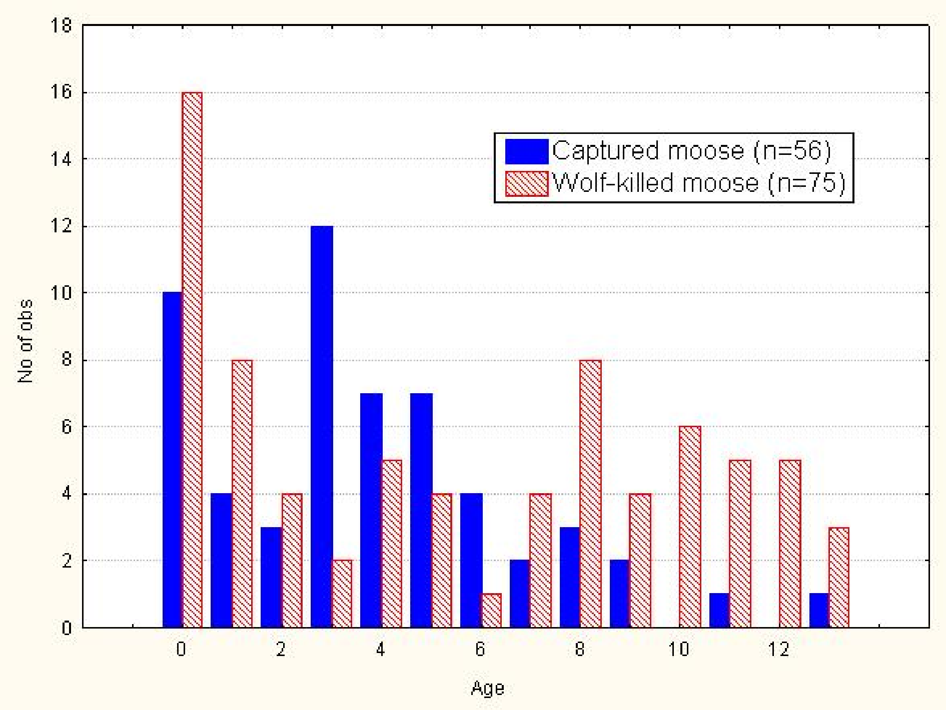


Figure 6. Age distribution of moose captured 2006-2007 vs wolf-killed/probable wolf-killed moose in Algonquin Park 2003 - 2007. The number of calves per captured moose were estimated assuming a cow:calf ratio of 100:20 from 2006 moose aerial inventory.

Table 3. Age distribution of wolf-killed and probable wolf-killed moose in areas of moose harvest vs non-harvest in Algonquin Park, Ontario, 2003-2007.

| Wolf-killed/probable wolf-killed moose, Algonquin Park, 2003-2007 | | | | | |
|---|---|---|---|---|---|
| Harvested area | | | Non-Harvested area | | |
| **age** | **n** | **%** | **age** | **n** | **%** |
| 0-1 | 15 | 40 | 0-1 | 88 | 28 |
| 2-5yo | 10 | 26 | 2-5yo | 4 | 14 |
| 6-10yo | 6 | 16 | 6-10yo | 13 | 45 |
| ≥11yo | 7 | 18 | ≥11yo | 4 | 14 |
| total | 38 | | total | 29 | |

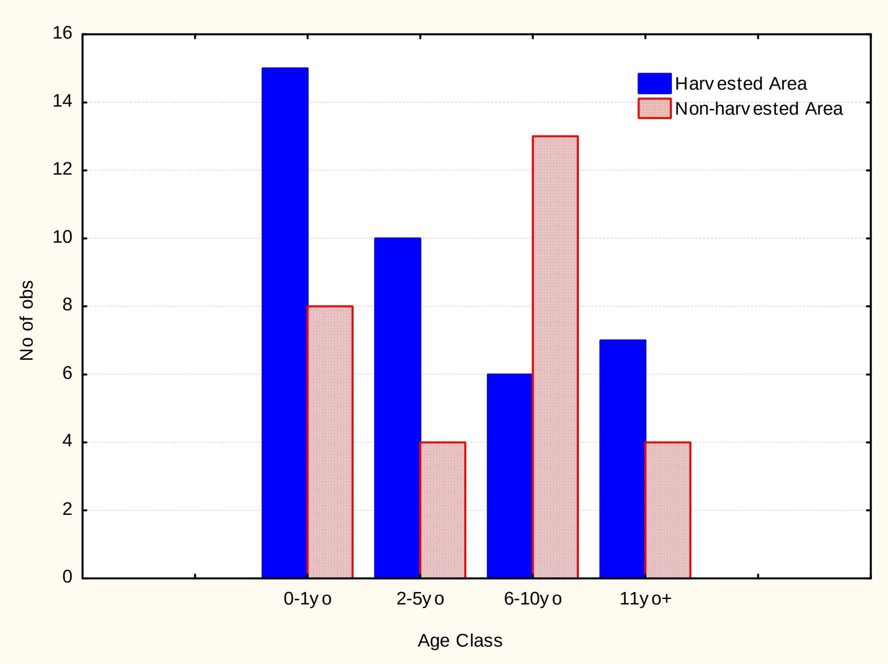


Figure 7. Wolf killed and probable wolf-killed moose by age class and moose harvest policies in Algonquin Park, 2003-2007.

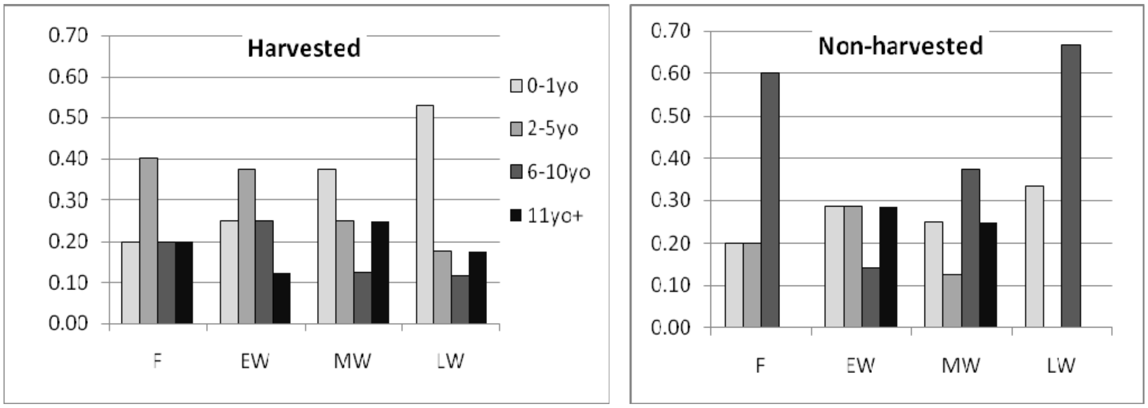


Figure 8. Proportions of moose age-classes killed by wolves in each winter period, in areas where moose are hunted versus areas where moose are protected from harvest within Algonquin Park, Ontario, 2003-2007. (F=Fall, EW=early winter, MW=mid-winter, LW=late winter)

