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Foraging ecology of brown bears in the Mackenzie Delta region, NWT

by

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Abstract

The Mackenzie Delta region, NWT, has a short growing season and highly seasonal climate, and brown bears (*Ursus arctos*) there face many challenges obtaining their nutritional requirements. Consumption of meat by brown bears is linked to increases in population density, fecundity, growth and body size. I examined the use of Arctic ground squirrels (*Urocitellus parryii*), and broad whitefish (*Coregonus nasus*) as meat sources by Mackenzie Delta brown bears. As a preliminary step, I built an Arctic ground squirrel habitat model, using field-surveyed ground squirrel burrow locations. Using this model, I examined bears' selection for Arctic ground squirrel habitat as a population, by sex and as individuals, and linked this to results of stable isotope analysis and site investigations. Bears showed little evidence of Arctic ground squirrel use at the population and sex level, but some individual bears appeared to prey heavily on ground squirrels, particularly during hyperphagia. I also described observations of a brown bear using broad whitefish in autumn, and used telemetry locations to show that other bears may also feed heavily on broad whitefish during hyperphagia. My research provides prey-specific evidence for intrapopulation niche variation among Mackenzie Delta brown bears.

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Chapter 1 – Introduction

1.1 General introduction

Within the order Carnivora, the family Ursidae show remarkable dietary variation. Among the 8 extant bear species, diets range from near-obligate carnivory in polar bears (*Ursus maritimus*), to insectivory in sloth bears (*Melursus ursinus*), through varying degrees of omnivory among brown (*U. arctos*), black (*U. americanus*), spectacled (*Tremarctos ornatus*), sun (*Helarctos malayanus*), and Asiatic black bears (*U. thibetanus*), to herbivory in giant pandas (*Ailuropoda melanoleuca*; Peyton 1980, Stirling and Derocher 1990, Joshi et al. 1997, Mattson 1998, Wong et al. 2002, Mowat and Heard 2006). Within the omnivorous species exists a great deal of inter-population and individual variation in diet, ranging again within the spectrum between carnivory and herbivory (Rode et al. 2001, Mowat and Heard 2006, Edwards 2009). Physical adaptations to an omnivorous diet, notably the development of broad-crowned molars suitable for processing vegetation, allow bears to maximize their foraging efficiency by exploiting the most abundant and/or nutritionally valuable resources within the wide array of food items available to them (Herrero 1978, Stirling and Derocher 1990, Rode et al. 2001, Sacco and Van Valkenburg 2004). Brown, or grizzly, bears (hereafter brown bears) exemplify the within-species dietary plasticity of the omnivorous ursids. The catalogue of foods commonly eaten by brown bears is extensive; leaves, shoots, fruit and roots of grasses and forbs, fruit, nuts, leaves and bark of shrubs and trees, fungi, insects and their eggs, honey, birds, bird eggs and nestlings, small mammals, adult and neonate ungulates and salmonid fishes are all considered typical brown bear food (Pasitschniak-Arts 1993).

As a product of their ability to exploit a wide range of food items, brown bears have adapted to many different habitats across Eurasia and North America. The brown bear's historical range in Eurasia encompassed montane regions from the Mediterranean to northern Europe, through the Middle East to the Himalayas and the Tibetan Plateau, along the coastal forests of the Pacific Rim, and across the steppe and taiga of central Asia to the Arctic tundra (McLellan et al. 2008). In North America, brown bears range extended from the mountains of northern Mexico to the coastal tundra, inhabiting savannah, prairie grassland, taiga and coastal rainforest in between (Pasitschniak-Arts 1993). While brown bears have been extirpated from many parts of their former range, their current distribution still covers desert, temperate rainforest, grassland, montane, boreal and tundra biomes (McLellan et al. 2008).

1.2 Carnivory in omnivorous bears

Despite dental modifications to process vegetation, bears' digestive systems are not well adapted to a plant-based diet. Bears possess a short, non-caecal gastrointestinal tract typical of carnivores, and cannot digest cellulose (Bunnell and Hamilton 1983, Pritchard and Robbins 1990, Stirling and Derocher 1990). The ability of brown bears to digest vegetation is low, with reported dry matter digestibility for various berries and herbaceous plant parts ranging from 15 - 75%, whereas values for meat sources from mammals and fish range from 75 - 95% (Pritchard and Robbins 1990, Welch et al. 1997). As a result, bears feeding on plants are required to process much larger quantities of food than those feeding on meat sources rich in protein and lipids. The ability of bears to sustain themselves on plants can be constrained by encounter and bite rate, as the amount of low-digestibility plant matter required for body maintenance and growth can exceed a bear's capacity to detect, handle and consume it (Welch et al. 1997, Rode et al. 2001). Digestive processes may also limit intake, as the ability of the digestive system to accommodate and break down large amounts of plant material may determine maximum intake rates (Welch et al. 1997). The high metabolic costs associated with converting high carbohydrate - low protein fruit into body mass may also constrain intake in a high fruit diet (Rode and

Robbins 2000, Felicetti et al. 2003). Constraints related to foraging efficiency are of particular concern during the hyperphagic period before winter dormancy, when bears must gain sufficient fat stores to survive the winter (Watts and Jonkel 1988). In addition, some adult females bear the cost of gestation and lactation over winter, which must also be supported by autumn hyperphagy (Hellgren 1998).

Bears' large nutritional requirements, particularly during hyperphagy, and their relative inefficiency at handling, consuming and processing vegetation, point to the potential importance of meat in brown bear diets. Rich in protein and lipids, meat forms a large part of brown bear diet in regions where it is readily available (Mowat and Heard 2006). Across their range, brown bears use various meat sources; ungulates, whether as prey or carrion, are a common food item for inland brown bear populations, whereas anadromous salmonids are heavily exploited by coastal populations (Hilderbrand et al. 1999b, Hilderbrand et al. 2004, Mowat and Heard 2006). The consumption of large amounts of meat is not obligatory; many individuals and populations subsist mainly on plant materials, with berries acting as an important hyperphagia food source (Welch et al. 1997, Rode and Robbins 2000, Rode et al. 2001). Even in mainly herbivorous bears, however, occasional meat consumption confers metabolic and growth benefits (Rode and Robbins 2000, Felicetti et al. 2003). The proportion of meat in brown bears' diets has demonstrated significant correlation with bear population density, fecundity and female body size (Hilderbrand et al. 1999a,b). By consuming meat, brown bears can accrue significant growth, survival and reproductive benefits.

Selection of resources, such as dietary meat, occurs over a continuum of spatiotemporal scale. Selection at one scale can also affect selection at another; e.g. selection for a particular resource patch constrains an organism’s choices to the specific resource types within that patch. Johnson (1980) proposed a hierarchically ordered concept of resource selection, such that selection occurring at higher orders was conditional on lower-order selection processes. This concept proposes four levels of selection: first-order selection involves processes defining a species' geographic range, second-order selection involves processes determining an individual's (or group's) home range, third-order selection involves processes determining selection of resource patches within a home range, and fourth-order selection pertains to processes determining within-patch selection of food or other resources (Johnson 1980). While fourth- and third-order selection processes deal with choices surrounding individual resource units most directly, these are underpinned by larger-scale second- and first-order selection processes. Johnson's (1980) hierarchical orders, however, should be seen as overlapping concepts rather than discrete entities; as distinctions blur between the scale of home range and resource patch, and between resource patch and individual food items, so do the separations between selection orders (Mayor et al. 2009).

For Mackenzie Delta brown bears, a sensitive population in a highly seasonal environment, the ability to exploit scarce resources and withstand extreme environmental conditions is likely a major driver of population growth (Ferguson and McLoughlin 2000, McLoughlin et al. 2000). As such, the identification of exploited resources, particularly those that are temporally or spatially limited, is critical to understanding their distribution and abundance. Locating and handling food items form a large part of a brown bear's non-denning activities (Atwell et al. 1980, Phillips 1987, White et al. 1999, MacHutchon 2001), and the distribution of foraging resources are thought to have a strong effect on their habitat use (Servheen 1983, Waller and Mace 1997, McLellan and Hovey 2001, Nielsen et al. 2003, 2010). By identifying the distribution of key resources and the bears using them, it is possible to gain insight into foraging, habitat use and survival strategies at the individual and population level.

1.3 Study area

Broadly, the study area for my thesis was the Mackenzie Delta region of northwestern Northwest Territories (hereafter NWT), Canada. The study area encompasses the Mackenzie Delta lowlands, extending northwest from the town of Inuvik to Mackenzie Bay and the Beaufort Sea, and the adjacent uplands, extending east from the delta lowlands to a line running between the community of Tuktoyaktuk and the western shore of Sitidgi Lake (Fig. 1.1). This area lies within the Inuvialuit Settlement Region (DIAND 1984).

The study area consists of two adjacent, yet ecologically distinct, regions; the delta lowlands in the west, and the boreal and tundra uplands in the east. The Mackenzie Delta lowlands consist of floodplains and deltaic deposits of silt, clay, sand and fine organic sediments, and are dotted with thousands of shallow lakes and meandering channels (Mackay 1963, Rampton 1988). Large spruce trees (*Picea mariana* and *P. glauca*) reach their northern limit approximately 50 km north of Inuvik (Rampton 1988). The central and northern delta is composed of willow thickets (*Salix* spp.) and marshes of aquatic sedge (*Carex aquatilis*) and common horsetail (*Equisetum arvense*; Mackay 1963, Rampton 1988). The Mackenzie Delta is underlain by discontinuous permafrost (Rampton 1973).

The upland habitat east of the Mackenzie Delta consists of rolling morainal and glaciofluvial deposits of clay, sand and gravel (Rampton 1988). Lakes cover 15 – 30% of the surface area of this region (Mackay 1963). Thermokarst processes shape much of the topography of this region, contributing to extensive pingos, ice slumps, mudflows and tundra polygons (Rampton 1973, 1988). Upland habitat in the southern third of the study area consists of woodland tundra, with open stands of white and black spruce and larch (*Larix laricina*) interspersed with muskeg, peat-bog and sedge marsh communities (Mackay 1963, Lambert 1973). The northern two-thirds of the upland study area is a mixture of tussock tundra and polygonal peatlands. Better-drained areas host dwarf shrub-heath tundra vegetation (Lambert 1973, Rampton 1988). The upland area is underlain by continuous permafrost (Mackay 1963, Rampton 1988).

As an Arctic environment, the climate in the Mackenzie Delta region is highly seasonal and unpredictable. The growing season is short and primary productivity is low and exhibits high interannual variation (Ferguson and Messier 1996, CAFF 2001). The study area has short, cool summers, with 95 and 106 frost-free days/year for Tuktoyaktuk and Inuvik respectively, and July mean temperatures between 11-14°C (Environment Canada 2010). Continuous daylight extends from 24 May until 19 July (NRC 2010). Winters are long and cold, with mean January temperatures of -27°C and an extreme cold record of -56.7°C for Inuvik (Environment Canada 2010). Continuous night extends from 6 December to 4 January (NRC 2010).

1.4 Ecological and anthropomorphic constraints on Mackenzie Delta brown bears

The Arctic boreal and coastal tundra habitats of the Mackenzie Delta region represent the northern limit of brown bear distribution in Canada (Ross 2002, but see Doupé et al. 2007 for discussion of possible northward range expansion). The ecophysical conditions of this region, with its harsh and unpredictable climate, short growing season and low primary productivity, present unique challenges to the Mackenzie Delta brown bear population (Nagy et al. 1983, Edwards 2009). Coupled with this volatility of their biotic and abiotic environment, brown bears must contend with a relatively low level of ecological resiliency, as dictated by their low fecundity, limited propensity for long-range dispersal and requirement for large quantities of high quality foods, particularly during hyperphagia in late summer and autumn (Weaver et al. 1996). This low resilience in the face of a harsh and unpredictable environment means the Mackenzie Delta brown bear population may be sensitive to additional environmental disruption. Disturbance, however, is predicted at both a local and global scale. At a local scale, the proposed construction of a major natural gas pipeline through the Delta, with a subsequent increase in anthropogenic activity, will likely affect bear behaviour and habitat use (Pearson 1980, Edwards et al. 2006). On a global scale, the effects of a warming Arctic climate are expected to have large repercussions for ecological function across the circumpolar north (CAFF 2001, Hassol et al. 2004, IPCC 2008).

1.4.1 Climate change

The warming climate is expected to lead to ecological disturbance in the Mackenzie Delta region. The western Canadian Arctic has experienced an increase in winter temperatures of 3-4°C since the 1960s, with a further rise of 4-7°C over the next 100 years anticipated under moderate emissions scenarios (Hassol 2004, IPCC 2008). Consequences of a warming Arctic climate, such as increased precipitation, thawing permafrost, an increased frequency of icing events and the encroachment of sub-arctic boreal forest into tundra regions, will affect the quality and spatiotemporal distribution of resources (CAFF 2001, Hassol 2004, IPCC 2008). The effects of a warming Arctic climate on brown bears are difficult to predict; a longer growing season, deepening active layer and increased primary productivity may confer foraging benefits, whereas phenological disruption, changing precipitation regimes and losses in biodiversity would have negative consequences for bears' survival, growth and reproduction. A northward advancing treeline, for instance, could have a profound impact on the distribution and abundance of Arctic ground squirrels (*Urocitellus parryii*, formerly *Spermophilus parryii*; Helgen et al. 2009), a food resource for Mackenzie Delta bears (see Chapter 2).

1.4.2 Anthropogenic development

Brown bears populations respond negatively to anthropogenic development and human activity. Brown bears are affected by increases in development and human presence within their range through direct mortality (increased hunting, poaching and cull of nuisance bears; McLellan 1998, McLellan et al. 1999, Nielsen et al. 2004, Schwarz et al. 2010, higher vehicle-caused mortality; Huber et al. 1998, Gibeau and Herrero 1998, Kaczensky et al. 2003), direct habitat loss (Schoen 1990) and indirect habitat loss and increased energetic costs caused by avoidance of human activity (McLellan and Shackleton 1988, Reinhart and Mattson 1990, Johnson et al. 2005, Rode et al. 2007, Martin et al. 2010). Habitat fragmentation and anthropogenic barriers to bear movement can also have implications for brown bear genetic diversity (Proctor et al. 2002, Proctor et al. 2005, Haroldson et al. 2010).

Extensive anthropogenic disturbance, in the form of petroleum extraction and transportation development, is projected for the Mackenzie Delta region. An estimated 5.7 trillion cubic feet of natural gas and natural gas liquids exist in the Niglintgak, Taglu and Parsons Lake reserves (Imperial Oil Ltd. et al. 2007, Voutier et al. 2008). Extraction and transportation of these reserves to southern markets has been proposed by the Mackenzie Gas Project, a joint venture between ExxonMobil Canada Properties, Imperial Oil Resources Ventures Ltd., ConocoPhillips Canada (North) Ltd., ShellCanada Ltd., and the Aboriginal Pipeline Group. Development in Mackenzie Delta study area would include gathering and conditioning facilities at the Niglintgak, Taglu and Parsons Lake fields, a Storm Hills pigging facility and lateral gas pipelines joining these installations to a proposed processing and storage station in Inuvik, as well as permanent and ice roads, camps, airstrips and barge landing sites to facilitate construction, operation and maintenance of facilities and pipelines (Imperial Oil Ltd. et al. 2007, Voutier et al. 2008). Construction of facilities, pipelines and associated infrastructure will see an influx of people into the Mackenzie tundra uplands, with ten remote camps capable of holding a total of 1750 workers slated for construction within the Mackenzie Delta study area (Imperial Oil et al. 2007). Regulatory approval for development of the Mackenzie Gas Project was recently granted (NEB 2010), with the first shipments of natural gas and natural gas liquids along a completed pipeline anticipated by 2018 (O'Meara 2010).

1.5 Goal of my research

Meat sources commonly used in other brown bear populations are scarce or absent in the Mackenzie Delta region; salmon (*Oncorhynchus* spp.) and char (*Salvelinus* spp.) do not make significant migrations in the region's streams, and shifting migration patterns and herd declines have resulted in few caribou (*Rangifer tarandus*) using the region during bears' active season (Scott and Crossman 1998, Nagy et al. 2005, Nagy and Johnson 2006). Inability to exploit meat sources would reduce the ability of Mackenzie Delta brown bears to withstand ecological and anthropogenic change. Stable isotope analysis of Mackenzie Delta bears, however, has shown foraging strategies spanning herbivory, omnivory and carnivory (Edwards et al. 2010). What meat sources, then, are Mackenzie Delta bears exploiting, and where and when does this occur?