Table 4. Demographics of wolf-killed deer in Algonquin Park, Ontario, 2006-07 by (a) age class, and (b) ages of adults from incisor cementum annuli.

a.

| Deer age class | n | % |
|---|---|---|
| total | 108 | |
| Fawn | 38 | 35 |
| Adult | 70 | 65 |

b.

| Adult Deer ages | n | % |
|---|---|---|
| Total | 20 | |
| 1yo | 1 | 5 |
| 2-5yo | 12 | 60 |
| >5yo | 7 | 35 |

## Admixture

One hundred thirty-four Algonquin wolves were included in the admixture analysis. Of these, 74 (55%) had >80% probability of membership in *C. lycaon*, 25 (19%) had >20% probability of membership in *C. latrans,* and 34 (25%) had >20% probability of membership in *C. lupus*. Three individuals were influenced equally by both outgroups (~50:50), three others were primarily influenced by *C. lupus* but had >0.2 probability of *C. latrans* as well, and 6 individuals had <0.8 probability of *C. lycaon* but <0.2 probability of either outgroup (range 0.14-0.19). Three of these were influenced by *C. lupus* and 3 by *C. lycaon*. *C. lupus* influenced individuals were more likely to be associated with packs than individuals with *C. latrans* influence; transients represented 24% (n=6) of *C. latrans* influenced wolves, and 8% (n=2) of *C. lupus* influenced animals, whereas the overall rate of transient individuals in the population was 13% (n=17).

Fifty-two wolves included in the admixture analysis were associated with packs used in the prey use analysis. Of these, 31 wolves (60%) were grouped with the *C. lycaon* population and 21 (40%) individuals were categorized as admixed, with 20% or greater probability of membership in either *C. lupus* or *C. latrans* outgroups. Of these, 6 were admixed with *C. latrans* (range 0.20–0.68) and 15 were admixed with *C. lupus* (range 0.24-0.97). FCA results corroborated all but 3 of the 52 admixture classifications from STRUCTURE results. Results presented and discussed below are based on analysis using the more conservative pack-average measure of admixture, consistent with all FCA results (Table 5). We also present results with the pack-maximum measure (Table 6b), in order to explore whether low levels of admixture influence prey use.

Table 5. Estimated likelihood scores of population membership (*q*) by wolf pack, from STRUCTURE admixture analysis of wolves in Algonquin Park, Ontario, 2003-2007. “Individual admixture” represents maximum *q* value within each pack, and “average admixture” represents averaged q values for all sampled pack members. Populations are represented as: LC = *C. lycaon* (Algonquin), LP = *C. lupus* (NE Ontario), LT=*C. latrans* (SE Ontario). Admixture scores ≥0.20 are highlighted.

| | **"Individual admixture"** | | **"Average admixture”** | |
|---|---|---|---|---|
| **Pack** | **Max *lupus*** | **Max *latrans*** | **Avg *lupus*** | **Avg *latrans*** |
| Achray | 0.08 | 0.05 | 0.04 | 0.04 |
| Big Crow | 0.07 | 0.05 | 0.05 | 0.04 |
| Buckhill | 0.08 | 0.67 | 0.05 | 0.34 |
| Jocko | 0.11 | 0.11 | 0.05 | 0.05 |
| Lefleur | 0.18 | 0.68 | 0.1 | 0.4 |
| Louisa | 0.09 | 0.54 | 0.04 | 0.19 |
| McKaskill | 0.93 | 0.04 | 0.91 | 0.03 |
| Pine | 0.62 | 0.08 | 0.33 | 0.08 |
| Potter | 0.69 | 0.09 | 0.34 | 0.06 |
| Radiant | 0.23 | 0.02 | 0.09 | 0.02 |
| Rain | 0.09 | 0.21 | 0.09 | 0.14 |
| Stevenson | 0.08 | 0.67 | 0.05 | 0.36 |
| Sunday | 0.23 | 0.03 | 0.14 | 0.03 |

## Prey Use by Pack

Prey use differed significantly among packs, with proportional use of deer vs moose ranging from 0.00–1.00. When all packs were pooled, there was a shift from deer to moose over the course of the winter, with moose and deer use roughly equal in mid-winter, which was also the time period of maximum biomass consumption.

Results of full winter linear regression analysis, without considering the influence of winter progression, showed significant effects of distance to deer yard (F=23.9, df=4, 11, p=0.010), pack size (F=6.5, df=4, 11, p=0.009) and moose density (F=4.2,df=4, 11 p=0.045). *C. latrans* admixture was not significant, but was retained in the model as it improved $R^2$. For the full winter ANCOVA including winter periods, assumptions of homogeneity of slopes was violated for the fall period only, so ANCOVA included early, mid and late winter periods only. ANCOVA results were consistent with the full winter regression model, with significant effects of pack size (F=19.00, df=5, 32, p<0.001), deer distance (F=15.70, df=5, 32, p<0.001) and moose density (F=6.90, df=5, 32 p=0.013; Table 6). Using ANCOVA to incorporate winter progression did not increase explanatory power (ANCOVA $R^2$ =0.62 vs regression $R^2$= 0.77; table 6).

Though prey distribution and pack size were the most important factors for full winter prey use, there were no distinct thresholds for distance to deer yard or moose density that consistently predicted reliance on deer vs moose for full winter prey use. Pack size was positively correlated with proportion of moose in diet however it was not the primary determining factor in prey use or specialization. Packs with >0.5 proportion of moose ranged in size from 3–9 wolves, and those with >0.5 proportion deer ranged from 4-8. If specialization on prey is defined as >0.7 proportion of moose or deer, then moose specialist packs ranged in size between 5-9, and deer specialist packs ranged from 4-8 individuals. Though assumptions of no multicollinearity were met, with tolerance values >0.45 for all independent variables, there were significant correlations between *C. latrans* admixture and distance to deer yard (r=-0.61, p=0.011)), and *C. lupus* admixture and pack size (r=0.59, p=0.015). No other correlations among independent variables were significant.

Factors influencing prey use varied by winter period. The fall period did not have any significant factors, with 78% of variation unexplained. In early winter there were significant effects of pack size (F=4.8, df=3, 9, p=0.03) and deer yard distance (F=5.6, df=3, 9, p=0.05). There was a negative relationship between proportion of deer in diet and pack size, and deer reliance decreased with increasing distance to deer yard. All packs with a territory boundary within 10 km of the deer yard, or 20 km average distance across the territory, made foraging trips during early winter; above these thresholds migratory foraging was variable, with the maximum observed migration distance being 42 km from the territory boundary.