In my thesis, I focus at the level of third- and fourth-order resource selection by Mackenzie Delta brown bears, examining processes occurring within seasonal ranges and resource patches, to understand bears' use of specific food resources. By identifying which meat sources bears use, and how and when they use them, we can better understand which resources are most critical to bears, and how their distribution and use might be affected by anthropogenic change. My thesis focuses specifically on Arctic ground squirrels, a species known to be a common food source for some Arctic brown bear populations, and broad whitefish (*Coregonus nasus*), a novel food source whose use by brown bears has been recorded only within the Mackenzie Delta region. This thesis builds on earlier work by Edwards (2009), who examined lower-order selection, focusing at the home range and within-home-range scale, to identify seasonally important habitats and determinants of home range size in Mackenzie Delta brown bears.

1.5.1 Thesis chapters

My thesis is comprised of three data chapters. Chapter 2, Habitat selection by Arctic ground squirrels in the Mackenzie Delta region, NWT, lays the groundwork for investigation into the use of Arctic ground squirrels by Mackenzie Delta brown bears. Arctic ground squirrels have been proposed as an important food item for northern brown bear populations (Pearson 1980, Miller et al. 1982, Nagy et al. 1983, Hechtel 1985, Mueller 1995, MacHutchon and Wellwood 2003). Unlike other, more mobile mammalian prey species, Arctic ground squirrels are near-sessile when considered at scales larger than tens of metres, and their distribution can be mapped in much the same way as vegetation types. The location and distribution of vegetative brown bear food resources in the Mackenzie Delta region have been modeled (C. Squires-Taylor, NWT Centre for Remote Sensing, *pers. comm.*), but no such data exist for Arctic ground squirrels. In Chapter 2, I constructed and evaluated a set of Arctic ground squirrel resource selection function (RSF) models, considering covariates for vegetation type, topography, surficial geology and spatial autocorrelation among Arctic ground squirrel locations. The final model predicted Arctic ground squirrel habitat selection at multiple scales, gave insight into the factors driving Arctic ground squirrel distribution, and provided a baseline against which to measure the effects of future climate change and anthropogenic disturbance on Arctic ground squirrels.

In Chapter 3, Use of Arctic ground squirrels by brown bears in the Mackenzie Delta region, NWT, I used the Arctic ground squirrel habitat model developed in Chapter 2 to evaluate selection for Arctic ground squirrel habitat by 37 GPS collared brown bears, and the relationship between this selection and bears' foraging behaviour, as estimated generally by stable isotope analysis, and specifically by bear activity site visits. I examined selection for Arctic ground squirrel habitat by bears at both the individual and population level, to determine the contribution of individual bears to population-level selections. I also divided bears into sex-segregated groups, and examined differences in foraging patterns between sexes. I also examined the difference in selection for Arctic ground squirrel habitat among seasons. While the results show no significant evidence of selection for Arctic ground squirrel habitat at the population or sex-segregated level, some individual bears demonstrated strong selection for Arctic ground squirrel habitat. These results support the hypothesis that a high level of intrapopulation variation in resource use exists among Mackenzie Delta brown bears, with a component of the population specializing on Arctic ground squirrel predation.

In Chapter 4, Use of broad whitefish by brown bears in the Mackenzie Delta region, NWT, I described observations of a brown bear feeding on migrating broad whitefish in Pete's Creek, a small tributary of the Mackenzie River. I also examined GPS-collar location data from other study bears for evidence of broad whitefish predation, and discussed the potential importance of this food source to the Mackenzie Delta brown bear population.

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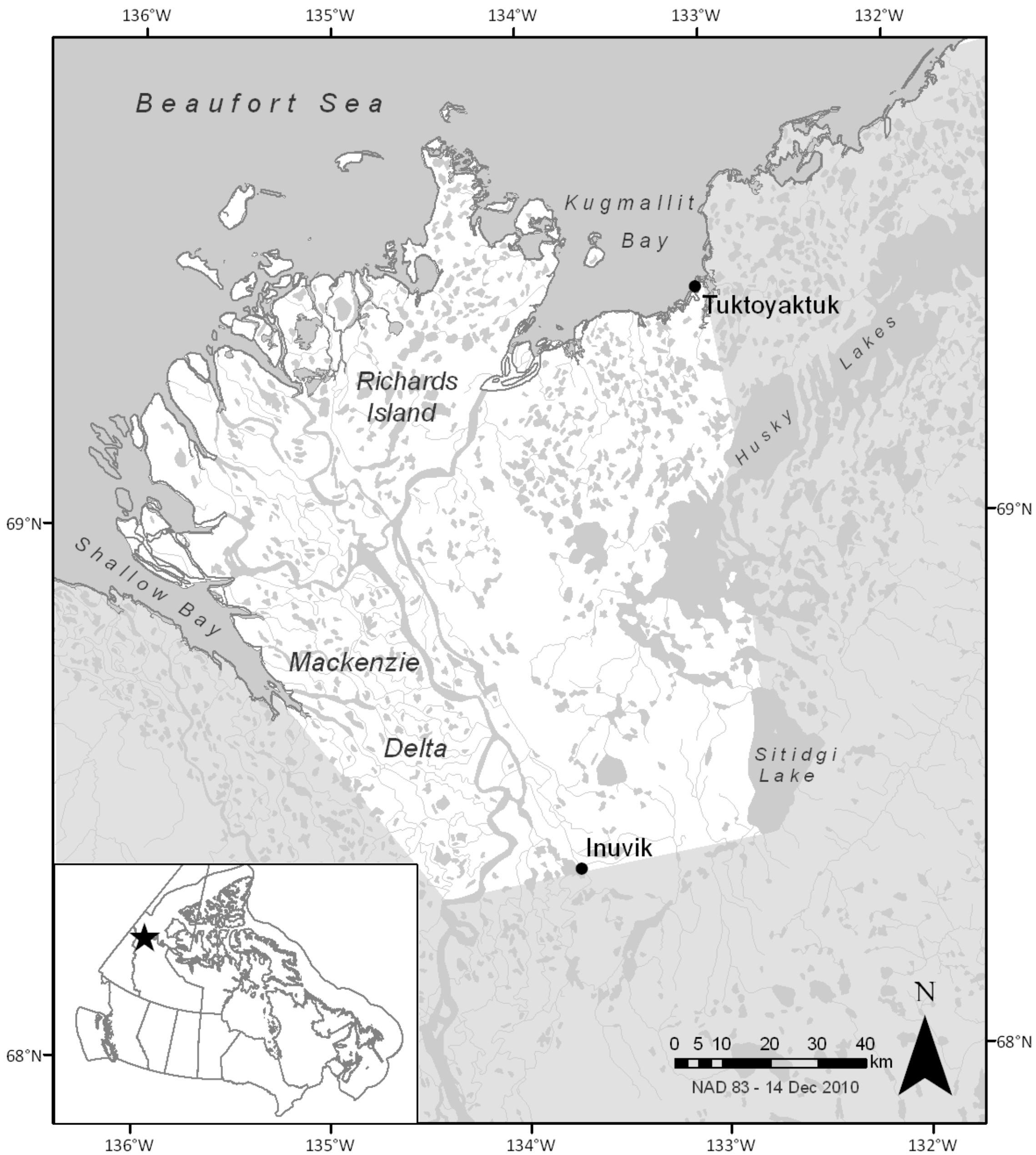

Figure 1.1 - The Mackenzie Delta region, NWT, showing the study area (white) and location within Canada (inset).

Chapter 2 – Habitat selection by Arctic ground squirrels in the Mackenzie Delta region, NWT[1]

2.1 Introduction

Indicators are often used to monitor large, complex ecosystem processes. Ideal indicators are monitored easily and accurately, match the scale of the underlying processes of interest, and give credible information about these processes (Storch and Bissonette 2003, Goodsell et al. 2009). Indicator species are often fauna with direct cultural or economic importance, such as birds, harvestable mammals, and apex predators (Ray et al. 2005, Laidre et al. 2008, Sergio et al. 2008, Einoder 2009). Less economically and culturally significant species are often overlooked, even in well-studied ecosystems (Tisdell and Swarna Nantha 2007, Berger 2008).

Arctic ecosystems are defined increasingly by the rapidity of their alteration. At a global level unprecedented climate change threatens to disrupt ecosystem function by changing abiotic conditions, decoupling ecological linkages, and facilitating northward advancement of southern species (Hassol 2004, Parmesan 2006, Intergovernmental Panel on Climate Change 2008, Sommerkorn and Hamilton 2008). At more local scales the demands of an increasing Arctic population, and expanding natural resource extraction and attendant development, also place strain on ecosystem function (Truett and Johnson 2000, Nassichuk 2003, Hassol 2004, Johnson et al. 2005). Monitoring ecosystem change is critical to identifying and conserving threatened system components and managing anthropogenic impacts.

Arctic ground squirrels inhabit the subarctic and Arctic mainland from the

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western shore of Hudson Bay to eastern Siberia (MacClintock 1970, Woods 1991). Arctic ground squirrels are ubiquitous in tundra habitats and present in alpine meadows and clearings within the boreal forest (Woods 1991). Arctic ground squirrels live colonially in complex, shallow burrow systems that serve as predator refuge, maternal dens, and hibernacula (Carl 1971, McLean 1981).

Relatively large rodents (600-900 g) with seasonally high fat content, Arctic ground squirrels are prey for brown bears, foxes (*Vulpes* spp.), wolverines (*Gulo gulo*), wolves (*Canis lupus*), rough-legged hawks (*Buteo lagopus*), peregrine falcons (*Falco peregrinus*), and snowy owls (*Bubo scandiacus*) (Carl 1971, Ballard et al. 1987, Bradley and Oliphant 1991, Reid et al. 1997). A territorial species, the Arctic ground squirrel consists of populations that are thought to be regulated by competition for suitable habitat (Carl 1971, Batzli and Sobaski 1980, Batzli 1983). Arctic ground squirrels are distinct from most tundra-dwelling rodents because their populations are noncyclical and are thought to maintain populations of Arctic tundra predators during the crash and recovery phase of cyclically fluctuating small mammal species (Reid et al. 1997).

Arctic ground squirrels have significant influence on their surrounding biotic and abiotic environment. Through selective feeding and deposition of body wastes, ground squirrels can alter the composition of plant communities near their burrows (Batzli and Sobaski 1980, McKendrick et al. 1980). In addition to these top-down effects, Arctic ground squirrels have significant indirect effects on their environment. Their excavations, averaging 18 tonnes/ha/year in one alpine site, displace large amounts of earth and influence erosion, soil compaction, and depth of the permafrost (Price 1971). Combined with waste deposition and food caching, this biopedturbation results in extensive nutrient redistribution (Price 1971, Batzli and Sobaski 1980, McKendrick et al. 1980). For burrowing mammals in better-studied systems, burrow creation and maintenance, selective herbivory, and nutrient redistribution affect nutrient availability, landscape heterogeneity, and regional species diversity (Huntly and Reichman 1994, Whitford and Kay 1999). Affecting the availability of resources to other organisms through the alteration of their physical environment, Arctic ground squirrels act as physical ecosystem engineers (Jones et al. 1994, 1997).

As a widespread, noncyclical tundra mammal that influences top-down, bottom–up, and indirect ecological processes over large geographic space, the Arctic ground squirrel may be important for monitoring Arctic ecosystems. Despite the potential importance of Arctic ground squirrels to ecosystem dynamics, studies on their ecology in tundra environments are scarce, and the majority of those that exist predate current technologies and analytical methods (Mayer 1953, Carl 1971, Batzli and Sobaski 1980, Batzli 1983). I modeled habitat selection by Arctic ground squirrels, a key ecosystem component as both a prey item and herbivore predator, in the Mackenzie Delta region, NWT. I used these models to examine patterns of Arctic ground squirrel distribution and to provide baseline data against which to compare future distributions of this component as the Mackenzie Delta ecosystem is affected by changes occurring at local and global scales.

2.2 Study Area

The study area was bounded by the Beaufort Sea to the north and the Mackenzie Delta in the west, in the northwestern part of NWT, and straddled the ecotone between forest and tundra. The southern one-third of the study area had open stands of stunted white and black spruce and larch interspersed with muskeg and peat bog communities. These boreal communities graded to tundra in the northern two-thirds of the study area, with moist sites dominated by tussock cottongrass (*Eriophorum vaginatum*), sedges and *Drepanocladus* and *Sphagnum* mosses, and well-drained uplands consisting of heath tundra typified by Labrador tea (*Rhododendron subarcticum*), crowberry (*Empetrum nigrum*), mountain avens (*Dryas integrifolia*), dwarf birch (*Betula nana*) and *Vaccinium* spp. (Lambert 1973, Rampton 1988). Underlain by permafrost, substrates consisted mainly of rolling morainal and glaciofluvial deposits, with lakes covering 15-30% of the surface area (Mackay 1963, Rampton 1988).

2.3 Methods

2.3.1 Data collection

I divided the area into 3-km x 3-km plots and randomly selected 115 plots to survey for Arctic ground squirrel use, excluding those that fell mostly on habitat unsuitable for ground squirrels (i.e., water or seasonally flooded delta plain). I used Arctic ground squirrel burrow systems as an indicator of recent ground squirrel use. I surveyed plots for Arctic ground squirrel burrow systems by helicopter, flying at 5-15 m above ground. When I encountered a burrow I hovered directly over it and recorded a georeferenced image using a GPS-linked Nikon D2Xs digital camera (Nikon Inc., Melville, New York). Plot size was such that thorough searches lasted ≤ 15 min. One vegetation cover, willow thicket, was too dense to allow searches from the air; I selected a sample of 15 areas of willow thicket areas within survey plots for ground searches to evaluate Arctic ground squirrel habitat use in these areas.

2.3.2 Habitat modeling

I evaluated Arctic ground squirrel habitat selection by comparing characteristics of used to available locations using exponential resource selection functions (RSFs), estimated using logistic regression (Boyce and McDonald 1999, Manly et al. 2002). I based modeling effort on a 30-m grid (corresponding to the grain size of other geospatial data collected), with grid cells containing at least one burrow considered used. I randomly assigned 10,000 cells as available. After assigning available cells, I excluded those that fell in habitats unsuitable for permanent colonization by Arctic ground squirrels (i.e., water and seasonally flooded delta plain), leaving 7,378 available cells for my analyses. Candidate RSF models incorporated covariates for topography, surficial geology, and vegetation type.

Topography covariates considered in RSF model construction were slope in degrees (SLP); easterly aspect (EAS); terrain ruggedness (RUG), calculated as the standard deviation of slope values; and cell curvature (CRV), calculated as the second derivative of the cell surface on values from its eight nearest neighbour cells. Topography covariates were derived from a 30-m resolution digital elevation model available from NWT Centre for Geomatics (www.gnwt geomatics.nt.ca).

Surficial geology covariates classified surficial deposit composition and texture and were chosen for consideration based on their hypothesized impacts on burrow construction and suitability. Surficial geology classes considered were hummocky moraine (MOH), consisting of coarse till (gravel to boulders) deposited in hummocks and ridges with relief of 15 – 50 m; rolling moraine (MOR), consisting of flat to gently sloping plains of fine morainal till; glaciofluvial plain (GLF), consisting of gently sloping plains of sand and gravel, often with eolian sand veneer; and lacustrine plain (LAC), consisting of gently sloping plains of silt and clay overlain by sand or organic materials. Surface water (WAT) also was considered. Surficial geology covariates were derived from Rampton et al. (1988).

Vegetation types, particularly those relating to vegetative cover and to moist environments, were hypothesized to affect burrow site selection by Arctic ground squirrels. Vegetation classes considered were sparse vegetation (SPB), consisting of areas with >50% bare ground; deciduous tall shrub (DTS), consisting of areas with >25% cover of *Alnus* spp. and *Salix* spp. ≥1.3 m in height; deciduous low shrub (DLS), consisting of areas with >25% cover of *Alnus* spp. and *Salix* spp. <1.3 m in height; and moist tussock (TUS), consisting of areas of tussock tundra, wet low-centre polygons, dwarf shrub/tussock tundra and graminoid wetlands. Vegetative greenness values (GRN) also were considered. Vegetation covariates were derived from Landsat 5 Thematic Mapper satellite imagery classified on a 28.5-m grid (C. Squires-Taylor, NWT Centre for Remote Sensing, *pers*. *comm*.).