Mid-winter variation in prey use was most influenced by distance to deer yard (F=26.3, df=3, 9, p=0.001), with significant effects of *C. lupus* (F=5.8, df= 3, 9, p=0.016) and nearly significant effects of *C. latrans* (F=4.0, df=3, 9, p=0.07) admixture. There was a negative correlation between *C. lupus* scores and proportion deer in diet, and a positive correlation between *C. latrans* scores and proportion deer in diet. The significance of admixture was consistent with both the average and individual measures, though the strength of the effect was slightly greater with the average measure (Table 6). There was a strong pattern of prey specialization in mid-winter; 10 out of 13 packs relied exclusively on one or the other prey species, and the 3 packs that used both prey relied heavily on moose, making 1 or 2 deer kills on territory. There were no instances of packs killing moose on territory and also making deer yard excursions during mid-winter. When distance to the deer yard was averaged across each territory there was an apparent threshold of 20 km for deer yard excursions; packs with average distances greater than 20 km (n=6) did not travel to the deer yard in mid-winter, and all packs below the threshold (n=7) made regular trips. If the distance to the deer yard was measured as the minimum distance from the territory boundary, there was a less distinct threshold; packs with territory boundaries less than 10 km from deer yards (n=6) all made deer yard excursions, those between 10 km and 15 km were mixed (n=2), and none of those above 15 km away (n=5) made excursions.

Variation in late winter prey use was explained by moose density (F=14.6, df= 2, 7, p=0.002) and pack size (F=6.6, df= 2, 7, p=0.030), with less reliance on deer as moose density and pack sizes increased. In late winter there was some degree of specialization as well; 3 out of 12 packs preyed exclusively on deer, 4 exclusively on moose and 5 packs used both prey. Four of the five packs that utilized both deer and moose during late winter used them in roughly equal proportions (range 0.40-0.60). Packs with moose densities >0.47/km$^2$ relied exclusively on moose. Below this threshold, there was variability in the level of reliance on moose. Pack size explained 31% of modeled variation in late winter prey use, however there was no distinct threshold of pack size that determined moose reliance.

Table 6. Multiple regression results for effects of distance to deer yard, moose density, pack size and admixture of *C. latrans* and *C. lupus* on proportion of deer in diet of wolf packs in Algonquin Park, Ontario, 2006-2007, for each winter period and full winter. ANCOVA results for full winter with winter period as discrete factor. (a) presents results with average admixture, whereas (b) shows individual-maximum admixture.

a. Models with average admixture scores per pack

| Winter period | DF | Multiple $R^2$ | Model F | Model p | significant factors | Coef | SE | t / F | p | % variation explained |
|---|---|---|---|---|---|---|---|---|---|---|
| Early | 3, 9 | 0.57 | 4.00 | 0.046 | Deer Dist | -0.020 | 0.009 | -2.22 | 0.053* | 27% |
| | | | | | Pack Size | -0.128 | 0.051 | -2.52 | 0.033** | 23% |
| | | | | | Av *C. latrans* | -0.014 | 0.011 | 1.26 | 0.238 | 7% |
| Mid | 3, 9 | 0.79 | 11.41 | 0.002 | Deer Dist | -0.031 | 0.006 | -5.10 | <0.001** | 58% |
| | | | | | Av *C. lupus* | -0.921 | 0.308 | -2.99 | 0.015** | 13% |
| | | | | | Av *C. latrans* | -1.573 | 0.809 | -1.94 | 0.084* | 9% |
| Late | 2, 9 | 0.70 | 10.62 | 0.004 | Moose Density | -1.520 | 0.362 | -4.20 | 0.002** | 70% |
| | | | | | Pack size | -0.098 | 0.038 | -2.57 | 0.030** | 31% |
| Full Winter | 4, 11 | 0.77 | 8.99 | 0.002 | Deer Dist | -0.013 | 0.005 | -2.84 | 0.016** | 57% |
| | | | | | Pack Size | -0.139 | 0.044 | -3.14 | 0.009** | 16% |
| | | | | | Moose Density | -0.696 | 0.308 | -2.26 | 0.044** | 10% |
| | | | | | Av *C. latrans* | -0.644 | 0.562 | -1.15 | 0.276 | 3% |
| ANCOVA Full winter | 5, 32 | 0.58 | 8.75 | <0.001 | Pack Size | | | 19.00 | <0.001** | 43% |
| | | | | | Deer Dist | | | 15.70 | <0.001** | 36% |
| | | | | | Moose Density | | | 6.90 | 0.013** | 16% |
| | | | | | Winter | | | 0.95 | 0.396 | 5% |

b. Models with individual-maximum admixture scores per pack

| Winter period | DF | Multiple $R^2$ | Model F | Model p | significant factors | Coef | SE | t / F | p | % variation explained |
|---|---|---|---|---|---|---|---|---|---|---|
| Early | 2, 10 | 0.50 | 4.90 | 0.033 | Deer Distance | -0.010 | 0.005 | -2.13 | 0.059* | 53% |
| | | | | | Pack Size | -0.094 | 0.044 | -2.12 | 0.060* | 47% |
| Mid | 3,9 | 0.87 | 19.39 | <0.001 | Deer Distance | -0.034 | 0.005 | -7.22 | <0.001** | 67% |
| | | | | | Ind *C. latrans* | -1.151 | 0.333 | -4.23 | <0.001** | 21% |
| | | | | | Ind *C. lupus* | -0.981 | 0.232 | -3.45 | 0.007** | 13% |
| Late | 2, 9 | 0.70 | 10.62 | 0.004 | Moose Density | -1.520 | 0.362 | -4.20 | 0.002** | 70% |
| | | | | | Pack size | -0.098 | 0.038 | -2.57 | 0.030** | 31% |
| Full Winter | 3, 12 | 0.74 | 11.26 | <0.001 | Deer Distance | -0.010 | 0.004 | -2.66 | 0.021** | 69% |
| | | | | | Pack Size | -0.114 | 0.039 | -2.92 | 0.013** | 19% |
| | | | | | Moose Density | -0.614 | 0.302 | -2.03 | 0.065* | 12% |
| ANCOVA Full winter | 7, 30 | 0.62 | 6.99 | <0.001 | Deer Dist | | | 18.70 | <0.001** | 43% |
| | | | | | Pack Size | | | 12.10 | 0.002** | 28% |
| | | | | | Moose Density | | | 4.16 | 0.050* | 10% |
| | | | | | Ind *C. latrans* | | | 3.43 | 0.072* | 9% |
| | | | | | Ind *C. lupus* | | | 2.40 | 0.132 | 5% |
| | | | | | Winter | | | 0.64 | 0.535 | 3% |

*p <0.1, **p <0.05

## DISCUSSION

### **Patterns of Deer and Moose Reliance**

This study revealed variation and complexity in prey use related to changes in accessibility and vulnerability of prey with winter progression, differences in pack size, and genetic admixture. We found deer distribution to be a significant driver of prey use during early and mid-winter; however, some packs used moose regardless of deer availability, whereas other packs relied exclusively on deer in spite of changes in deer distribution, and most packs used both prey items to some degree. Though some packs made long excursions to forage on deer in early winter, there was an apparent threshold in mid-winter of 20 km average territory distance beyond which wolves did not travel to forage on deer. This resulted in two distinct wolf-prey systems; a wolf-deer system in which wolves left territories to forage on wintering deer then returned to territories between kills, and a wolf-moose system in which wolves hunted their territories for moose. Accessibility was an important factor influencing deer predation in this system, and predation on moose was driven by vulnerability to some extent, however, the influence of vulnerability was variable among packs.