I examined potential model covariates at five scales: 30 m (input cell size) and for circles of 50-, 100-, 200-, and 500-m radii. I used the scale that demonstrated the greatest differentiation between used and available cells for building candidate RSF models. Covariates were screened for collinearity, and I did not include covariate pairs having a Pearson correlation (*r*) of ≤ -0.70 or ≥ 0.70 within the same model.

I approached the construction and evaluation of the candidate model set with the goal of identifying a descriptive model of Arctic ground squirrel habitat selection. I constructed 12 candidate models from the screened covariates: ten models based on prior ecological knowledge of Arctic ground squirrel habitat relationships, incorporating hypothesized selection patterns for terrain characteristics, surficial geology and vegetation types, and two models produced by forward and backward conditional covariate selection methods (α-to-enter = 0.05, α-to-remove = 0.10—Burnham and Anderson 2002, SPSS Inc. 2006). I ranked candidate models using Bayesian Information Criterion (BIC), which selects more parsimonious models than Akaike's Information Criterion with large sample sizes (Schwarz 1978, Burnham and Anderson 2002).

2.3.3 Spatial autocorrelation

The existence of spatial autocorrelation among animal use locations can lead to spurious conclusions about resource selection patterns (Legendre 1993, Legendre et al. 2002, Manly et al. 2002). To examine the effects of possible spatial autocorrelation among Arctic ground squirrel burrow locations, I added autocovariates of various neighbourhood sizes to the top-ranked RSF model (Augustin et al. 1996, 1998). I calculated an initial autocovariate value for each cell by taking a distance-weighted mean of predicted relative probability of cell use (derived from the top-ranked RSF) for a neighbourhood of cells surrounding each focal cell. I used square neighbourhoods of three, seven, 13, 19, and 25 cells on a side, corresponding to a nearest-neighbour and neighbourhoods equal to one, two, three and four mean home-range diameters of Arctic ground squirrels obtained from the literature (Table 2.1). Cell weights in each neighbourhood were calculated as the inverse of their distance to the focal cell, and any cells falling in water or other unavailable habitat were censored. Autocovariate values for each training cell were introduced to the original RSF model, and new predicted relative probability of use values were calculated. I then used neighbourhoods of these new RSF values to build new autocovariate values. I continued autocovariate recalculations for ten iterations to allow autocovariate values and β coefficients to stabilize (Augustin et al. 1996). I evaluated the final models for parsimony using BIC.

2.3.4 Model validation and predictive performance

I withheld 20% of the used locations and assessed the predictive performance of our final model with that data set, following Johnson et al. (2006). Using the final model, I predicted pixel RSF values, and aggregated pixel values into ten ranked bins. Bin widths were determined by examining RSF values for used pixels in the model-building data set, such that each bin contained a roughly equal number of used pixels. For each bin I calculated a utilization value ($U(x_i)$), where

$$U(x_i) = w(x_i)\,A(x_i) \,/\, \Sigma\, w(x_j)\,A(x_j) \ ,$$

with $w(x_i)$ is the midpoint RSF value of bin i and $A(x_i)$ the area of bin i (Boyce and McDonald 1999, Johnson et al. 2006). I calculated expected used pixels for each bin (n_i), where

$$n_i = n \cdot U(x_i) \ ,$$

with n = used pixel locations within the out-of-sample validation data set. Comparing n and n_i, I evaluated proportionality of the RSF model to probability of habitat use using the slope and intercept of a linear regression on the data. I assessed model fit to validation data using R^2 and a G-test for goodness-of-fit, and tested for departure of the slope from zero and one using t-tests.

I also compared the correlations of area-adjusted frequencies of predicted RSF values from the out-of-sample validation data set to the rank values of their containing bins using the Spearman rank correlation (Boyce et al. 2002). Area-adjusted frequencies were calculated by dividing raw frequencies from each bin by the bin area in km^2.

2.4 Results

I surveyed 115 randomly selected 3-km x 3-km plots between 6 July – 28 August 2007, identifying 1,030 burrow systems of Arctic ground squirrels, which were aggregated into 820 used 30-m grid cells. No Arctic ground squirrel burrows were found during ground searches in willow thickets. I withheld a randomly selected 20% (n = 164) sample of the used cells for out-of-sample model validation.

For the majority of habitat values the greatest differentiation between used and available was seen at the 200-m buffer size. Only cell curvature, slope, and percent deciduous tall shrub differed significantly at the 100-m buffer size, whereas the 30-m focal cell and 500-m buffer size showed no significant difference among used and available locations. Among the candidate models the top-ranked model was the forward conditional covariate selection (Table 2.2). Models 2 - 12 received poor empirical support.

I used Model 1 as a starting point for iterative autocovariate calculation. In no case was the autocovariate a significant addition to the RSF model, nor was any autocovariate's β coefficient significantly different from zero (Table 2.3). BIC comparisons gave a posterior probability of 0.55 for the original RSF, compared to 0.10 for the highest-ranked models containing autocovariates (Table 2.4). With the fewest parameters and greatest posterior probability, the original Model 1 remained the most parsimonious model of predicted probability of Arctic ground squirrel habitat use (Table 2.4).

Model 1 demonstrated good fit as evidenced by a large coefficient of determination ($R^2 = 0.89$) and a nonsignificant G-test ($G_9 = 0.22$, p = 0.99), which indicated agreement between model predictions and validation data (Fig. 2.1). Although the slope was significantly different from zero ($t_8 = 7.97$, $p < 0.01$), it also was significantly different from one ($t_8 = 6.31$, $p < 0.01$), indicating that Model 1 predictions perform better than random but are not directly proportional to the probability of habitat use by Arctic ground squirrels (Fig. 2.1). Area-adjusted frequency of Arctic ground squirrel habitat use showed significant positive correlation with bin rank (Fig. 2.2).

Model 1 predicts that Arctic ground squirrels show selection for rolling moraine and glaciofluvial deposits and select against hummocky moraine, high mean greenness values, and total surface area of water within 200 m of their burrows (Table 2.3). Arctic ground squirrels appear to select for terrain with high mean convexity values or in proximity to steep slope but against terrain possessing both proximity to steep slope and high mean convexity. At a larger spatial scale Arctic ground squirrels were predicted to show stronger selection of northern tundra habitat than of forested areas in the southern third of the study area (Fig. 2.3). Strongly selected habitats in the south were concentrated along creek valleys and delta and coastal bluffs. Large swaths of both tundra and boreal forest habitats were predicted to be nearly devoid of Arctic ground squirrels.

2.5 Discussion

The exponential resource selection model outperformed autologistic-derived exponential models. As such, spatial autocorrelation among Arctic ground squirrel burrows likely was driven exogenously by the spatial arrangement of preferred habitat rather than endogenously by factors such as social bonds (Augustin et al. 1996, 1998, van Teeffelen and Ovaskainen 2007). The specific habitat preferences of Arctic ground squirrels, combined with the patchy nature of such preferred habitat, accounted for ground squirrel distribution.

The resource selection model performed well at predicting Arctic ground squirrel presence within a RSF bin relative to other bins. A comparison of expected versus observed proportions of Arctic ground squirrel locations from the validation data set, however, demonstrated that model predictions were not directly proportional to true probability of habitat use. The validation data revealed a tendency of the model to overestimate selection in high-ranked bins and underestimate selection in low-ranked bins. As such, the model is best suited to provide a ranked index of resource selection, with RSF values denoting relative rank of Arctic ground squirrel habitat selection for each map pixel, rather than scalar selection values.

Unequal detection probability of Arctic ground squirrel burrows using the chosen sampling method could obscure true patterns of habitat selection (Manly et al. 2002, MacKenzie 2006). Reduced sightability of burrows in a specific habitat type would spuriously decrease the predicted selection for that habitat. Although boreal forest did account for a portion of our study area, trees were slender, stunted, and widely spaced, as is typical near treeline. Reduced burrow sightability as a result of such sparse forest was likely negligible. The only vegetation type in which I was not confident of my ability to thoroughly detect burrows was willow thicket. In the Mackenzie Delta region dense stands of willow, 2-4 m tall, are found along seasonally flooded creek banks and on revegetating permafrost slumps (Mackay 1963). I detected no Arctic ground squirrel burrows in ground searches of willow thickets and found the moist substrates characterizing these thickets to be unsuitable for ground squirrel burrows.

Arctic ground squirrels construct several types of burrows of various sizes, durability, and detectability. Current knowledge about Arctic ground squirrel burrow types and functions is derived from Carl (1971) and Batzli and Sobaski (1980). These authors described Arctic ground squirrel territories as centered on large burrow systems consisting externally of 10 – 50 openings within and surrounding a large spoil pile of bare earth (single and double burrow systems; all burrow designations *sensu* Carl 1971). Scattered throughout the territory were single burrows (boundary pits) or burrow systems consisting of one to four openings with a small spoil pile at one or two openings (duck holes). The simplest of these burrows, boundary pits, were excavated only in spring and by summer were often difficult to identify. Boundary pits and duck holes served as territorial markers and temporary refuges and were not described to be as central to Arctic ground squirrel activities as single and double burrow systems. Boundary pits and duck holes, however, are positive indicators of Arctic ground squirrel presence, and as such I did not distinguish between them and more complex burrows in my classification of used points. One burrow type, termed refugee burrows, were built by dispersing juveniles that had been excluded from their natal territories and resembled duck holes. Because they were built by Arctic ground squirrels that have been excluded from occupied territories, refugee burrows often were constructed in areas of marginal habitat, and the burrows and their occupants seldom lasted through the winter. Lacking a dependable method for distinguishing between refugee burrows and those in perennial territories, I likely incorporated refugee burrows into the sample of used locations. The inclusion of these presence data from suboptimal locations increased the ability of the model to identify overall Arctic ground squirrel distribution but decreased its ability to capture habitat selection under conditions of equal availability for all ground squirrels. Because of their ephemeral occupancy compared to perennial single and double burrow systems, however, refugee burrows contributed little to the used sample and to the overall habitat occupancy by Arctic ground squirrels.

Apparent selection for areas of low mean greenness by Arctic ground squirrels might reflect top-down and indirect habitat alteration by the ground squirrels themselves, with earthen spoil piles and herbivory contributing to lower greenness values in active ground squirrel colonies. Under such a dynamic the effects of spoil piles would be greatest at the smallest buffers examined (the 30-m x 30-m focal cell and its 50-m radius buffer), and the effects of grazing would be most detectable at or below home-range size (radii of ≤200 m). I found that differences between mean greenness values for used and available locations were greatest within 200-m radius buffers, supporting Arctic ground squirrel herbivory as a possible determinant of greenness values within ground squirrel colonies. If Arctic ground squirrels themselves determine greenness values in proximity of their burrows, these models would not be strictly modeling habitat selection but rather a combination of both selection and habitat alteration. Previous study, however, suggests that selection for areas of low mean greenness by Arctic ground squirrels might be a strategy for reducing predation risk, or a consequence of increased predation in greener, more heavily vegetated areas. By selecting for sloped or convex terrain in areas of low mean greenness values, Arctic ground squirrels might be choosing burrow sites that allow for more effective vigilance behaviour. Karels and Boonstra (1999) found that the presence of mammalian predators influenced survival of Arctic ground squirrels in a boreal habitat, with burrows in areas of flat terrain and restricted visibility less likely to remain occupied over time than those on slopes and open ground. The selection of habitats coinciding with creek valleys, bluffs, and bare slopes in the southern one-third of the study area could be a response to increased visibility in these areas compared to the surrounding open forest. In some areas boreal forests are sink habitats, with forest populations supported by immigration from source populations in higher elevation alpine tundra and open meadows (Gillis et al. 2005). The low observed densities and low predicted habitat selection of Arctic ground squirrels within open boreal habitat suggests a similar trend along the latitudinal boreal forest – tundra ecotone. If such dynamics exist, even moderate northward advancement of large trees and shrubs into tundra regions could reduce Arctic ground squirrel population growth rates over a large portion of their range (Hassol 2004, Kaplan and New 2006).

Besides being easy to invigilate, exposed areas of loose, dry substrates are typified by a depressed permafrost layer (Zoltai and Pettapiece 1973, Smith 1975, Everett 1980). A deep active layer benefits Arctic ground squirrels by allowing excavation of deeper, warmer, and more secure burrows, which in turn confer higher rates of survival and fecundity (Carl 1971, Batzli and Sobaski 1980). Although global climate change is expected to bring circumpolar permafrost degradation, a potential benefit for Arctic ground squirrels, attendant changes in soil moisture caused by altered precipitation and evapotranspiration regimes could temper these benefits (Hassol 2004).

The effects of localized change on Arctic ground squirrels, in the form of development and expansion of direct human influence, are more difficult to predict. Large reserves of oil and natural gas lie beneath the Mackenzie Delta and Beaufort Sea, and the construction of an extensive extraction, processing, and transportation infrastructure is scheduled for the area (Imperial Oil et al. 2007, Voutier et al. 2008). Arctic ground squirrels do not actively avoid proximity to human activity, but indirect effects on ground squirrel predators and anthropogenic landscape alteration could cause local changes in ground squirrel abundance and distribution (Mueller 1995). Assigning selection values to Arctic ground squirrels allows for informed development and management decisions concerning anthropogenic landscape disturbance and provides a model against which to compare future conditions.

Arctic ground squirrels constitute a prey item whose noncyclical abundance might maintain predators during the crash and recovery phase of other small mammal populations, and their distribution and abundance could be of cyclical or permanent importance to the ecology of many Arctic predators (Reid et al. 1997). As selective herbivores and agents of soil biopedturbation and nutrient redistribution, Arctic ground squirrels also could have large impacts on vegetation communities and active layer dynamics (Price 1971, Batzli and Sobaski 1980, McKendrick et al. 1980). Both local- and global-scale changes in Arctic ground squirrel abundance and distribution could have consequences for plant and soil communities and Arctic predator and small mammal guilds, considering its role as a prey item, herbivore, and ecosystem engineer.

Arctic ground squirrels are an important ecosystem component across a large segment of the Arctic and subarctic. Easily detected and showing strong selection for habitat types that are projected to undergo alteration by global climate change and local anthropogenic disturbance, Arctic ground squirrels deserve continued attention by Arctic ecologists. The models I constructed provide quantitative, landscape-scale support to previous qualitative observations of habitat selection by Arctic ground squirrels (Carl 1971, Batzli and Sobaski 1980, Karels and Boonstra 1999, Gillis et al. 2005). By modeling current habitat selection at this scale, I have established a baseline against which to measure the effects of future changes on Arctic ground squirrels and their ecosystem.

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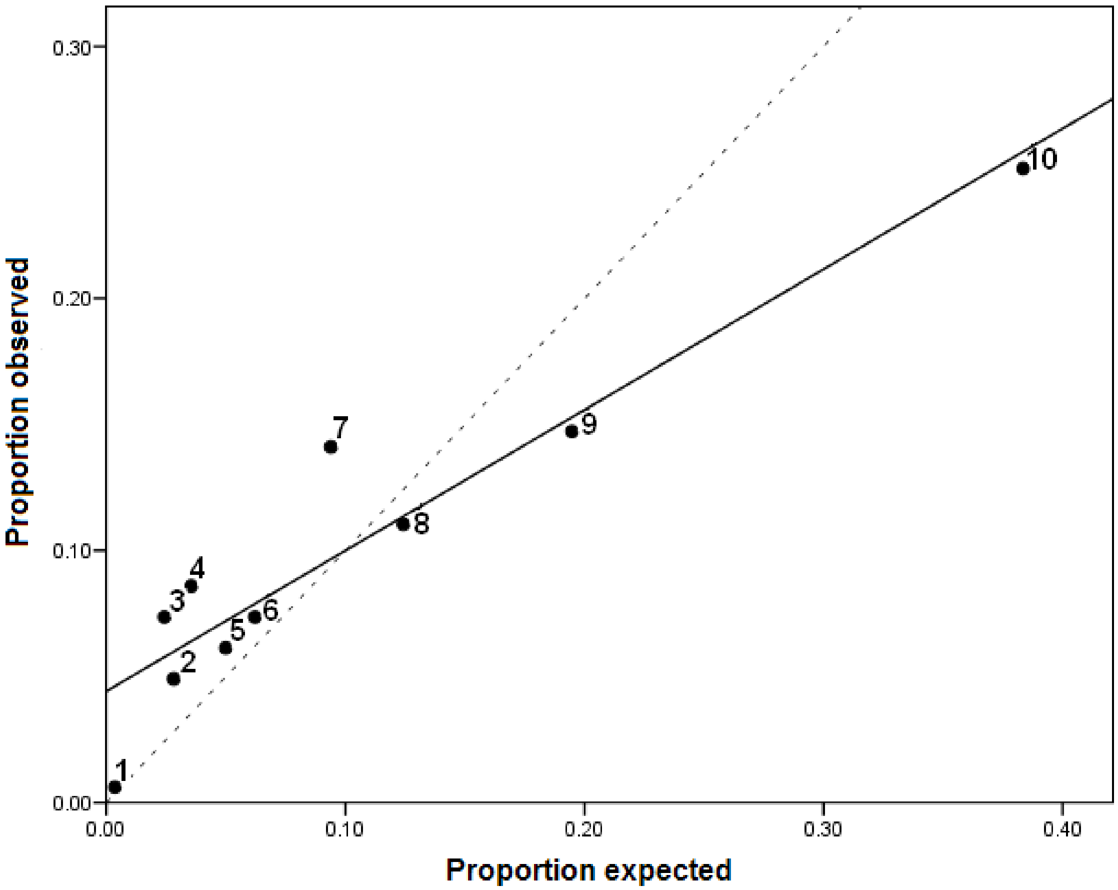

Figure 2.1 - Proportions of expected and observed Arctic ground squirrel locations from a validation data set (n = 164) within ten ranked RSF bins (labels). Included are the fitted regression line for the results of Model 1 (solid) and a dashed line indicating results of a RSF model directly proportional to habitat selection by ground squirrels, with a slope of one and intercept of zero. The regression model (expected versus observed) was $y = 0.56x + 0.04$.

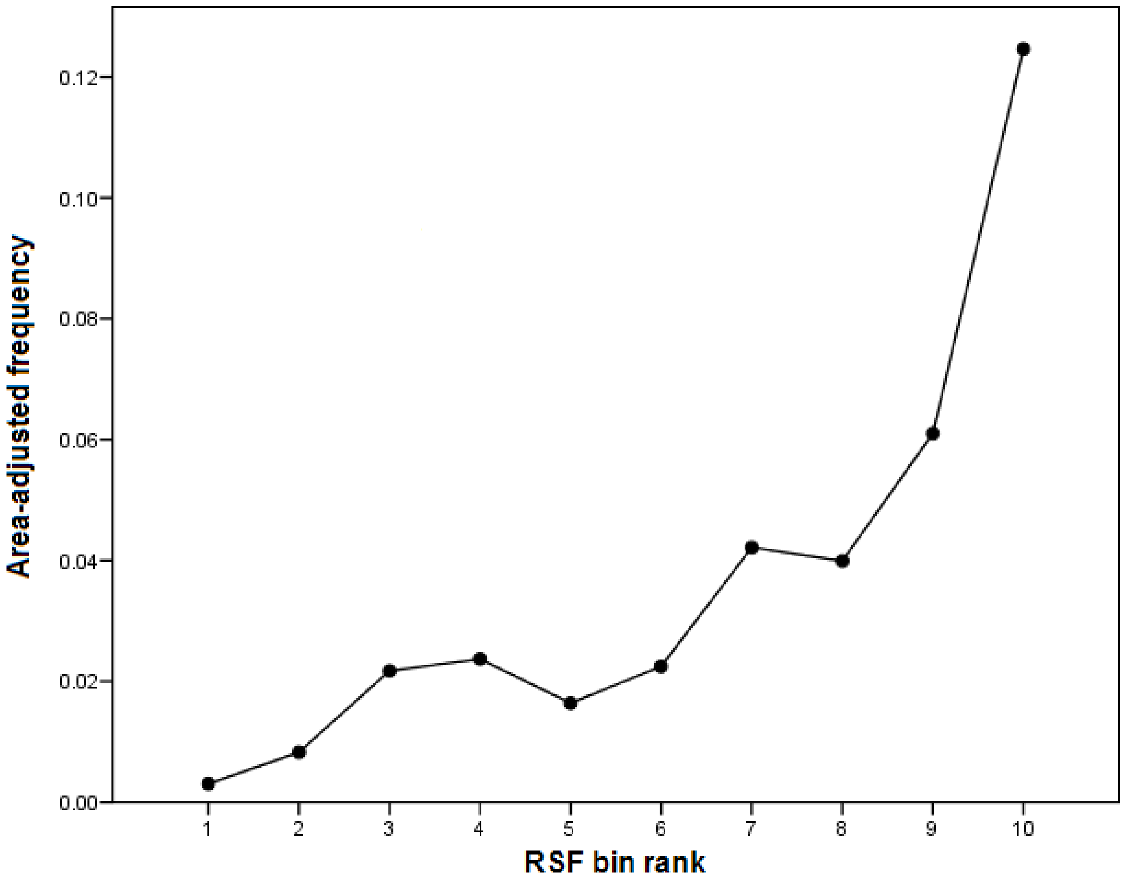

Figure 2.2 - Area-adjusted frequencies of Arctic ground squirrel burrows from an out-of-sample validation data set within ten ranked RSF bins. The Spearman rank correlation was $r_s = 0.93$, $p < 0.01$.

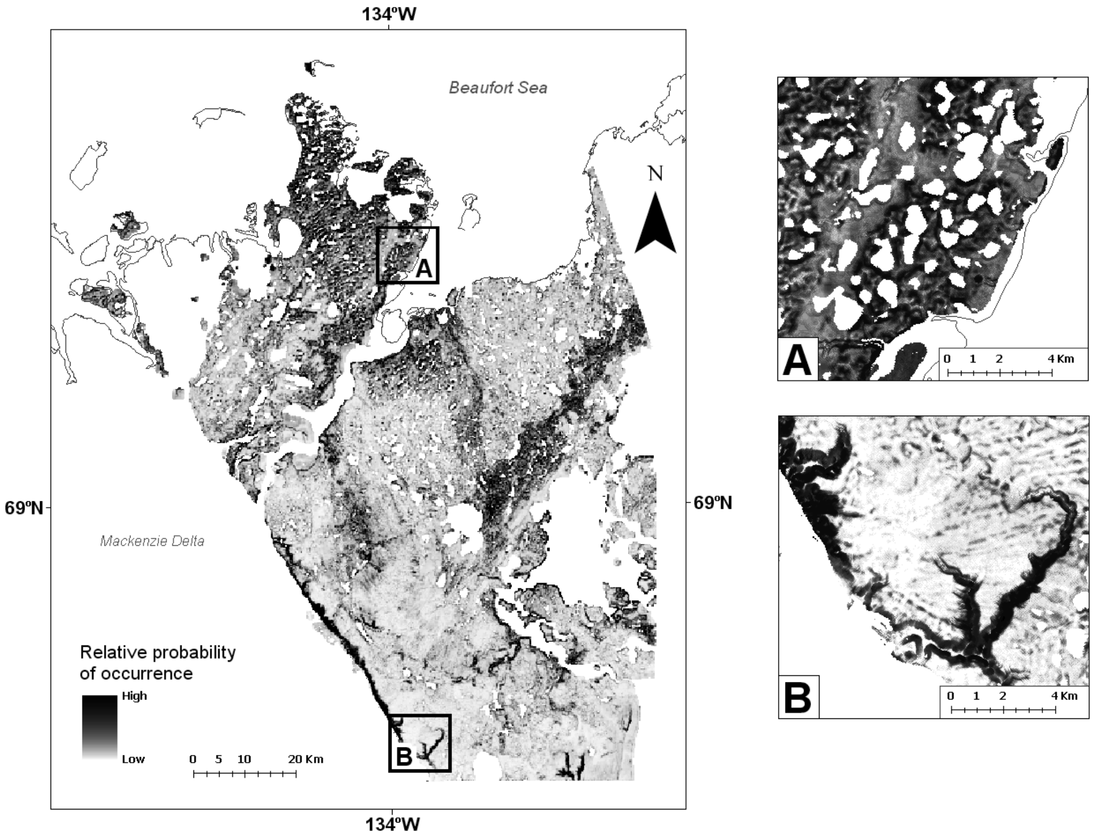

Figure 2.3 - Relative probability of use (occurrence) by Arctic ground squirrels in the study area, as predicted by Model 1, the best-supported exponential RSF model. White space represents habitat unavailable to ground squirrels (water and seasonally flooded delta plain). Areas A and B are shown at a larger scale at right.

Table 2.1 - Areas and extrapolated diameters of Arctic ground squirrel home ranges. Home-range diameters were calculated as the diameter of a circle of reported area of ground squirrel home range.

Source	Area (ha)	Extrapolated diameter (m)
Carl (1971)	0.3	60
	1.1	120
	2.1	160
	1.8	150
	1.5	140
	3.6	210
	2.5	180
	1.6	140
	2	160
mean	1.8	150
Batzli (1980) (male mean)	4.3	230
(female mean)	3.2	200
overall mean	**3.1**	**190**

Table 2.2 - Ranking of 12 exponential RSF models of Arctic ground squirrel habitat selection in the Mackenzie Delta region, NWT (cells used:cells available = 654:7,378). Models are shown with included covariates, log likelihood of model given the data (LL), number of parameters (K), Bayesian information criterion (BIC), the BIC difference from the best-supported model (ΔBIC) and the posterior probability. Covariate subscript 100 or 200 denotes that calculations were performed over a circle of radius 100 or 200 m centered on the focal cell, and that the maximum (a), sum (b), or mean (c) of these values were used. Subscript 200d denotes a special case in which terrain ruggedness was calculated as the SD of slope values over a 200-m radius circle centered on the focal cell.

Model #	**Model structure**	***LL***	**K**	**BIC**	**ΔBIC**	**Posterior probability**
1	SLP_{100a}+WAT_{200b}+CRV_{100c}+MOH_{200b}+MOR_{200b}+GLF_{200b}+GRN_{200b}+SLP_{100a}x CRV_{100c}	-2104	9	4243	0	0.98
2	SLP_{100a}+WAT_{200b}+CRV_{100c}+MOH_{200b}+MOR_{200b}+LAC_{200b}+GRN_{200b}+EAS_{200b}+ SLP_{100a}x CRV_{100c}+ SLP_{100a}x EAS_{200b}	-2100	13	4251	7.62	0.02
3	SLP_{100a}+WAT_{200b}+CRV_{100c}+MOH_{200b}+MOR_{200b}+LAC_{200b}+GRN_{200b}+SPB_{200b}+ TUS_{200b}+ SLP_{100a}xCRV_{100c}	-2124	11	4291	47.81	0
4	SLP_{100a}+WAT_{200b}+CRV_{100c}+EAS_{200b}+GRN_{200b}+SLP_{100a}x CRV_{100c}	-2164	7	4355	112.2	0
5	RUG_{100d}+WAT_{200b}+CRV_{100c}+EAS_{200b}+MOH_{200b}+MOR_{200b}+LAC_{200b}+LAC_{200b}+ GRN_{200b}+SPB_{200b}+ TUS_{200b}	-2166	11	4375	131.8	0
6	RUG_{100d}+WAT_{200b}+CRV_{100c}+MOH_{200b}+MOR_{200b}+LAC_{200b}+GRN_{200b}+SPB_{200b}+ TUS_{200b}	-2188	9	4411	168	0

7	SLP$_{100a}$+WAT$_{200b}$+MOH$_{200b}$+MOR$_{200b}$+LAC$_{200b}$+GRN$_{200b}$+SPB$_{200b}$+TUS$_{200b}$	-2192	8	4415	172.1	0
8	RUG$_{100d}$+MOH$_{200b}$+MOR$_{200b}$+LAC$_{200b}$+GLF$_{200b}$	-2243	5	4506	262.4	0
9	RUG$_{100d}$+MOH$_{200b}$+GRN$_{200b}$	-2252	3	4516	272.6	0
10	RUG$_{100d}$+GRN$_{200b}$+SPB$_{200b}$+TUS$_{200b}$+DTS$_{100b}$+DLS$_{200b}$	-2281	6	4585	342.3	0
11	RUG$_{100d}$+ WAT$_{200b}$+CRV$_{100c}$+EAS$_{200b}$	-2330	4	4676	432.5	0
12	RUG$_{100d}$+ WAT$_{200b}$+MOH$_{200b}$+MOR$_{200b}$+GRN$_{200b}$+SPB$_{200b}$	-2572	6	5167	924.3	0

Table 2.3 - Model coefficients (β), SE, Wald statistics (z; d.f. = 1 in all cases) and Wald significance (α) for the best-supported exponential RSF model (Model 1) and five autologistic-derived exponential RSF models of Arctic ground squirrel habitat selection in the Mackenzie Delta region, NWT (cells used: cells available = 654:7,378). Autocovariates in autologistic-derived RSF models were built using square neighbourhoods of three, seven, 13, 19, and 25 cells on a side, surrounding the focal cell.

		Covariates								
		AUT	**SLP$_{100a}$**	**WAT$_{200b}$**	**CRV$_{100c}$**	**MOH$_{200b}$**	**MOR$_{200b}$**	**GLF$_{200b}$**	**GRN$_{200c}$**	**SLP$_{100a}$xCRV$_{100c}$**
Model 1 RSF	β	-	0.119	-0.017	16.49	-0.004	0.002	0.006	-0.054	-0.442
	SE	-	0.005	0.002	1.601	0.001	0.001	0.001	0.005	0.048
	z	-	539.32	48.65	106.04	13.97	7.71	48.81	138.79	83.48
	α	-	<0.01	<0.01	<0.01	<0.01	0.01	<0.01	<0.01	<0.01
3x3 autologistic RSF	β	0.092	0.118	-0.017	16.354	-0.004	0.002	0.006	-0.054	-0.438
	SE	0.733	0.01	0.003	1.934	0.001	0.001	0.001	0.006	0.056
	z	0.02	40.01	40.01	71.53	13.92	7.57	45.22	69.19	60.36
	α	0.9	<0.01	<0.01	<0.01	<0.01	0.01	<0.01	<0.01	<0.01
7x7 autologistic RSF	β	0.959	0.114	-0.017	15.972	-0.004	0.002	0.006	-0.052	-0.428
	SE	1.613	0.011	0.003	1.822	0.001	0.001	0.001	0.007	0.054
	z	0.35	117.71	38.37	76.87	13.71	7.2	43.03	60.99	63.99
	α	0.55	<0.01	<0.01	<0.01	<0.01	0.01	<0.01	<0.01	<0.01

13x13 autologistic RSF	β	-0.66	0.121	-0.017	16.609	-0.004	0.002	0.006	-0.055	-0.445
	SE	3.236	0.01	0.003	1.706	0.001	0.001	0.001	0.007	0.05
	z	0.04	135.23	42.8	94.75	14	7.72	45.49	70.63	78.17
	α	0.84	<0.01	<0.01	<0.01	<0.01	0.01	<0.01	<0.01	<0.01
19x19 autologistic RSF	β	-2.82	0.124	-0.018	16.741	-0.004	0.002	0.006	-0.057	-0.447
	SE	4.755	0.01	0.003	1.657	0.001	0.001	0.001	0.006	0.049
	z	0.35	163.17	44.93	102.1	14.28	8.07	47.15	81.95	82.95
	α	0.55	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
25x25 autologistic RSF	β	-3.86	0.124	-0.018	16.7	-0.004	0.002	0.006	-0.057	-0.446
	SE	6.14	0.009	0.003	1.636	0.001	0.001	0.001	0.006	0.049
	z	0.4	186.84	45.14	104.21	14.33	8.12	47.45	87.74	83.89
	α	0.53	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01

Table 2.4 - Ranking of the best-supported RSF model from Table 2.2 (Model 1) and five exponential RSF models derived from autologistic regression estimator functions, modeling Arctic ground squirrel habitat selection in the Mackenzie Delta region, NWT (cells used:cells available = 654:7,378). Models are shown with included covariates, log likelihood of model given the data (LL), number of parameters (K), Bayesian information criterion (BIC), the BIC difference from the best-supported model (ΔBIC), and the posterior probability. Autocovariates in autologistic-derived RSF models were built using square neighbourhoods of three, seven, 13, 19, and 25 cells on a side, surrounding the focal cell.