Though deer were likely still available on wolf territories during the fall period, before snow accumulation or consistent freezing temperatures (Nelson 1994, Sabine et al. 2002), some packs made off-territory foraging excursions involving trespasses into neighboring territories towards the deer yard, likely a result of following deer on their migration routes. Our results are consistent with other reports of high wolf kill rates on deer during fall migration, (Nelson & Mech 1991), which is not fully understood as deer are in their best condition in early fall having benefited from abundant forage on their summer ranges, and deep snows increasing vulnerability to predation generally do not occur until after the deer have completed migration (Hoskinson and Mech 1976). Spatial predictability of deer during fall migration increases accessibility of deer to wolves, and is a plausible explanation for reliance on deer during this period.

In early winter, deer had become aggregated and were a sparse and unpredictable resource outside of the deer yards. Deer remaining outside the wintering area once snow reaches limiting levels are highly vulnerable to wolf predation once encountered (Nelson & Mech 1991). Predation on deer outside of the deer yards in early and mid-winter was depensatory (sensu Potvin et al. 1988), with instances of predation on deer declining to zero as the few deer remaining on territories were killed. Within the deer yards, deer were a predictable resource; however, accessibility varied depending on the distance and risk involved in travel for each pack. The cost of deer yard excursions increased if travel was initiated from the far reaches of territories, as was observed in packs utilizing both deer and moose in early winter, while some packs that specialized on deer minimized the cost of excursions by shifting habitat use to the area of their territory in closest proximity to the deer yard (K. Loveless et al., unpublished data).

In mid-winter, when conditions for travel were most costly, packs specialized on either deer or moose, with proximity to the deer wintering area explaining most variation. Mid-winter was also when levels of biomass consumption and daily kill rates were highest, consistent with other reports of high kill rates associated with deep snow (Huggard 1983, Jedrzejewski et al. 2002).

Once snow melt began and deer began to return to their summer range, wolves' overall reliance on deer decreased, and moose density became the most important factor driving prey use, followed by pack size. As spring migration progressed, deer became increasingly available to wolves on territories and migration routes, and wolves may have had less advantage over the remaining deer in the yards without snow to impede escape (Nelson & Mech 1991). The decreased concentration of deer, and lower vulnerability would explain the drop in deer kill rate and biomass consumption for deer specialist packs in late winter. Although some deer remained aggregated in the yards beyond snowmelt, consistent with other studies (Hoskinson & Mech 1976, Nelson et al. 2004), wolves did not continue making trips to the deer yard once snowmelt had commenced.

The highest reliance on moose occurred after snowmelt had begun, with high kill rates continuing beyond snowmelt, while kill rates on deer declined even among deer-specialist packs. Given that deep snow is associated with high kill rates on ungulates (Kolenosky 1972, Huggard 1993, Ballard et al. 1997), the observed decrease in kill rates on deer after snowmelt is not surprising; however, increased kill rates on moose were unexpected. The contrasting patterns in kill rates on deer and moose during and after snowmelt suggest that snow depth is not driving predation on moose on a population level, and that after snow melt moose must be a more advantageous prey item for wolves. Moose have a negative energy balance throughout winter, continuing until spring green up provides new forage, thus body condition likely continues to deteriorate with energetic demands during and after snowmelt (Peek 1998). With high moose vulnerability at the end of winter and lower costs of locomotion for wolves with snowmelt, hunting moose likely has an improved cost:benefit ratio. Thus moose may be a more advantageous prey type in late winter than deer, which provide less energetic benefit, are less predictable spatially after snowmelt, and are more difficult to capture without the hindrance of snow.

The high reliance on deer during fall migration compared to low reliance during spring migration has been noted in other studies and seems contradictory (Nelson and Mech 1991). In this system, it can be explained by the improved cost:benefit of moose predation in spring. Several packs that foraged only in the deer yards in mid-winter killed moose on territory during early winter when snow was not as limiting, lending support to the hypothesis that snow depth hindered predation on moose by deer specialist packs. Our results suggest that in mid-winter, the cost:benefit ratio of hunting moose was greater than the cost:benefit ratio of travelling to the deer yard to hunt deer for packs whose average travel distance to the deer yard was within 20 km. Conversely, for moose specialist packs, snow depth was associated with higher kill rates. Thus the mechanism of snow depth had contrasting effects of inhibiting or increasing predation on moose, depending on whether deer were accessible.

Wolves appeared to select old (>11 y.o.) and calf moose in greater proportions than occurred in the population, however, this pattern was temporally and spatially variable. Wolves were less selective in fall and early winter and highly selective for calves, mature (6 – 10 y.o.) and old moose in late winter. Selection for calves was also more pronounced in areas where moose are harvested. Harvest of ungulates may create a younger age structure, thus changing the availability of vulnerable individuals to wolves (Solberg et al. 1999). However, we did not observe decreased reliance on moose by wolves where moose were harvested, rather selection shifted from older individuals to calves, and a higher proportion of prime age moose were killed throughout the winter. Old moose were a small proportion of wolf-kills, however were strongly selected in relation to the population. Differences in the importance of old moose in this study compared with other studies may reflect different age structures of the moose population. The small proportion of old moose in the Algonquin population is similar to the <10% reported by Fuller and Keith (1980), but contrasts with other studies that have found higher proportions of old moose both within wolf-killed samples and the moose population (Peterson et al. 1977, Peterson et al. 1984, Ballard et al. 1987). Given that there were very few old moose in the sample of captured individuals (4% in this study, vs 27% in Ballard et al. 1987), and that harvest tends to decrease the age structure of moose populations, high reliance on mature adults (6-10 y.o.) in the harvested portions of the study area likely reflects very limited availability of old moose. Population structure normally conforms to a Poisson distribution, as cohorts diminish with attrition over time. The captured moose sample, with calves estimated from aerial surveys, showed a bi-modal distribution with low numbers of yearling and 2-year old moose. This could reflect low recruitment in recent years, or capture bias towards reproductive females for the purposes of the demographic study. However selection by wolves was most evident among calves and old moose, and these results were not affected by proportion of yearling and 2-year old moose in the population.