Model structure	***LL***	**K**	**BIC**	**ΔBIC**	**Posterior probability**
Model 1 RSF	-1680	9	3394	0	0.55
25x25 autologistic RSF	-1679	10	3398	3.5	0.1
7x7 autologistic RSF	-1679	10	3398	3.5	0.1
19x19 autologistic RSF	-1679	10	3398	3.5	0.1
13x13 autologistic RSF	-1680	10	3398	3.9	0.08
3x3 autologistic RSF	-1680	10	3398	3.9	0.08

Chapter 3 - Use of Arctic ground squirrels by brown bears in the Mackenzie Delta region, NWT

3.1 Introduction

In a food-limited environment, absent concerns of mate-searching, competition and predator avoidance, animals' distribution should be driven by the location of available food resources (Fleming 1992, Johnson and Sherry 2001, Guitian and Munilla 2008). Selection of habitat for food availability is especially strong when food resources are patchy, vary in temporal availability and are of high nutritional quality (Fleming 1992). Brown bears exemplify exploitation of rich and patchy resources available for only short periods each year (Elgmork and Kaasa 1992, MacHutchon and Wellwood 2003, Mowat and Heard 2006, Munro et al. 2006, Naves et al. 2006). Brown bear diets, however, vary widely among individuals, locations, seasons, and between sexes (Mace and Jonkel 1986, Hamilton and Bunnell 1987, Gau et al. 2002, Munro et al. 2006). While some bears may exist on a largely vegetarian diet, protein consumption has been linked to increased body mass, population density and litter size in brown bears (Hilderbrand et al. 1999a,b, Rode et al. 2001).

In Arctic and sub-arctic environments, common meat sources for brown bears are caribou and salmon near the Pacific coast (Young and McCabe 1997, Gau et al. 2002, Collins et al. 2005, Mowat and Heard 2006). For Mackenzie Delta region bears, however, the typical major meat sources in the north, caribou, and salmon, are scarce or absent during non-denning periods (Nagy et al. 2005, Nagy and Johnson 2006, M. Branigan, Government of NWT; *pers. comm.*). Other local sources of meat may include moose (*Alces alces*), muskox (*Ovibos moschatus*), semi-domestic reindeer (*R. t. tarandus*), beaver (*Castor canadensis*), whitefish (*Coregonus* spp.) and marine mammals (beluga, *Delphinapterus leucas*; ringed seal, *Pusa hispida*; bearded seal, *Erignathus barbatus*), snow geese (*Chen caerulescens*) and their eggs, and small mammals such as muskrat (*Ondatra zibethicus*), voles (*Microtus* spp.), lemmings (*Dicrostonyx groenlandicus* and *Lemmus trimucronatus*), and Arctic ground squirrels (Nagy et al. 1983, Fehr et al. 1997, Edwards et al. 2010).

Small mammals are an important prey item in some regions, with brown bear populations observed feeding heavily on marmots (*Marmota* spp.) in the Pakistan and Nepal (Nawaz 2008, Aryal et al. 2010), and pikas (*Ochotona* spp.) in northwestern China (Aichun et al. 2006). For brown bear populations in northern North America, however, Arctic ground squirrels are the most commonly reported small mammal prey (e.g. Murie 1981, Miller et al. 1982 Nagy et al. 1983, Hechtel 1985, Phillips 1987, Mueller 1995, Reid et al. 1997, MacHutchon and Wellwood 2003). Unlike most other tundra-dwelling rodents, Arctic ground squirrels do not undergo dramatic population cycles, and are available in relatively constant numbers from year to year (Reid et al. 1997). As a prey item, Arctic ground squirrels are of particularly high nutritional value in late summer and autumn, when accumulated fat stores account for up to 40% of their total body weight (Galster and Morrisson 1976, Buck and Barnes 1999a,b). Vulnerability of Arctic ground squirrels to predation is also highest in late summer and autumn, as permafrost has reached its seasonal ebb and burrows are fully excavatable, and Arctic ground squirrels have begun hibernation and are not easily roused from torpor, even by burrow excavation (Mayer 1953, Carl 1971, Buck and Barnes 1999a,b). Arctic ground squirrel remains were a significant component of brown bear scats collected in the Mackenzie Delta region in late summer and autumn, and extensive excavation of Arctic ground squirrel colonies has also been reported (Nagy et al. 1983). The peak of Arctic ground squirrel condition and availability corresponds with the pre-dormancy hyperphagic period in brown bears, and exploitation of this fat-rich resource by brown bears may be important in attaining proper condition for over-winter survival and successful reproduction. Given the potential importance of Arctic ground squirrels to Mackenzie Delta bears, I examined seasonal selection patterns for Arctic ground squirrel habitat, and related these selection patterns to carnivory using stable isotope analysis.

Many examinations of resource use focus entirely on population-level phenomena, and overlook the contribution of individual variation to that of the population (Łomnicki 1988, Bolnick et al. 2003). To capture both group-level selection patterns and individual variation in selection, I examined selection for Arctic ground squirrel habitat by brown bears at the population level, in sex-segregated groups, and by individual bears.

3.2 Study area

The study area extended north from the town of Inuvik, NWT, to Richards Island and the Beaufort Sea, and extended east to a line between the hamlet of Tuktoyaktuk and the western shore of Sitidgi Lake, and west to the margin of the Mackenzie Delta. The study area encompassed the ecotone between boreal forest and tundra, with the southern third characterized by open stands of white and black spruce. Low lying areas in boreal forest consisted of muskeg and peat bog. Boreal forest gave way to tundra in the northern two-thirds of the study area, typified by Labrador tea, dwarf birch, crowberry, *Arctostaphylos* spp. and *Vaccinium* spp., with moist areas vegetated with cottongrass, sedges and mosses (*Drepanocladus* spp. and *Sphagnum* spp.). Riparian zones in both forest and tundra host dense stands of willow and alder (*Alnus* spp.; Mackay 1963, Lambert 1973, Lantz et al. 2010a,b). Lakes and ponds cover 15-30% of the study area, and permafrost is ubiquitous (Mackay 1963, Rampton 1988).

3.3 Methods

I took a three-pronged approach to investigating past and current use of Arctic ground squirrels by brown bears; 1) modeling bears' selection for Arctic ground squirrel habitat using resource selection functions, 2) investigation of recent bear activity sites for evidence of Arctic ground squirrel predation, and 3) comparing modeled selection for Arctic ground squirrel habitat to stable isotope signatures.

Between 2003 – 2008, 96 brown bears were captured in the study area. Captures were effected by aerial darting from a helicopter, with bears chemically immobilized with 8mg/kg Telazol (Wyeth, Madison, NJ). Of these, 37 adult bears (30 females and seven males) were fitted with either Gen II or Gen III TGW 3680 GPS Argos satellite-linked collars (Telonics Inc., Mesa, AZ; CLS America Inc., Largo, MD). The harvest and sale of bear hides, particularly those of adult males, provides economic and cultural benefits for some Inuvialuit beneficiaries within the study area, and collar deployments on male bears were limited to reduce conflict with local hunters. Collars were programmed to collect 6 locations/day from 1 April – 30 November, and were shut down over the remainder of the year when bears were presumed to be in winter dormancy. Collars were fitted with CR-2a programmable release mechanisms (Telonics Inc., Mesa, AZ), with collar deployments lasting two years. I collected a sample of foreleg guard hairs from captured adult bears for stable isotope analysis. All animal handling procedures were approved by the University of Alberta Animal Care Committee, and permitted under Wildlife Research Permits issued by Government of NWT – Inuvik Region: Environment and Natural Resources.

3.3.1 Resource selection functions

My approach to evaluating selection for Arctic ground squirrel habitat by bears was to construct seasonal RSFs for each bear, incorporating Arctic ground squirrel habitat as a model covariate, and to use these individual RSFs to estimate population-level models by averaging individual RSF model coefficients (Nielsen et al. 2002, Sawyer et al. 2006, Sawyer et al. 2009). By creating population-level models from individual models, and treating the individual as the experimental unit, I was able to use the complete GPS collar location dataset without concern for within-season temporal or spatial autocorrelation (Nielsen et al. 2002, Sawyer et al. 2006, Thomas and Taylor 2006, Sawyer et al. 2009). I also combined individual bear models to create aggregate models segregated by sex. I also compared models for seasonal variation in selection for Arctic ground squirrel habitat at the individual, population and sex-segregated level. I hypothesized that Arctic ground squirrel predation would be highest during hyperphagia (August-October), when bears are feeding heavily and Arctic ground squirrel burrows are readily excavatable, and considered bear locations from this period separately from spring/early summer locations (April-July). I also considered that interannual variation in abundance of other food items (such as berry crops or cyclical small mammal populations) might influence population-level use of Arctic ground squirrels as prey, and evaluated interannual variation in population-level selection of Arctic ground squirrel habitat by bears.

3.3.1.1 Individual RSFs

I divided GPS collar locations for each bear into spring/early summer (April-July) and hyperphagia (August-October) for each year, and used these locations to build individual 100% Minimum Convex Polygon (MCP) seasonal home ranges (White and Garrott 1990). Within each seasonal 100% MCP, I randomly seeded ‘available’ locations at a density of 2 locations/km^2. I considered GPS collar locations collected for individual bears within seasons for each year as ‘used’ locations. I used environmental variables collected at each ‘available’ and ‘used’ locations from each bear-season-year to build exponential RSFs, estimated using logistic regression (Manley et al. 2002). Variables considered terrain, vegetation and an index of Arctic ground squirrel habitat selection. Terrain variables were slope, in degrees, site aspect, and distance to water (m). Terrain variables were derived from a 30-m resolution digital elevation model available from the NWT Centre for Geomatics (www.gnwtgeomatics.nt.ca). Vegetation variables included; tall shrub, consisting of areas with >25% cover of deciduous shrubs (*Salix* spp. and *Alnus* spp.) ≥1.3 m in height; upland shrub, consisting of upland areas with >25% cover of deciduous and coniferous shrubs <1.3 m in height; lowland shrub, consisting of flooplain and marsh areas with >25% cover of deciduous shrubs <1.3 m in height; dwarf shrub, consisting of areas with deciduous shrubs <0.25 m tall; tussock-lichen, consisting of wet areas of tussock and lichen cover without shrubs; and wet herbaceous, consisting of emergent and aquatic vegetation. Variables for vegetative greenness and soil wetness were also considered. Vegetation type, greenness and wetness variables were derived from Landsat 5 Thematic Mapper satellite imagery, with a 28.5-m resolution (C. Squires-Taylor, NWT Centre for Remote Sensing, *pers*. *comm*). For an index of Arctic ground squirrel habitat selection, I used the model built in Chapter 2 (Barker and Derocher 2010, see Chapter 2). Variables were screened for multicollinearity, and pairs of variables with Pearson's $r > |0.70|$ were not included in the same model.

3.3.1.2 Model selection and population-level RSFs

Information-theoretic model selection methods, such as Akaike's Information Criterion or Bayesian Information Criterion, are inappropriate where population-level models are built by averaging individual RSF coefficients (Sawyer et al. 2006), so I used backward stepwise model building to select population-level RSF model covariates. I began with ten covariates, representing hypothesized habitat selection patterns of bears in spring/early summer and hyperphagia, and consecutively removed covariates with the highest Wald test p-value, until all remaining covariates had $p \leq 0.10$. Because my interest focused on selection of Arctic ground squirrel habitat, if the Arctic ground squirrel habitat covariate was removed during stepwise model building, I replaced it in the final models. In addition to general population-level RSF models, I also selected covariates for male-only and female-only models for both spring/early summer and hyperphagia seasons using this method.

3.3.2 Bear activity site investigations

To determine the frequency of Arctic ground squirrel excavation by bears, I selected bear GPS collar locations for field investigation. Sites for investigation for each bear were chosen at random, with the constraint that they be >12h apart (to minimize spatiotemporal autocorrelation) and <48h apart (to maintain sample size). Site investigations were limited to female bears. I investigated 308 locations from eight female bears, recorded 1 July - 30 September 2007 and 2 July - 31 August 2008. Early snowfall precluded investigating locations recorded in September 2008. I conducted site investigations from a helicopter hovering at five to ten m above ground level, recording habitat, noting available food items, and bear sign, including Arctic ground squirrel excavation. To avoid disturbing bears and to investigate sites before signs of feeding were obliterated, site investigations took place between 2-30 days after they were recorded. The observed frequency with which individual bears excavated Arctic ground squirrels was compared to bears' modeled selection for Arctic ground squirrel habitat.

3.3.3 Stable isotope analysis

I performed stable isotope analysis of hairs plucked from the forelimb of captured bears, and used resulting δ^{15}N signatures to examine the relationship between selection for Arctic ground squirrel habitat and carnivory among study bears. I prepared each hair sample for stable isotope analysis by rinsing in distilled water, and then washing three times for 10 minutes each in 2:1

methanol:chloroform solution to remove lipids. Samples were then freeze-dried and ground finely before analysis.

Stable isotope analyses were performed on 1mg hair subsamples at the University of Saskatchewan Centre for Soil Science (Department of Soil Research, University of Saskatchewan, Saskatoon, SK, Canada), using an isotope mass spectrometer. Resultant ratios ($\delta^{15}N$) represent the difference between sample and atmospheric N_2, in parts per thousand, as determined by Peterson and Fry (1987):

$$\delta^{15}N = [(^{15}N:{}^{14}N_{sample} / {}^{15}N:{}^{14}N_{atmosphere}) - 1] \times 1000$$

I examined the correlation between $\delta^{15}N$ values and selection for Arctic ground squirrel habitat, hypothesizing that carnivorous bears depend heavily on Arctic ground squirrels as a protein source, and would show a subsequent positive selection for Arctic ground squirrel habitats, particularly during hyperphagia.

Bear guard hairs begin growth in May, continue growing over the active season, stop at hibernation, and are shed the following spring (Mizukami et al. 2005). Guard hairs collected just after bear emergence in May, therefore, represent a stable isotopic archive of diet over the previous active season. GPS collars deployed on captured bears, however, recorded locations for 1-2 subsequent years. Where stable isotope values and GPS collar data did not overlap temporally, I considered past stable isotope values as indicators of subsequent foraging patterns. In cases where stable isotope values for more than one year existed for individual bears, I assigned stable isotope values to GPS collar location data based on proximity of the year the collar data were collected to the year represented by the stable isotope data (i.e., the year previous to the

May the bear was captured and sampled).

3.4 Results

3.4.1 Resource selection functions

Covariates denoting Arctic ground squirrel habitat were not significant additions to the general, male-only or female-only population-level spring/early summer bear RSF models (Tables 3.1-3.3). During backward stepwise model selection, Arctic ground squirrel habitat was the fourth covariate removed for the general and female-only models, and the third removed for the male-only model (Tables 3.1-3.3). Replacing Arctic ground squirrel covariates into the models showed negative but non-significant selection for Arctic ground squirrel habitat in the general and female-only models, and positive but non-significant selection in the male-only model (Tables 3.1-3.3). Nine of the 75 bear-seasons examined (12%) showed significant positive selection for Arctic ground squirrel habitat using the general population-level model structure (two bear-seasons from two males, and seven bear-seasons from six females). Four bear-seasons from four females, and one bear-season from one male, showed significant negative selection for Arctic ground squirrel habitat using the general population-level model structure.

Arctic ground squirrel habitat covariates were likewise non-significant additions to the general, female-only or male-only population-level hyperphagia RSF models (Tables 3.4-3.6). Arctic ground squirrel habitat was the first covariate removed from the general model population-level model, the second covariate removed from female-only population-level model, and the third removed from male-only population-level model (Tables 3.4-3.6). Replacement of the Arctic ground squirrel habitat covariate into the final population-level models showed positive but non-significant selection for Arctic ground squirrel habitat in the general and male-only models, and negative but non-significant selection in the female-only model (Tables 3.4-3.6). Thirteen of the 46 bear-seasons examined (28%) showed significant positive selection for Arctic ground squirrel habitat using the general population-level model structure (two bear-seasons from two males and 11 bear-seasons from nine females). Two bear-seasons, from two individual females, showed significant negative selection for Arctic ground squirrel habitat using the general population-level model structure.

There was no evidence for interannual variation in population-level selection for Arctic ground squirrel habitat by bears; coefficients for the Arctic ground squirrel habitat covariate did not differ significantly among years for general population-level models for spring/early summer (Kruskal-Wallis H = 1.65, d.f. = 5, p = 0.90) or hyperphagia (Kruskal-Wallis H = 1.34, d.f. = 5, p = 0.93).

3.4.2 Bear activity site investigations

Of the 308 site investigations of locations recorded by GPS collars on study bears between 1 July 2007 - 30 September 2007 and 2 July 2008 – 31 August 2008, ten (3.8%) found evidence of bears foraging on Arctic ground squirrels. Of these sites, one was from a female presumed to be without cubs, and the rest from females presumed to be accompanied by cubs (observations of cub presence during bear captures the preceding springs). Four of the ten Arctic ground squirrel foraging sites were from locations from one bear, two locations from 2007 and two from 2008, accounting for 11% of that individual's investigated sites. Another bear accounted for three of the remaining Arctic ground squirrel foraging locations, all recorded in 2007 (7% of investigated sites for that bear). The three remaining Arctic ground squirrel foraging locations were at single locations from other bears, accounting for 6, 5 and 2% of investigated sites. Only one bear, that responsible for four Arctic ground squirrel foraging sites, showed significant positive selection for Arctic ground squirrel habitat (β = 1.712 , SE = 0.819 in 2007, β = 5.493, SE = 2.093 in 2008); Arctic ground squirrel habitat β coefficients for other bears did not differ significantly from zero.

3.4.3 Stable isotope analysis

The correlation between individual bears' $\delta^{15}N$ signatures and Arctic ground squirrel habitat covariates from spring/early summer general population-level models (Table 3.1) was positive and significant for males and females combined (r = 0.31, d.f. = 1, p = 0.02), females only (r = 0.31, d.f. = 1, p = 0.04), and positive but non-significant when males only were considered (r = 0.36, d.f. = 1, p = 0.25). The correlation between individual bears' $\delta^{15}N$ signatures and Arctic ground squirrel habitat covariates from hyperphagia population-level models (Table 3.4) was negative and non-significant for males and females combined (r = -0.19, d.f. = 1, p = 0.28), females only (r = -0.18, d.f. = 1, p = 0.34), and males only (r = -0.61, d.f.= 1, p = 0.27). When compared against rates of Arctic ground squirrel foraging sign observed at investigated sites, the correlation between Arctic ground squirrel foraging activity and individual bears' $\delta^{15}N$ signatures was negative and non-significant (r = -0.49, d.f. = 6, p = 0.22).

3.5 Discussion

Previous work has found Arctic ground squirrels to be a seasonally important component of Arctic brown bears' diet (Murie 1981, Nagy et al. 1983, MacHutchon and Wellwood 2003). In other brown bear populations, food resource models have shown to be predictive of bear habitat use (Nielsen et al. 2010). My own site investigations found that study bears excavated Arctic ground squirrels occasionally, with some bears appearing to forage on Arctic ground squirrels more often than others. Given these observations, the universally non-significant effect of the addition of an Arctic ground squirrel habitat covariate to the seasonal population-level and sex-segregated bear RSF models is surprising. Arctic ground squirrels are ubiquitous across large parts of the study area, and their availability and body condition reach their peak in autumn, yet a correlation between $\delta^{15}N$ signatures and bears' selection for Arctic ground squirrel habitat was not evident during hyperphagia. Examined as a population, why do Mackenzie Delta bears appear to spend so little time seeking out this resource during hyperphagia?

The discrepancy between my observations and previously-reported significance of Arctic ground squirrels in the diet of Arctic brown bears could indicate that this method of studying foraging behaviour by bears was unable to detect Arctic ground squirrel use. The level of detail provided by methods for studying forage use by bears is inversely related to the time elapsed since food ingestion; direct observation of feeding bears can provide minute-by-minute accounts of specific food items consumed, while scat analysis offers a less detailed record of food items consumed over a wider timespan (Greenwood 1979, Hewitt and Robbins 1996, Spaulding et al. 2000). Moving further away in time from the foraging activity of interest, stable isotope and fatty acid signature analysis give accounts of diet composition that span weeks, months or years, and provide estimates of diet composition that become less reliable as the number of possible food items increases (Phillips and Gregg 2003). Without direct observations or scat collections, and faced with a wide range of foods contributing to stable isotope signatures, analysis of archived GPS-collar data appears to be a promising method for determining spatiotemporal patterns of Arctic ground squirrel use by Mackenzie Delta bears. GPS collar locations collected every four hours may not be sufficient to detect behaviour as complex as searching out, capturing and consuming prey, particularly for prey species as small and rapidly consumable as Arctic ground squirrels.

The lack of conclusive evidence for heavy Arctic ground squirrel predation by Mackenzie Delta brown bears could stem from bears’ relatively infrequent use of Arctic ground squirrels as a food source. Rich in fat and protein, Arctic ground squirrels are nevertheless relatively small animals, with adults weighing 600-1200g (Batzli and Sobaski 1980, Buck and Barnes 1999a). During late summer and autumn, when permafrost levels have reached their lowest point and burrows are fully excavatable, Arctic ground squirrels become solitary, with each individual occupying a separate burrow (Carl 1971). To obtain a single Arctic ground squirrel, a bear must excavate an entire burrow, often to depths >0.5m (Carl 1971, Batzli and Sobaski 1980). For non-hibernating Arctic ground squirrels, predation success by bears excavating their burrows has been reported to be just over 50% (Carl 1971). The net energy gain from consuming an Arctic ground squirrel may be less than the energetic costs required to obtain it. Arctic ground squirrels may, however, provide nutritional value beyond their caloric content, particularly to bears that are otherwise herbivorous. Meat sources such as Arctic ground squirrels contain specific amino acids, vitamins and other nutrients that may be difficult or impossible to obtain from plant sources (Rode and Robbins 2000, Felicetti et al. 2003). In the Mackenzie Delta region, plant foods, such as berries, roots and leaves, are more abundant and less energetically costly to obtain than meat sources, which may be relatively uncommon and capable of evasion and/or defence. For many brown bear populations, berries, not meat, forms the bulk of their diet during hyperphagia (Elgmork and Kaasa 1992). By meeting the majority of their caloric requirements by feeding on plants (particularly berries), and expending the effort required to handle and consume Arctic ground squirrels (or other meat sources) to obtain valuable nutrients they cannot acquire from plants, Mackenzie Delta bears could be adopting a foraging strategy that provides adequate caloric and nutrient intake while minimizing costs associated with encountering and handling animal prey (Welch et al. 1997, Rode and Robbins 2000, Rode et al. 2001, Felicetti et al. 2003). If this strategy entails foraging for meat only occasionally, with the majority of foraging effort spent feeding on plants, then selection for habitat related to meat sources may be neither positive nor significant.

Another explanation for the non-significance of selection for Arctic ground squirrel habitat in the male-only, female-only and population-level models could be that a small proportion of bears are responsible for the majority of the visible signs of Arctic ground squirrel predation (excavations), with the remainder of the population spending little time foraging on Arctic ground squirrels. Significant selection for Arctic ground squirrel habitat by some individual bears, most commonly observed during hyperphagia, provides support for the presence of Arctic ground squirrel predation specialists among Mackenzie Delta bears. Other evidence for diet specialization among Mackenzie Delta brown bears also exists. A small proportion of the population is thought to forage heavily on migrating broad whitefish during hyperphagia (Barker and Derocher 2009, see Chapter 4), and isotopic evidence suggests that brown bears in this population exist at multiple trophic levels, with some bears highly herbivorous and others tending much more towards carnivory (Edwards et al. 2010). Predation of Arctic ground squirrels could be one of many possible strategies for Mackenzie Delta bears to meet their protein and fat intake requirements, with other bears exploiting other meat sources, or subsisting on a predominantly herbivorous diet.

If a small number of Arctic ground squirrel predation specialists were gaining a significant amount of protein by foraging on Arctic ground squirrels, one would expect a positive correlation between selection for Arctic ground squirrel habitat and $\delta^{15}N$ signature. I discovered such a correlation, but only between $\delta^{15}N$ signatures and selection for Arctic ground squirrel habitat in spring/early summer, (though not among the small sample of male bears). This indicates that some bears may specialize on Arctic ground squirrel predation during spring /early summer, gaining a measurable degree of $\delta^{15}N$ enrichment through Arctic ground squirrel consumption. The availability of refugia (in the form of burrows extending into frozen ground) to Arctic ground squirrels at this time of year likely precludes their capture by burrow excavation, and previous work in the Mackenzie Delta region has shown Arctic ground squirrel consumption to be low in spring (Nagy et al. 1983). In northeastern Alaska and northern Yukon, however, brown bears have been observed foraging on Arctic ground squirrels in spring, capturing them aboveground (Phillips 1987, MacHutchon 2001). Alternatively, the presence of other, unexamined meat sources may have a profound impact on the δ^{15}N values for some bears, such that the δ^{15}N enrichment signal from Arctic ground squirrel predation may be overwhelmed. Bears that do not specialize in Arctic ground squirrel predation could have high δ-^{15}N values from exploiting other prey, such as muskrats, moose, beaver or whitefish, or scavenging on marine mammal carcasses. Such δ^{15}N enrichment in bears that do not select for Arctic ground squirrel habitat would obscure a correlation between δ^{15}N values and inferred Arctic ground squirrel predation.

Intrapopulation variation in resource use can shape social and competitive interactions, influence evolutionary trajectories, and affect individual exposure to mortality risk and resource depletion or abundance (Łomnicki 1988, Bolnick et al. 2002, 2003, Ackermann and Doebeli 2004, Svanbäck and Persson 2004). These processes have important ecological consequences, and can inform management and conservation decisions about species and ecosystems. Information about individual niche width, however, is ignored when populations are examined as a whole (Bolnick et al. 2003, Vander Zanden et al. 2010). Population niche width is a product of individual niche widths, such that a broad population niche width can be composed of many individual generalists, individuals with niche specializations that remain consistent over time, individuals whose niche specializations vary with time, or combinations of all three (Vander Zanden et al. 2010). By examining the contribution of individual niche widths to the niche width of a population, we can describe the relationship of both the individual and the population with its environment. In the case of

Mackenzie Delta brown bears, general population-level, male-only and female-only resource selection models showed no selection for Arctic ground squirrel habitat. Individual models, however, show a range of behaviours, from selection against, no selection, to selection for this habitat. Combined with site investigation data, individual resource selection model results provide strong evidence for specialization on Arctic ground squirrel predation by a component of the Mackenzie Delta brown bear population. By examining resource selection at both the population and individual level, I revealed a more complete picture of my study organism, and its role in its ecosystem, than would have been provided by population-level analysis alone.

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Table 3.1 - Backward stepwise selection of model covariates for general population-level resource selection functions for male and female brown bears (n=75 bear seasons from 37 individual bears) during spring and early summer (April – July). The least significant addition to the model (as determined by Wald test p-values) was dropped and model covariate values recalculated until all covariates had p ≤ 0.10.

		Model covariates									
		South	**West**	**Slope**	**Greenness**	**Squirrel Habitat**	**Distance to Water**	**Tall Shrub**	**Upland Shrub**	**Dwarf Shrub**	**Tussock-Lichen**
Model 1	β	-1.0E-03	0.01	0.07	0.01	-0.30	-3.0E-03	-3.61	-0.15	0.54	2.77
	SE	0.04	0.06	0.01	3.0E-03	0.34	-3.0E-04	1.07	0.75	0.70	1.24
	Wald	1.0E-03	0.04	62.31	11.27	0.78	99.48	11.33	0.04	0.60	5.02
	p	**0.98**	**0.84**	**<0.01**	**<0.01**	**0.38**	**<0.01**	**<0.01**	**0.84**	**0.44**	**0.03**
Model 2	β		0.01	0.07	0.01	-0.30	-3.0E-03	-3.62	-0.16	0.53	2.69
	SE		0.05	0.01	3.0E-03	0.34	-3.0E-04	1.07	0.75	0.70	1.22
	Wald		0.07	60.68	10.81	0.78	102.47	11.37	0.05	0.58	4.86
	p		**0.80**	**<0.01**	**<0.01**	**0.38**	**<0.01**	**<0.01**	**0.83**	**0.45**	**0.03**
Model 3	β		4.0E-03	0.06	0.01	-0.47	-3.0E-03	-3.29		0.84	3.12
	SE		0.05	0.01	2.0E-03	0.40	-2.6E-04	1.10		0.35	1.05
	Wald		0.01	66.67	24.87	1.40	131.59	8.94		5.86	8.74
	p		**0.94**	**<0.01**	**<0.01**	**0.24**	**<0.01**	**<0.01**		**0.02**	**<0.01**
Model 4	β			0.06	0.01	-0.49	-3.0E-03	-3.30		0.84	3.12
	SE			0.01	2.0E-03	0.40	-2.5E-04	1.10		0.35	1.05
	Wald			66.44	24.84	1.46	141.03	9.01		5.83	8.77
	p			**<0.01**	**<0.01**	**0.23**	**<0.01**	**<0.01**		**0.02**	**<0.01**

Model 5	β			0.06	0.01		-3.0E-03	-3.32		0.83	3.12
	SE			0.01	2.0E-03		-2.7E-04	1.09		0.35	1.06
	Wald			66.56	26.46		122.08	9.18		5.43	8.73
	p			**<0.01**	**<0.01**		**<0.01**	**<0.01**		**0.02**	**<0.01**

Table 3.2 - Backward stepwise selection of model covariates for population-level resource selection functions for female brown bears only (n=60 bear seasons from 30 individual bears) during spring and early summer (April – July). The least significant addition to the model (as determined by Wald test p-values) was dropped and model covariate values recalculated until all covariates had p ≤ 0.10.

		Model covariates									
		South	**West**	**Slope**	**Greenness**	**Squirrel Habitat**	**Distance to Water**	**Tall Shrub**	**Upland Shrub**	**Dwarf Shrub**	**Tussock-Lichen**
Model 1	β	0.01	0.01	0.07	0.01	-0.41	-3.0E-03	-4.08	-0.38	0.40	1.01
	SE	0.04	0.05	0.01	0.00	0.42	3.7E-04	1.30	0.95	0.88	1.28
	Wald	0.08	0.07	50.90	6.76	0.97	64.38	9.87	0.16	0.21	0.62
	p	**0.78**	**0.79**	**<0.01**	**0.01**	**0.33**	**<0.01**	**<0.01**	**0.69**	**0.65**	**0.43**
Model 2	β	0.01		0.07	0.01	-0.42	-3.0E-03	-4.07	-0.35	0.41	1.02
	SE	0.04		0.01	3.0E-03	0.43	3.7E-04	1.30	0.94	0.87	1.27
	Wald	0.05		52.16	7.94	0.97	66.27	9.82	0.14	0.22	0.64
	p	**0.83**		**<0.01**	**0.01**	**0.32**	**<0.01**	**<0.01**	**0.71**	**0.64**	**0.42**
Model 3	β			0.07	0.01	-0.44	-3.0E-03	-4.08	-0.36	0.41	1.02
	SE			0.01	3.0E-03	0.43	3.6E-04	1.30	0.93	0.87	1.27
	Wald			51.21	7.34	1.01	68.96	9.88	0.15	0.22	0.64
	p			**<0.01**	**0.01**	**0.31**	**<0.01**	**<0.01**	**0.70**	**0.64**	**0.42**
Model 4	β			0.07	0.01	-0.60	-3.0E-03	-3.66	0.84		1.49
	SE			0.01	2.0E-03	0.50	3.1E-04	1.33	0.44		1.01
	Wald			58.82	20.00	1.42	92.03	7.54	3.68		2.20

	p			**<0.01**	**<0.01**	**0.23**	**<0.01**	**0.01**	**0.06**		**0.14**
Model 5	β			0.06	0.01		-3.0E-03	-3.68	0.83		1.49
	SE			0.01	2.0E-03		3.4E-04	1.33	0.45		1.01
	Wald			56.79	21.64		78.57	7.64	3.45		2.17
	p			**<0.01**	**<0.01**		**<0.01**	**0.01**	**0.06**		**0.14**
Model 6	β			0.06	0.01		-3.0E-03	-3.60	0.86		
	SE			0.01	2.0E-03		3.1E-04	1.36	0.43		
	Wald			62.28	33.41		94.12	7.02	4.04		
	p			**<0.01**	**<0.01**		**<0.01**	**0.01**	**0.05**		
Model 7	β			0.07	0.01	-0.61	-3.0E-03	-3.60	0.86		
	SE			0.01	2.0E-03	0.50	3.0E-04	1.36	0.42		
	Wald			66.38	31.84	1.46	103.10	7.01	4.15		
	p			**<0.01**	**<0.01**	**0.23**	**<0.01**	**0.01**	**0.04**		

Table 3.3 - Backward stepwise selection of model covariates for population-level resource selection functions for male brown bears only (n=15 bear seasons from seven individual bears) during spring and early summer (April – July). The least significant addition to the model (as determined by Wald test p-values) was dropped and model covariate values recalculated until all covariates had p ≤ 0.10.