Due to the patterns of prey specialization in Algonquin, most predation on moose during early and mid-winter was done by the few moose specialist packs. The low selectivity in early and mid-winter reflect these packs ability to kill prime age moose, likely due to experience and skill at subduing moose. The dramatic increase in selectivity in late winter can be partially explained by an increase in the diversity of packs making moose kills. Though most packs showed some degree of age specific selection, packs which relied on deer for most of the winter were more likely to be limited to highly vulnerable moose than packs which specialized on moose throughout the winter. Moose vulnerability appeared to be lower in 2007 than in 2006, with less selectivity for calves, lower kill rates on moose, and numbers of scavenged winter killed moose dramatically lower in 2007 compared to 2006, however the tendency to specialize in mid-winter, and the population-level increase in moose reliance in late winter occurred in both years. We conclude that on a population level moose vulnerability was an important factor, resulting in higher kill rates on moose during late winter when moose are known to be most vulnerable. However high vulnerability of moose was not required for packs to successfully exploit and rely on moose.

Pack size was a significant factor predicting prey use during early and late winter, with a tendency for larger packs to rely more heavily on moose. However in mid-winter packs ≥20 km from the deer yard relied heavily or exclusively on moose regardless of pack size. A shift in prey use by one pack studied over both winters may have been influenced by changes in pack size. This was a *C. lupus* influenced pack bordering the deer yard, and it relied on both moose and deer in 2006 when the pack had 5 members, but relied almost exclusively on deer in 2007 when the pack dropped to 4 animals and the conditions were overall milder. However predation on moose by packs of 3 wolves was documented in this study and by single or pairs of wolves elsewhere (Thurber and Peterson 1993), and the relationship of pack size to foraging success on large prey is inconsistent among studies (Schmidt and Mech 1997). Large packs may be advantageous (Vucetich et al. 2004), but not critical for subsisting on large prey such as moose (Thurber and Peterson 1993), however skill and experience of individual pack members may be key to successful handling of large prey (Sand et al. 2006). More data is needed to disentangle the effects of pack size, winter severity, or other unknown factors on the shift in prey use by this pack. The other two packs with repeat measures showed consistent foraging patterns between the two winters.

## Genetic Admixture and Predation

Prey distribution was the most important factor driving prey use; however admixture was significant in the overall prey use model, and the mid-winter model. There was an overall, significant trend for *C. lupus* influenced packs to specialize on moose, and for *C. latrans* influenced packs to specialize on deer, which became more distinct with higher levels of admixture. Strongly *C. latrans* influenced packs (defined here as >0.5 average admixture) were unlikely to prey on moose. There was one moose kill that may have been made by a strongly *C. latrans* pack, however it occurred at an intersection of territories with 2 *C. lupus* influenced packs that regularly killed moose, and we could not be sure which pack had made the kill. Conversely, deer were a minor prey item for strongly *C. lupus* influenced packs, comprising only 10-15% of diet.

Though results were largely consistent between the more sensitive and conservative measures of admixture per pack, packs with low (<0.2) to moderate (0.2–0.5) levels of admixture were variable in their predation patterns. This was reflected in model results, which were stronger when the pack average was used to represent admixture, indicating that measures based on individual variation within packs introduced noise into the model (Tables 6a&6b). Examples of this variability included a pack which was primarily *C. lycaon* (pack average score 0.19 *C. latrans*) however one member was highly *C. latrans* (individual score 0.54 *C. latrans*) influenced. This pack was observed to prey on deer and moose in early winter, however preyed exclusively on moose in mid- and late-winter while it was GPS monitored. Another pack that was not considered admixed by the pack average scale but had one *C. lupus* influenced individual (0.23 *C. lupus*), made long distance foraging excursions to the deer yard in early winter then foraged exclusively on moose during mid-winter.

The pattern of shifting prey use with winter progression was distinctly different between admixture categories, with *C. lupus* influenced packs using moose from early winter through late winter, and *C. latrans* influenced packs making limited use of moose in fall before shifting completely to deer for the remainder of winter. *C. lycaon* patterns of prey use were more variable; mean use of deer was higher in mid and late winter, however wide confidence intervals overlapped with *C. lupus* mean prey use (Fig. 9). Data on fall prey use for *C. lupus* packs is likely not representative because no strongly *C. lupus* packs were monitored during fall.

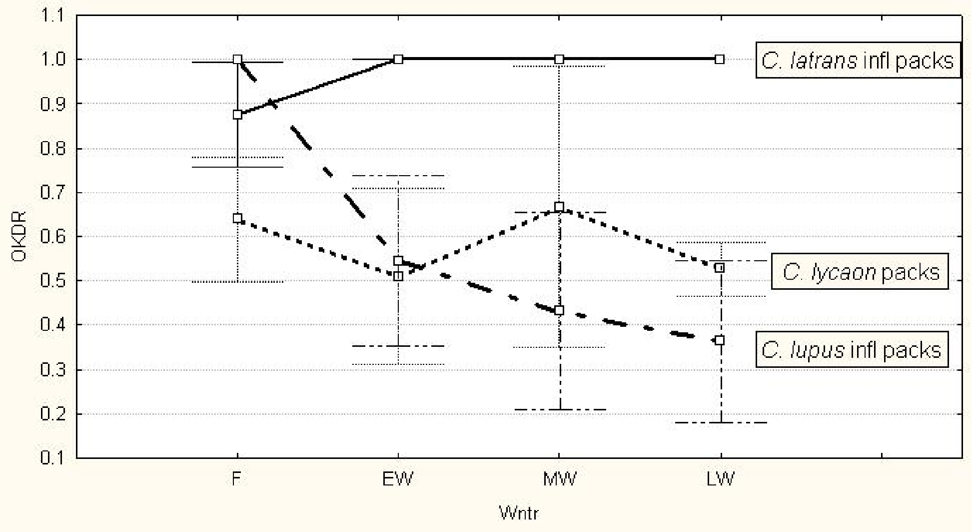


Figure 9. Proportion of time spent on deer kills (OKDR) versus moose kills by wolf packs in Algonquin Park, Ontario with winter progression, among *C. lycaon* packs (≤0.2 likelihood of hybridization) compared with hybrid influenced packs (>0.2 likelihood of membership in *C. latrans* or *C. lupus* dominated populations) F=Fall, EW=early winter, MW=mid-winter, LW=late winter)

The *C. lycaon* tendency to be more generalist than either the strongly *C. lupus* or *C. latrans* influenced packs could simply represent their intermediate morphological position between coyote and gray wolf-like animals. This could ultimately be an advantage in a system with high variability in the vulnerability and accessibility of prey, and may explain the persistence of eastern wolves in spite of genetic introgression from other canid types. Though highly *C. latrans* influenced packs were spatially associated with the deer yard, there was evidence of *C. latrans* genetic influence in low and moderate levels across the study area. *C. lupus* packs were not clumped spatially, but were less likely to be in proximity to the deer yard. Admixed packs that tend to specialize may be more likely to establish when prey variation is low; for example, areas having low moose density but in proximity to the deer yard, or areas distant from deer wintering areas with obligate reliance on moose. Further monitoring over time and with larger sample sizes would be required to validate this hypothesis.