		Model covariates									
		South	**West**	**Slope**	**Greenness**	**Squirrel Habitat**	**Distance to Water**	**Tall Shrub**	**Upland Shrub**	**Dwarf Shrub**	**Tussock-Lichen**
Model 1	β	-0.05	0.00	0.04	0.01	0.17	-3.0E-03	-1.71	0.73	1.10	9.81
	SE	0.13	0.22	0.01	4.0E-03	0.30	4.3E-04	1.53	0.26	0.27	3.05
	Wald	0.16	0.00	15.43	8.75	0.34	48.78	1.24	8.13	16.16	10.33
	p	**0.69**	**0.99**	**<0.01**	**<0.01**	**0.56**	**<0.01**	**0.27**	**<0.01**	**<0.01**	**<0.01**
Model 2	β	-0.02		0.04	0.01	0.18	-4.0E-03	-2.12	0.72	1.08	10.51
	SE	0.12		0.01	4.0E-03	0.30	5.6E-04	1.72	0.25	0.27	3.08
	Wald	0.03		15.25	9.06	0.34	50.68	1.51	8.05	15.79	11.62
	p	**0.87**		**<0.01**	**<0.01**	**0.56**	**<0.01**	**0.22**	**0.01**	**<0.01**	**<0.01**
Model 3	β			0.04	0.01	0.17	-4.0E-03	-1.68	0.71	1.06	9.78
	SE			0.01	4.0E-03	0.31	5.3E-04	1.55	0.25	0.27	3.05
	Wald			14.09	8.92	0.30	57.18	1.18	7.92	15.49	10.25
	p			**<0.01**	**<0.01**	**0.59**	**<0.01**	**0.28**	**0.01**	**<0.01**	**<0.01**
Model 4	β			0.04	0.01		-3.0E-03	-1.73	0.70	1.03	9.78
	SE			0.01	4.0E-03		3.9E-04	1.54	0.25	0.27	3.06
	Wald			17.69	8.20		57.71	1.26	7.54	14.96	10.23

	p			**<0.01**	**<0.01**		**<0.01**	**0.26**	**0.01**	**<0.01**	**<0.01**
Model 5	β			0.04	0.01		-3.0E-03		0.72	1.06	9.81
	SE			0.01	4.0E-03		3.9E-04		0.26	0.26	3.06
	Wald			17.26	10.22		57.71		8.02	16.90	10.29
	p			**<0.01**	**<0.01**		**<0.01**		**0.01**	**<0.01**	**<0.01**
Model 6	β			0.04	0.01	0.18	-4.0E-03		0.72	1.08	
	SE			0.01	3.0E-03	0.31	5.3E-04		0.26	0.26	
	Wald			13.45	10.92	0.31	57.18		7.82	16.76	
	p			**<0.01**	**<0.01**	**0.58**	**<0.01**		**0.01**	**<0.01**	

Table 3.4 - Backward stepwise selection of model covariates for population-level resource selection functions for male and female brown bears (n=46 bear seasons from 37 individual bears) during hyperphagia (August-October). The least significant addition to the model (as determined by Wald test p-values) was dropped and model covariate values recalculated until all covariates had p ≤ 0.10.

		Model covariates									
		North	**East**	**Slope**	**Wetness**	**Squirrel Habitat**	**Distance to Water**	**Lowland Shrub**	**Dwarf Shrub**	**Tussock-Lichen**	**Wet Herbaceous**
Model 1	β	-0.03	-0.04	0.05	0.01	0.02	-2.0E-03	-1.2	1.24	6.5	-0.29
	SE	0.05	0.06	0.01	3.0E-03	0.28	3.1E-04	0.6	0.55	1.55	0.77
	Wald	0.35	0.36	33.24	15.92	0	41.04	4.08	5.13	17.67	0.14
	p	**0.55**	**0.55**	**<0.01**	**0**	**0.95**	**<0.01**	**0.04**	**0.02**	**<0.01**	**0.7**
Model 2	β	-0.04	-0.05	0.06	0.01		-2.0E-03	-1.21	1.23	6.5	-0.3
	SE	0.05	0.06	0.01	3.0E-03		3.1E-04	0.59	0.56	1.55	0.77
	Wald	0.64	0.77	34.64	16.35		41.48	4.14	4.83	17.65	0.15
	p	**0.42**	**0.38**	**<0.01**	**<0.01**		**<0.01**	**0.04**	**0.03**	**<0.01**	**0.7**
Model 3	β	-0.04	-0.06	0.06	0.01		-2.0E-03	-1.24	1.16	6.36	
	SE	0.05	0.06	0.01	3.0E-03		3.1E-04	0.58	0.55	1.54	
	Wald	0.61	0.8	37.73	11.63		40.97	4.55	4.39	17.14	
	p	**0.44**	**0.37**	**<0.01**	**<0.01**		**<0.01**	**0.03**	**0.04**	**<0.01**	
Model 4	β		-0.05	0.05	0.01		-2.0E-03	-1.26	1.18	6.5	
	SE		0.06	0.01	3.0E-03		3.0E-04	0.59	0.56	1.55	
	Wald		0.74	35.58	10.32		44.76	4.63	4.47	17.66	

	p		**0.39**	**<0.01**	**<0.01**		**<0.01**	**0.03**	**0.04**	**<0.01**	
Model 5	β			0.05	0.01		-2.0E-03	-1.26	1.17	6.49	
	SE			0.01	3.0E-03		2.9E-04	0.59	0.56	1.55	
	Wald			37.08	10.82		46.64	4.65	4.45	17.66	
	p			**<0.01**	**<0.01**		**<0.01**	**0.03**	**0.04**	**<0.01**	
Model 6	β			0.05	0.01	0.02	-2.0E-03	-1.26	1.19	6.49	
	SE			0.01	3.0E-03	0.27	3.0E-04	0.59	0.55	1.55	
	Wald			36.31	10.17	0.01	44.13	4.61	4.71	17.67	
	p			**<0.01**	**<0.01**	**0.94**	**<0.01**	**0.03**	**0.03**	**<0.01**	

Table 3.5 - Backward stepwise selection of model covariates for population-level resource selection functions for female brown bears only (n=42 bear seasons from 30 individual bears) during hyperphagia (August-October). The least significant addition to the model (as determined by Wald test p-values) was dropped and model covariate values recalculated until all covariates had p ≤ 0.10.

		Model covariates									
		North	**East**	**Slope**	**Wetness**	**Squirrel Habitat**	**Distance to Water**	**Lowland Shrub**	**Dwarf Shrub**	**Tussock-Lichen**	**Wet Herbaceous**
Model 1	β	0.00	-0.05	0.06	0.01	-0.68	-2.0E-03	-1.17	0.70	5.95	-0.40
	SE	0.06	0.06	0.01	3.0E-03	0.70	3.3E-04	0.65	0.13	1.58	0.84
	Wald	0.00	0.70	34.71	13.74	0.95	35.99	3.21	30.90	14.29	0.23
	p	**0.96**	**0.40**	**<0.01**	**<0.01**	**0.33**	**<0.01**	**0.07**	**<0.01**	**<0.01**	**0.63**
Model 2	β		-0.05	0.06	0.01	-0.02	-2.0E-03	-1.21	0.65	6.24	-0.49
	SE		0.05	0.01	3.0E-03	0.29	3.3E-04	0.67	0.12	1.60	0.86
	Wald		0.93	34.13	12.67	0.00	37.75	3.31	30.17	15.17	0.32
	p		**0.34**	**<0.01**	**<0.01**	**0.95**	**<0.01**	**0.07**	**<0.01**	**<0.01**	**0.57**
Model 3	β		-0.07	0.06	0.01		-2.0E-03	-1.19	0.63	6.10	-0.42
	SE		0.05	0.01	3.0E-03		3.2E-04	0.66	0.12	1.59	0.85
	Wald		1.61	34.96	13.98		40.23	3.25	27.89	14.76	0.25
	p		**0.20**	**<0.01**	**<0.01**		**<0.01**	**0.07**	**<0.01**	**<0.01**	**0.62**
Model 4	β		-0.07	0.06	0.02		-2.0E-03	-1.24	0.52	-0.41	
	SE		0.05	0.01	3.0E-03		3.1E-04	0.66	0.11	0.85	
	Wald		1.58	36.87	24.32		41.56	3.56	21.64	0.23	
	p		**0.21**	**<0.01**	**<0.01**		**<0.01**	**0.06**	**<0.01**	**0.63**	

Model 5	β		-0.08	0.06	0.01		-2.0E-03	-1.30	0.48		
	SE		0.06	0.01	3.0E-03		3.2E-04	0.65	0.11		
	Wald		1.83	38.36	16.96		40.00	3.99	17.88		
	p		**0.18**	**<0.01**	**<0.01**		**<0.01**	**0.05**	**<0.01**		
Model 6	β			0.06	0.01		-2.0E-03	-1.30	0.47		
	SE			0.01	3.0E-03		3.1E-04	0.65	0.11		
	Wald			40.07	17.95		41.19	3.99	18.15		
	p			**<0.01**	**<0.01**		**<0.01**	**0.05**	**<0.01**		
Model 7	β			0.06	0.01	-0.19	-2.0E-03	-1.34	0.49		
	SE			0.01	3.0E-03	0.27	3.2E-04	0.67	0.11		
	Wald			38.58	15.52	0.48	37.91	4.06	19.48		
	p			**<0.01**	**<0.01**	**0.49**	**<0.01**	**0.04**	**<0.01**		

Table 3.6 - Backward stepwise selection of model covariates for population-level resource selection functions for male brown bears only (n = five bear seasons from four individual bears) during hyperphagia (August-October). The least significant addition to the model (as determined by Wald test p-values) was dropped and model covariate values recalculated until all covariates had p ≤ 0.10.

		Model covariates									
		North	**East**	**Slope**	**Wetness**	**Squirrel Habitat**	**Distance to Water**	**Lowland Shrub**	**Dwarf Shrub**	**Tussock-Lichen**	**Wet Herbaceous**
Model 1	β	-0.20	0.13	0.01	0.01	0.56	-2.0E-03	-1.35	6.13	9.81	0.73
	SE	0.11	0.30	0.02	0.01	0.53	1.0E-03	0.28	4.83	5.72	0.45
	Wald	3.73	0.19	0.41	2.97	1.13	6.54	23.16	1.61	2.94	2.67
	p	**0.05**	**0.66**	**0.52**	**0.09**	**0.29**	**0.01**	**<0.01**	**0.21**	**0.09**	**0.10**
Model 2	β	-0.20		0.01	0.01	0.58	-2.0E-03	-1.35	6.12	9.83	0.75
	SE	0.09		0.02	0.01	0.55	1.0E-03	0.27	4.83	5.73	0.46
	Wald	4.94		0.44	2.52	1.10	10.29	25.52	1.61	2.94	2.69
	p	**0.03**		**0.51**	**0.11**	**0.29**	**<0.01**	**<0.01**	**0.21**	**0.09**	**0.10**
Model 3	β	-0.22			0.01	0.54	-2.0E-03	-1.31	6.15	9.99	0.75
	SE	0.10			0.01	0.51	1.0E-03	0.24	4.82	5.69	0.46
	Wald	5.05			3.10	1.11	10.29	29.62	1.63	3.09	2.59
	p	**0.03**			**0.08**	**0.29**	**<0.01**	**<0.01**	**0.20**	**0.08**	**0.11**
Model 4	β	-0.22			0.01		-2.0E-03	-1.27	6.12	9.99	0.68
	SE	0.10			0.01		1.0E-03	0.25	4.90	5.64	0.43
	Wald	5.56			2.70		6.54	26.69	1.56	3.14	2.57
	p	**0.02**			**0.10**		**0.01**	**<0.01**	**0.21**	**0.08**	**0.11**

Model 5	β	-0.19			0.02		-3.0E-03	-1.55		9.51	0.46
	SE	0.09			0.01		1.0E-03	0.29		5.65	0.46
	Wald	4.45			7.01		12.07	29.45		2.84	1.00
	p	**0.04**			**0.01**		**<0.01**	**<0.01**		**0.09**	**0.32**
Model 6	β	-0.19			0.02		-3.0E-03	-1.53		9.53	
	SE	0.10			0.01		1.0E-03	0.28		5.65	
	Wald	3.86			6.20		12.07	29.29		2.85	
	p	**0.05**			**0.01**		**<0.01**	**<0.01**		**0.09**	
Model 7	β	-0.20			0.02	0.14	-3.0E-03	-1.56		9.49	
	SE	0.10			0.01	0.16	1.0E-03	0.28		5.66	
	Wald	4.00			7.02	0.71	14.70	30.38		2.81	
	p	**0.05**			**0.01**	**0.40**	**<0.01**	**<0.01**		**0.09**	

Chapter 4 – Use of broad whitefish by brown bears in the Mackenzie Delta region, NWT[2]

4.1 Introduction

Fish provide a lipid-rich, highly digestible and spatially concentrated food source for many brown bear populations, and predation on salmon, trout, and charr by bears is well documented (Kistchinski 1972, Reinhart and Mattson 1980, Hilderbrand et al. 1999ab, Mowat and Heard 2006). The Mackenzie Delta, however, lacks major runs of salmon, trout, and char, and is likewise depauperate in caribou, a terrestrial source of protein typically available to Arctic brown bears (Scott and Crossman 1998, Nagy et al. 2005, Nagy and Johnson 2006). While bears may exist on vegetarian diets, the consumption of meat has been linked to increased body mass, population density and litter size in brown bears (Hilderbrand et al. 1999ab, Rode et al. 2001). Arctic ground squirrels and a limited number of semi-domestic reindeer are available to Mackenzie Delta bears (Nagy et al. 1983), however, the exploitation of alternative sources of meat protein, such as fish, may be important to meeting bears' nutritional requirements, and may serve as a major determinant of survival and fecundity.

Broad whitefish are a riverine and anadromous species, distributed along the Arctic Ocean coast from the Ural Mountain drainages in Russia to the Perry River, Nunavut (Scott and Crossman 1998). Broad whitefish undertake migrations between the Arctic Ocean and large rivers to smaller lakes and streams to feed, reproduce and overwinter (Reist et al. 1987, Treble and Tallman 1997, Tallman et al. 2002). During these migrations, broad whitefish may be vulnerable to predation by bears (Reist et al. 1987). Here I describe the predation of broad whitefish by at least one brown bear in the Mackenzie Delta region, NWT.

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[2] *A version of this chapter has been published. Barker and Derocher 2010. Arctic **62**: 312-316.*

4.2 Methods

The study area encompasses the Arctic boreal forest and upland tundra lying between the towns of Inuvik and Tuktoyaktuk, and the adjacent Mackenzie Delta floodplain, NWT (Fig. 4.1). Pete's Creek (69° 11′ N, 134° 08′ W), located centrally in the study area, is a 1-3 m wide creek 16 km long, lined with dwarf willow, flowing northward across scrub tundra from a small unnamed lake to the east branch of the Mackenzie River (Fig. 4.1; Mackay 1963).

Since 2003, an ongoing study has examined the food habits, movement patterns, denning, and reproductive ecology of brown bears in the study area (Edwards 2009). Between 2003-2007, 45 bears were fitted with Argos satellite-linked GPS radio-collars, with GPS positions recorded every four hours (Edwards 2009). Bear handling protocols were approved by the University of Alberta Animal Care Committee, and field work has been conducted under Wildlife Research Permits issued by Government of NWT – Inuvik Region: Environment and Natural Resources.

In August 2007, eight bears were wearing GPS collars. For each bear, a random selection of GPS positions, recorded 24-48 h apart, were investigated in the field for evidence of bear feeding activity. Site investigations were done from a helicopter hovering at 5-15 m altitude, and a site description, available food resources, and signs of bear activity, as well as photographs of the site, were recorded. Site investigations were conducted on 6 September and 2 October 2007.

To assess the possible use of the Pete's Creek area by study bears, I calculated annual 100% minimum convex polygon (MCP) home ranges for each GPS-collared bear in an ArcGIS database using Hawth's Analysis Tools (White and

Garrott 1990, Beyer 2004). For bears with 100% MCP home ranges incorporating Pete's Creek, I counted GPS collar locations that fell within 200 m of the creek's centre line.