If variation in prey use is influenced by hybridization in Algonquin, the plausible mechanisms could be 1) behavioral predisposition affecting hunting or social patterns, or 2) morphological differences which influence the cost:benefit of prey use. Both coyotes and gray wolves are social, though wolves tend to have more cohesive pack structure than coyotes, which often hunt singly or in small groups when foraging for small prey or deer (Bekoff et al. 1981, Geffen et al. 1996, Patterson and Messier 2001). Coyote-type canids would benefit from pack cohesiveness when large prey are available, however they may hunt individually and sustain themselves on small prey if necessary, whereas wolves are too large to effectively sustain themselves on small prey and are thus obligated to hunt in packs. We did not observe differences in pack cohesiveness among packs in Algonquin, though pack sizes of *C. latrans* influenced packs tended to be smaller than average, and *C. lupus* influenced packs were larger than other packs, including *C. lycaon* moose specialist packs. This could be confounded by differences in prey specialization, though a review of wolf-prey studies did not find moose-reliant packs to be larger than deer-reliant packs (Fuller et al. 2003). Wolves are thought to be less adaptable to human disturbance than coyotes, perhaps due to their reliance on large prey and the larger home ranges necessary to support a sufficient prey base (Bekoff and Wells 1980). Measurement of a behavioral predisposition for pack cohesiveness, adaptability to human disturbance, hunting strategy or prey preferences may not be possible in a natural system; however, many behavioral differences between canid species can be explained by the constraints of body size. A threshold in body size for predators that can sustain themselves on small prey has been suggested to occur between 21.5 and 25 kg (Carbone et al. 1999). Anecdotal evidence of body size as a factor in selection between moose and deer within a multiple prey system was documented in Scandinavia (Sand et al. 2006), and body size was found to be an important factor in foraging success in Yellowstone (McNulty et al. 2009). Given the range in body sizes of Algonquin wolves observed in this study (adult male wolves 18–40 kg) this would seem a likely mechanism. Prior experience and learning is a possible mechanism for genetic association with prey use; if *C. lupus* introgression is occurring in Algonquin due to dispersers from the northern *C. lupus* dominated population, these individuals would bring knowledge and experience of handling moose, the primary prey for northern Ontario wolves (J. Holloway et al., unpublished data).

Whether body size, genetic predisposition, or individual experience drive variation in prey use among hybrid classes, the important question is whether and to what extent hybridization is affecting the predator-prey system, and what implications this may have for Algonquin and the larger hybrid zone extending from the Great Lakes region to Quebec. Definitive conclusions on the influence of admixture on predatory behavior cannot be made on the basis of such limited sample size; however, the tendency for packs strongly influenced by admixture to specialize seems clear. Though most packs that grouped strongly with the *C. lycaon* population utilized both deer and moose, some *C. lycaon* packs subsisted primarily on moose, and others relied heavily on deer, indicating that this genotype is not limited to one or the other prey species. However, admixed packs may be more effective specialists on either moose or deer, and perhaps could out-compete *C. lycaon* packs when conditions favor specialization. Algonquin park forest management is guided by the goal of restoring a mature even-age forest similar to pre-settlement stand types by implementing selective-cut harvest regimes and fire suppression. Though both moose and deer prefer mosaic of early successional and mature forests (Maier et al. 2005, Courtois et al. 2002), moose are better able to subsist on limited understory growth with selective harvest (Peek 1998). Thus Algonquin forestry practices are in effect managing for moose, and winter habitat for deer in the park will continue to decline. Though we observed packs with low *C. latrans* influence to utilize moose, we could not confirm any moose kills made by strongly *C. latrans* packs. If *C. latrans* influence limits a packs ability to exploit moose, then this would likely limit the establishment of strongly of *C. latrans* packs to the areas where deer are accessible. It is not clear whether *C. lupus* packs have any competitive advantage over *C.*

*lycaon* packs, or vice versa. Large-scale patterns of hybridization in Ontario indicate higher gene flow between the *C. lupus* dominated population to the north than the *C. latrans* population to the south, so the differences between *C. lycaon* animals and the *C. lycaon* x *C. lupus* animals may be less distinct than the differences brought on by hybridization with coyotes. Further study is warranted to determine the trend of hybridization in Algonquin, and how this could influence the ongoing development of this predator-prey system.

### Measures of Prey Use

Variation in estimates of prey reliance at the pack level, and among winter periods, revealed extreme discrepancies among prey use measures. For population-wide estimates of prey use, the differences among measures were less pronounced; biomass and GPS handling time did not differ significantly, whereas daily handling time had significant differences from each. Because of wide variability in prey use among packs, pooling across the population inflated the variance, decreasing the power for detecting differences between mean prey use estimates. Therefore population level differences between the GPS and biomass measures may be important to consider in spite of the lack of significance.

The biomass measure represents relative amount of meat available for consumption from all deer and moose kills made by each pack, however in this study we could not measure the exact amount of meat actually consumed. When hours spent at each kill site were calculated, it became clear that in many cases wolves did not spend sufficient time at kill sites to consume the amount of meat estimated by the biomass method. For example, one pack that was monitored in fall and early winter 2006 relied on deer except for one moose kill. Because this pack's kill rates were low, and moose biomass is high in relation to deer, the inclusion of one moose in this packs diet resulted it being categorized as a moose-reliant pack, with >50% of biomass composed of moose. On examination of GPS data, this pack spent 16.5 hours at the moose carcass, in comparison to 74 hours on a total of 6 deer kills. Wolves can consume organs and meat at a rate of 24.78 grams per kilogram body mass per minute (Wilmers and Stahler 2002), but total intake is thought to be limited to 20% of their body mass per day (Mech 1970). Thus the maximum biomass that a 28 kg wolf could ingest in one day is 5.6 kg, and the maximum amount of meat this pack of 5 could have removed in the time spent on this moose kill was 28 kg. In contrast, the biomass measure estimate for this kill was 146 kg. This example is one of many observed in this study, where estimates of biomass consumed by packs were unrealistic when compared to time spent at the kill site, even with inclusion of associated resting sites where scraps of prey were carried and consumed.

Both GPS and daily handling time measures showed a population level trend of increased reliance on deer in late winter 2007, contrary to the biomass measure which showed increased reliance on moose (Fig. 5c). Compared to the actual kill rates, there was a sharp drop in the rate of deer kills and only a slight decrease in the rate of moose kills between mid and late winter. If utilization had been consistent with kill rates, patterns shown by handling time and biomass measures would have been consistent. This discrepancy was due to a decrease in time spent per moose kill in late winter 2007; however, incomplete utilization of carcasses was not detected in field investigations. A plausible explanation for this pattern would be higher incidence of kills being fed upon by multiple packs in late winter in 2007, when there were few winter killed carcasses available for scavenge compared to 2006. Also, it was not uncommon to find evidence of bear activity at carcasses investigated in late winter and spring, and given the importance of scavenging to bears emerging from hibernation (Hilderbrand et al. 1999) and the scarcity of this resource in late winter 2007, it is possible that bears may have competed with wolves for carcasses as well. Regardless, this population-wide trend was only detected with the handling time measures, and the biomass measure overestimated both the amount of meat packs could have consumed, and the relative importance of moose relative to deer on a population level. If research priorities are to measure the relative importance of different prey items, or energetic benefits per kill, caution should be used in interpreting biomass estimates of prey consumption unless precise measurements of utilization are possible, such as observations of wolves consumption at kill sites (e.g. Wilmers et al. 2003), or measurements of carcass consumption upon abandonment of kills (e.g. Hayes et al. 2000).

Differences between daily handling time and both other measures were due to predation on beaver. Though predation on small alternate prey is often difficult to detect in field investigations, we did not address detection bias in this study. In this study, small alternate prey may have been missed if wolves consumed and left the kill site in less than 3 hours, or some of the shorter clusters were not detected due to GPS error. However most studies of predator-multiple prey systems face similar challenges and are faced with decisions on how to quantify use of alternate prey. For this reason, we retained alternate prey in our analysis in order to investigate how analytical methods may influence representation of both primary and alternate prey, in spite of variation in detection error. When prey use is measured in terms of prey biomass, or proportion of hours spent on a kill, the importance of small alternate prey is negligible. However when it is measured in the traditional handling time of days between kills the time represented by alternate prey becomes more significant, as the number of days between kills determines the importance of the preceding prey item, rather than the biomass the prey item provided or hours spent handling. This highlights a weakness of the daily handling time measure, in which the number of days between kills is attributed to the energetic gain derived from the preceding kill, with no distinction between days spent satiated by a previous kill, and days spent fasting and nutritionally stressed. Therefore, when wolves kill small prey during long stretches of time between ungulate kills, the energetic contribution of small alternate prey is likely over-represented using the daily handling time method. Likewise, any prey that are taken during times of low kill rates are subject to the same error. Because of this, daily handling time may be more useful for considering rates of predation on individual prey species than calculating relative importance of prey, or energetic costs and benefits for predators. However if wolves are able to rely on small prey items when large prey are scarce or difficult to capture, they are an important resource, and biological importance in this regard is likely under-estimated by both the hourly handling time and biomass measures.

Accurate measurement of prey use is critical for modeling of prey switching or functional responses, and opportunities to quantify error in estimates of prey consumption are rare. Using fine scale GPS data to estimate utilization of prey is an improvement upon course scale handling time, as well as estimates based on biomass, and useful for identifying bias in these commonly used methods. We suggest that hourly handling time is the most precise measure available, and should be used when making inferences regarding prey consumption on a fine scale. Studies considering consumption rates or relative importance of different prey items should use caution when applying a biomass measure. In spite of advances in converting prey items to kilograms of edible meat and adjusting for scavenging (e.g. Wilmers and Stahler 2002, Selva et al. 2003, Vucetich et al. 2004), this remains an imprecise method. Even when all known influences are accounted for we found this method to overestimate importance of large prey items in relation to the GPS handling time measure. This error is likely based on imprecision of estimates of biomass lost to scavengers, edible biomass among individual prey, and variation in actual utilization by study animals which may not be detected from field investigations due to kleptoparasitism and scavenging by unmarked animals. For a more precise estimate of biomass consumed at each kill, hourly handling time could be multiplied by active consumption rates (Wilmers and Stahler 2002, Wilmers et al. 2003), up to the estimate of available biomass at each kill. Though this would also involve error in estimation of wolves' satiation point and digestive pauses, it may address the tendency to overestimate biomass consumed. If fine-scale tracking or GPS data is not available, or degree of carcass use cannot be assessed, researchers should be cautious of using such course scale data to draw conclusions about precise energetic gain derived from prey.

# CONCLUSION

Optimal foraging theory holds that animals make foraging decisions based on maximizing benefit and minimizing cost. Factors influencing costs and benefits of deer vs moose in this system include the distance that must be covered to locate prey, the difficulty in travelling that distance, the ease with which the pack subdues prey, the number and body sizes of the animals which will feed on the prey, and the potential losses to scavengers for packs of varying sizes. Accessibility is an important factor in this; though travelling to forage on deer is costly and risky, deer represent a spatially predictable resource with relatively low capture costs. Vulnerability of moose to predation is likely less predictable as it varies among individuals, and until moose body conditions deteriorate towards late winter environmental habitat factors may be more important for determining cost:benefit ratio of moose predation for wolves. Thus the factors influencing the threshold for when moose or deer are selected by each pack vary with seasonal changes that affect prey distribution, habitat associations and vulnerability, costs of locomotion for both predator and prey, as well as the composition of packs in terms of the number of wolves, degree of admixture, and the experience or skill level of individuals (Sand et al. 2006). In this system, the threshold for when wolves left territories to forage for a predictable resource rather than staying on territory to exploit a more dispersed and challenging resource was temporally and spatially variable. This highlights the fact that selection of prey depends not only on prey density, but a predator's ability to exploit, which varies with changing environmental conditions. Incorporating this variability will likely improve models of predator-prey dynamics.

We found that kill rates varied with vulnerability and accessibility of prey, with highest rates of kill on deer and moose corresponding to the time period in winter when conditions were most severe and deer were limited to the wintering area, representing a spatially predictable resource. For moose, kill rates remained high during and after snowmelt when moose body condition is known to be poor. Hebblewhite et al. (2003) pointed out the statistical flaws in extrapolating from short sampling periods to estimate kill rates for entire winters, as well as the implications for functional response models populated with data from short sampling periods. This study highlights an additional source of error arising from unrepresentative subsamples of kill rates. Hebblewhite et al. (2003) recommended that 25% of winter be sampled in order to stabilize variance, and noted that even with 55% of winter sampled there was high variability in kill rates. Our results indicate that kill rates and prey selection vary with winter progression. It follows then if kill rate sampling is pooled among time periods with varied winter conditions, high variance would be expected. Most studies do not have the resources to monitor predation continuously through winter on multiple packs, however sub-sampling should be designed to avoid temporal bias, and winter progression as well as variation on the pack level should be taken into account when extrapolating.

Research conducted in the 1960s indicated high deer densities, low moose densities and a low use of moose by Algonquin wolves, as indicated by 8.5% frequency of occurrence in scat, and only 4 moose kills found over the 7 year study, compared to 676 deer kills (Pimlott et al. 1969). Later research in the same study area concluded that Algonquin wolves are “deer specialists,” with use of moose mostly restricted to scavenges of winter killed moose and occasional kills (Forbes and Theberge 1992), but reported frequency of moose in wolf scat ranging from 27–49% frequency of occurrence and 65–87% biomass, by areas of varying moose and deer densities (Forbes & Theberge 1996). Kill rates were not measured, however wolf kills were examined opportunistically, and it was determined that 70% of moose consumed by wolves were scavenged winter-killed moose, with low rates of actual predation on moose. Although moose were found to be an important resource, Forbes and Theberge (1996) concluded that wolves in Algonquin were deer specialists, on the basis of predation on deer versus scavenging on moose, and the high incidence of off-territory movements to forage in the deer yards in spite of moose availability on territories. Theberge and Theberge (2004) later suggested that moose predation may be increasing, or perhaps was more prevalent than previously thought. There has clearly been an increase in moose predation since the 1960s, and possibly increased predation on moose since the early 1990s, the degree of which is difficult to determine in the face of major differences in protocol and technology. Results of this study indicate that specialization on moose has developed among some packs, with less selective predation occurring among the moose specialist packs, and in milder winters. Additionally, we have documented genetic introgression from *C. lupus* dominated populations to the north, as well as *C. latrans* dominated populations to the south, with implications for phenotypic and behavioral heterogeneity within the Algonquin population. Further examination of the energetic costs and benefits of specialization on moose versus deer, with changes in deer distribution and winter conditions, and continued monitoring of the genetic composition of this population would help to answer whether we are likely to see a continuation of these trends.

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# APPENDIX

Initial transects conducted in January resulted in detection of deer in wolf territories adjacent to the known deer yard but not beyond, consistent with reports that deer may stage outside of deer yards before snow depths are limiting (Nelson 1995, Nelson et al. 2004). In order to quantifying the timing and extent of deer aggregation taking place, three areas within the adjacent territories were delineated, according to spatial gradients of transect results, with Area A furthest from the deer yard, Area B adjacent to the deer yard, and Area C representing the deer yard. Likewise, 3 time frames were defined according to temporal patterns in transect results as well as weather events that were likely to result in changes in deer distribution. Track densities along transects in each area and time period were averaged to reduce the effects of transect length and occasional pockets of deer encountered (Table 7). In time period 1 (Jan 13 – Feb 22), there was evidence of some aggregation in the deer yard, however deer were still dispersed outside of the deer yard as tracks were encountered on all transects in both areas A and B. Increased deer movements towards the yard were noted in field observations after a significant snow on February 9, however increased aggregation was not immediately detected with survey results.

On Feb 22 snow depth exceeded 30cm in higher elevation areas outside of the deer yard, which is considered to affect deer mobility (Telfer 1970, OMNR 2007). In time period 2 (Feb. 23 - Mar. 5), we detected high deer densities in areas B and C, and very low densities in outlying area A. During time period 3 (Mar. 6 - 15), only area C, the deer yard itself, had high densities of deer, with low densities in both areas A & B.

Boundaries of deer aggregation during period 2 were delineated using densities from track surveys, interpolated using inverse distance weighting in ARCview 9.2, where the boundary between high density and low density was drawn at the mid-point between the density values. The track survey results showed a distinct breakpoint of deer densities below 290 meters (Table 8), with the average density above this elevation 0.68 (range 0.18-1.25), and below 290m averaging 9.4 (range 4.2-16.2). The interpolated mid-point boundary fell approximately along this elevational gradient, and was adjusted to conform to the topography.

In summary, for winter 2007 deer were considered to be dispersed and in various stages of migration until the onset of snow on Jan 7. Deer were available within the territories adjacent to and in the deer yard between Jan 7 and February 22, and distance to deer yard for all packs was calculated from the boundaries of the deer yard-adjacent territories. Between February 23 and March 5 deer were aggregated within an expanded wintering area adjacent to the deer yard below 285m elevation. After March 5 until snowmelt, deer were considered to be aggregated within the traditional deer yard, and the boundaries as defined by MNR were used.

Table A1. Deer densities from track surveys conducted during winter of 2006-07, in Algonquin Park, Ontario.

| Date | Area | Km Surveyed | Tracks/km/day |
|---|---|---|---|
| Jan13-Feb22 | A | 25.6 | 0.6 |
| | B | 16.3 | 0.5 |
| | C | 12.5 | 1.6 |
| Feb23-Mar5 | A | 8.4 | 0.7 |
| | B | 14.5 | 9.1 |
| | C | 8.5 | 8.0 |
| Mar6-15 | A | 20.0 | 0.1 |
| | B | 3.0 | 0.1 |
| | C | 16.9 | 5.8 |

Table A2. Results of deer track surveys conducted during time period 2 (Feb 23-Mar 5, 2007) in Algonquin Park, Ontario. A threshold of high/low deer density was found at 290m elevation.

| **Transect Date** | **Area** | **Km surveyed** | **Tracks/ km/day** | **Elevation** | **Forest Type** | **Transect starting location** |
|---|---|---|---|---|---|---|
| 5-Mar | C | 0.81 | 9.9 | 191 | Mixed | N of Division |
| 1-Mar | B | 6.4 | 4.2 | 226 | Mixed | W Uppr Pine Lake |
| 27-Feb | C | 3.5 | 11.1 | 239 | Mixed/Hardwood | W. Bonn/SE Bear Lk |
| 27-Feb | C | 4.2 | 4.9 | 266 | Conifer/Mixed | Wh Mtn Chute |
| 1-Mar | B | 4.2 | 10.0 | 269 | Mixed | Gunns, E Lwr Pine |
| 1-Mar | B | 3.9 | 16.2 | 284 | Mixed/Hemlock | Walker Lk, Lwr Pine Lk |
| 28-Feb | A | 2 | 0.5 | 296 | Conifer | NW Basin Rd |
| 28-Feb | A | 3.2 | 0.2 | 329 | Conifer/Mixed | S Basin Rd, Foys Lk Rd |
| 28-Feb | A | 3.2 | 1.3 | 332 | Conifer | SE Foys Lake |
| 4-Mar | A | 12.3 | 0.9 | 355 | Hardwood | Beechnut Rd to Rories |