4.3 Results

On 2 October 2007, while investigating GPS locations for a lone subadult female bear, I traveled by helicopter to Pete's Creek. The temperature was -2 °C, there was 1-2 cm of snow on the ground, and the creek surface had recently frozen to a depth of 3 cm. Seven locations for investigation were adjacent to Pete's Creek. Three sites were located next to oxbow bends in the creek, two were centred on beaver dams, and two were located in bankside willow thickets. I observed large numbers of tracks from wolves, foxes, ravens (*Corvus corax*), bald eagles (*Haliaeetus leucocephalus*), and at least one bear in the snow at all investigation sites. At the last site I observed two patches of disturbed soil and vegetation 10 m from the creek bank, which upon investigation on the ground proved to be cached piles of partially-consumed broad whitefish (25-40 cm total length), buried under approximately 20 cm of soil, moss, and Labrador tea. Both caches were oval-shaped, about 150 cm long x 100 cm wide x 40 cm tall, and were 3 m apart. At least six grey, unconsolidated scats containing fish scales were in the immediate vicinity of the caches. A muddy, well-used trail led from the caches to a beaver dam bridging the creek, and ice in the pool upstream of the beaver dam had been freshly broken. Both the trail and excavated soil beside the caches showed clear pad and claw marks of a brown bear. Concerns about the proximity of bears precluded remaining at the cache site to count the cached whitefish.

After departure by helicopter, I observed a GPS-collared brown bear in a dwarf willow thicket at the creek edge, 400 m southeast of the caches. The bear remained in the willows until the helicopter approached within 100 m, and then ran into the open tundra. The bear appeared in excellent physical condition and was noticeably fat. Subsequent GPS collar locations suggest that this bear was the subadult female whose positions I had investigated.

I followed Pete's Creek southward to its source, where I observed a congregation of >20 ravens and five bald eagles at a fast-flowing riffle that was unfrozen. Upon investigation on the ground, I observed approximately 30 dead and dying whitefish in the 15 m stretch of unfrozen creek, with fish ranging from whole to almost entirely consumed. My species identification of broad whitefish was determined from a fish collected at the site and was confirmed by Department of Fisheries and Oceans staff (T. Stein, Department of Fisheries and Oceans, *pers. comm.*).

A review of GPS locations for the subadult female bear in question indicated that she remained in the vicinity of Pete's Creek from 26 July - 4 October 2007, with >59% of successful GPS locations (representing at least 796 hours) within 200 m of the creek itself (Fig. 4.2). The bear's arrival at Pete's Creek corresponded to the reported downstream migration of large juvenile broad whitefish (30-45cm; Bond and Erickson 1985, Reist and Chang-Kue 1997), and her departure from the area on 4 October coincided with completion of winter freeze-up.

Annual 100% MCP home ranges from seven of 45 (15.6%) GPS-collared brown bears in the study overlapped at least part of Pete's Creek, with three of the seven bears (including the one mentioned above) spending large amounts of time at Pete's Creek during the whitefish migration period. From 12 - 20 September 2003, an adult female with three cubs-of-the-year spent ≥176 hours within 200 m of Pete's Creek (44 locations, 93% of successful GPS fixes). This same bear returned in 2004, spending ≥48 hours within 200 m of the creek between 27 July – 4 August 2004 (12 locations, 27% of successful GPS fixes). From 1 – 10 September 2004, another adult female bear recorded ≥192 hours within 200 m of Pete's Creek (48 locations, 92% of successful GPS fixes) (Fig. 4.2).

4.4 Discussion

Published reports of brown bears feeding on fish other than salmon, trout or char are rare. Siberian brown bears have been observed feeding on grayling (*Thymallus arcticus*) and pike (*Esox lucius*), Tajikistani brown bears have been reported to feed on spawning osman (*Dyptichus* spp.), and late medieval documents suggest brown bears in Norway once fed on spawning eels (*Anguilla anguilla*; Storm 1881, Vaisfeld and Chestin 1993). The only evidence for bears feeding on fish other than salmon, trout and char in North America comes from the central Canadian Arctic, where small volumes of longnose sucker (*Catostomus catostomus*) remains were observed amongst fecal samples collected from brown bears in spring (Gau et al. 2002). Traditional knowledge reports from the Mackenzie Delta region, however, are clear that brown bears forage on whitefish, with Pete's Creek noted as an area where bears gather in late summer/autumn to take advantage of this seasonal resource (Fehr et al. 1997, MGP/ISR 2006). Broad whitefish are abundant in the Mackenzie Delta area, feeding and overwintering in many tributaries and side channels of the Mackenzie River (Reist et al. 1987, Treble and Tallman 1997, Tallman et al. 2002), and bear predation is likely at other streams as well.

Living at the northern limit of their range, with an active period as short as five months of the year, Mackenzie Delta bears face extreme pressure to gather adequate nutritional resources (Nagy et al. 1983). Meat, a highly digestible and nutrient-dense food, confers survival and reproductive benefits on bears consuming it (Hilderbrand et al. 199a,b, Rode et al. 2001), but access to typical meat sources for Arctic coastal brown bears (salmon, char, and caribou) is limited in the Mackenzie Delta region (Scott and Crossman 1998, Nagy et al. 2005, Nagy and Johnson 2006). A large, dependable source of meat, such as broad whitefish runs, could have a significant role in the fat and protein intake of some bears in this region. As such, predation on whitefish may influence the fitness of bears exploiting this resource. The spatial concentration of fishing activity at streams during whitefish migrations means that disruption of foraging behaviour in these areas could have negative implications for some bears' ability to meet their nutritional requirements. The proposed development of the Mackenzie Delta for natural gas should consider that we do not fully understand the food resources of brown bears in the area, and further investigation of is warranted.

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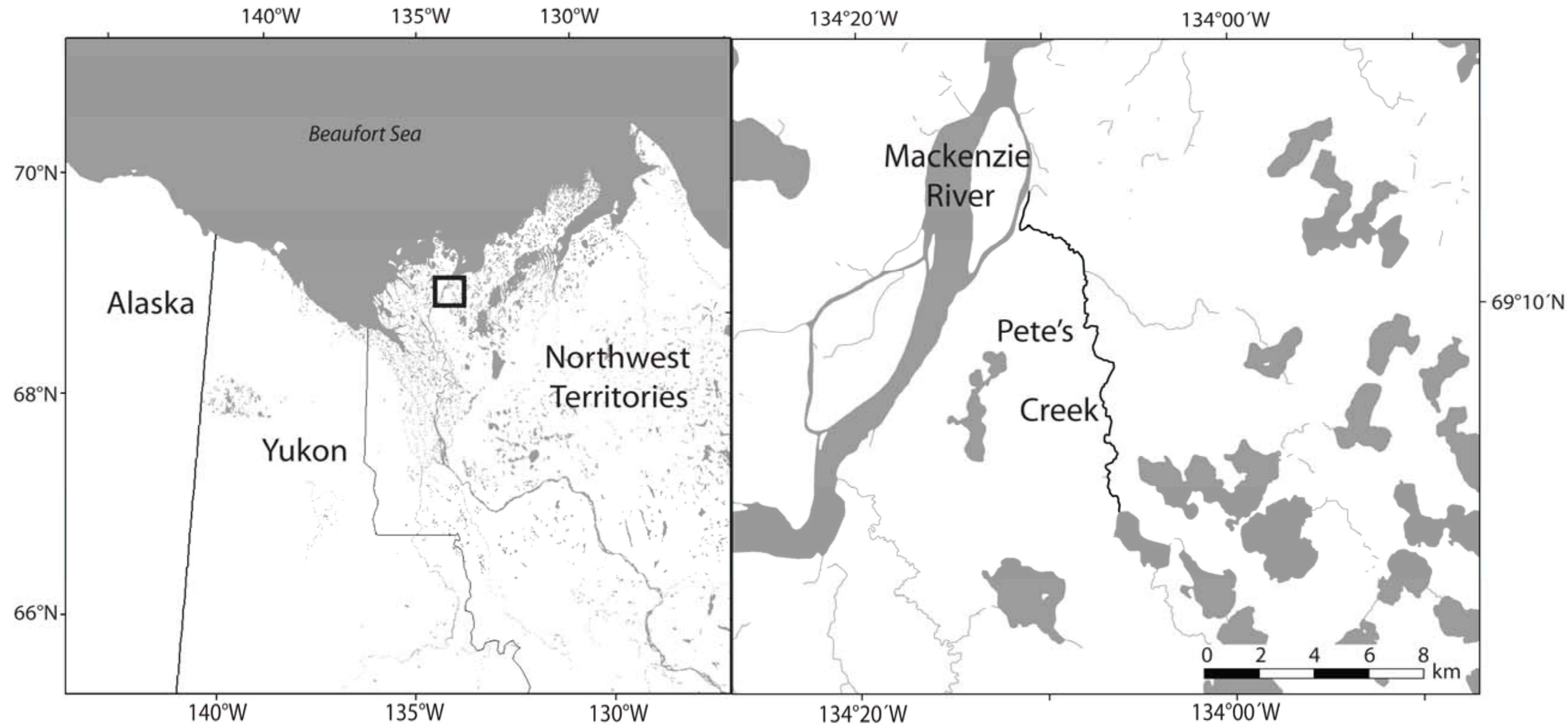

Figure 4.1 – Pete's Creek in a regional setting (left), and in detail (right).

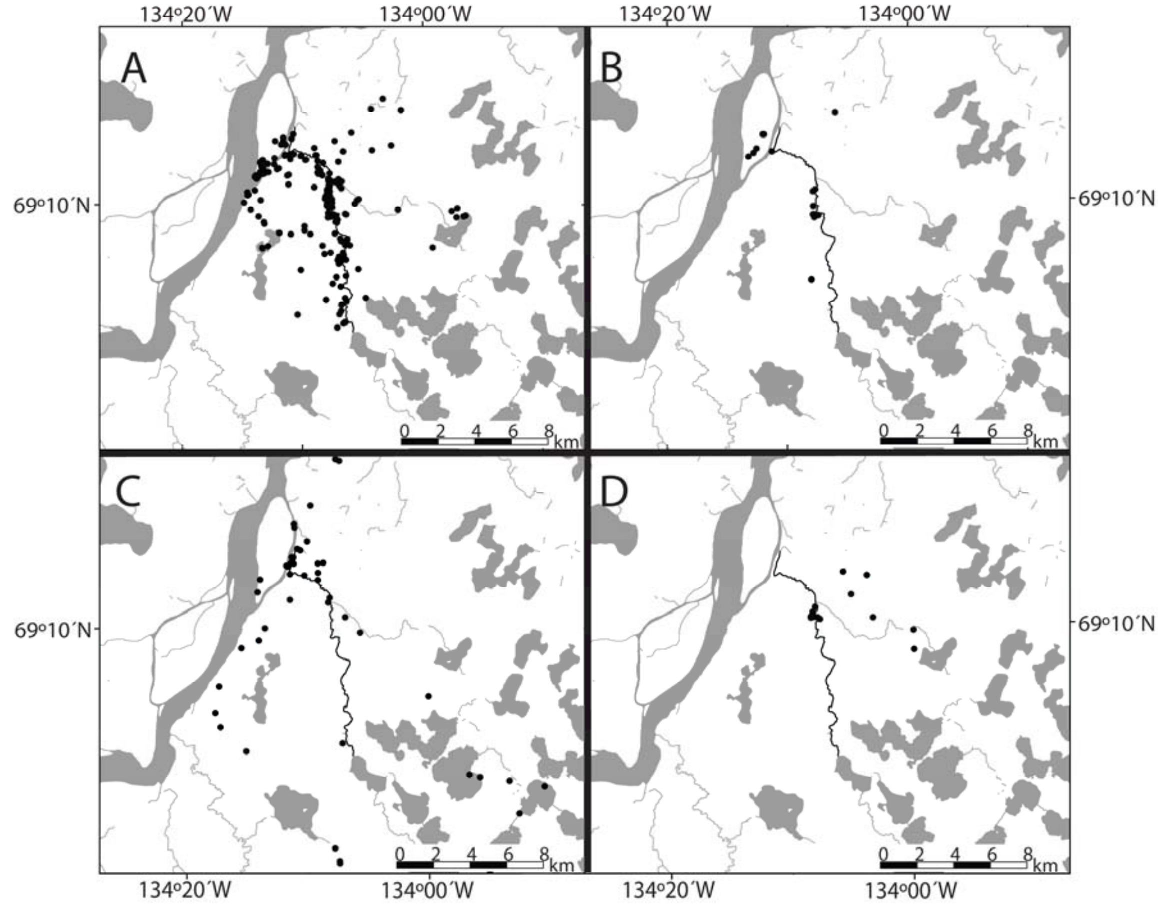

Figure 4.2 - Map of the Pete's Creek area showing: A) GPS collar locations recorded 26 July – 4 October 2007 for a subadult female brown bear observed near cached whitefish on 2 October 2007 (n = 337); B) GPS collar locations recorded from 12 – 20 September 2003 for an adult female brown bear with three cubs-of-the-year (n = 47); C) GPS collar locations recorded 27 July – 4 August 2004 for the same adult female (n = 44); and D) GPS collar locations recorded 1 – 10 September for another adult female brown bear (n = 52). GPS locations were recorded at four hour intervals.

Chapter 5 – General Discussion and Conclusion

5.1 Summary

In Chapter 2, Habitat selection by Arctic ground squirrels in the Mackenzie Delta region, NWT, I examined within-range habitat selection by Arctic ground squirrels. Arctic ground squirrels are an important ecosystem component throughout their Arctic and sub-arctic range. As a common prey item, they influence predator distribution and abundance (Carl 1971, Reid et al. 1997). Because their abundance is non-cyclical, they may play an important role in maintaining predator populations during the crash and recovery phase of other, cyclical small mammal populations (Reid et al. 1997). Through herbivory and deposition of wastes, Arctic ground squirrels modify plant communities within their home ranges (Batzli and Sobaski 1980, McKendrick et al. 1980). As an agent of biopedturbation, Arctic ground squirrels affect the distribution of soil and soil nutrients, and influence permafrost depth and erosional processes (Price 1971). Using resource selection functions, I found that Arctic ground squirrels selected for areas with steep slopes, high terrain convexity, and areas of rolling moraine and glaciofluvial deposits, and against high mean greenness, proximity to water, hummocky moraine, and areas possessing both steep slopes and high terrain convexity. Modeled habitat selection patterns predicted different Arctic ground squirrel distribution across the Mackenzie Delta region. Selected habitat was restricted to bluffs and creek valleys in the southern, forested portions of the study area, whereas selected habitat was more widely distributed in the northern tundra regions. The distribution of Arctic ground squirrel burrows did not show evidence of intrinsic, socially-driven spatial autocorrelation; the distribution of preferred habitat likely drives within-range habitat selection by Arctic ground squirrels. Using the results of this habitat modeling exercise, I discussed the potential impacts of climate change and habitat alteration on Arctic ground squirrel distribution and abundance. The model I created for Arctic ground squirrel habitat selection set the stage for my investigation into predation of Arctic ground squirrels by Mackenzie Delta brown bears in Chapter 3.

In Chapter 3, Use of Arctic ground squirrels by brown bears in the Mackenzie Delta region, NWT, I examined the importance of Arctic ground squirrels as a prey item for Mackenzie Delta brown bears. Arctic ground squirrels are an important component of the diets of some northern brown bear populations (Murie 1981, Phillips 1987, MacHutchon and Wellwood 2003), and other commonly-used meat sources (caribou and salmon) are rare or absent in the Mackenzie Delta region (Scott and Crossman 1998, Nagy et al. 2005, Nagy and Johnson 2006, M. Branigan, Government of NWT, *pers. comm.*). I tested for selection for Arctic ground squirrel habitat within bears' seasonal home ranges, and coupled this with site investigations of bear GPS-collar locations. I examined bears' selection for Arctic ground squirrel habitat and signs of Arctic ground squirrel predation (burrow excavation) against bears' level of carnivory, as inferred by $\delta^{15}N$ values in bears' tissues (Peterson and Fry 1987). Patterns in selection for Arctic ground squirrel habitat by bears, and signs of Arctic ground squirrel predation encountered during site visits, provide evidence for a pattern of individual specialization on Arctic ground squirrel predation by Mackenzie Delta brown bears. Arctic ground squirrels appeared to be an important food item for some bears, particularly during hyperphagia, but not for others. Carnivory, as derived from bears' $\delta^{15}N$ values, did not show a relationship with selection for Arctic ground squirrel habitat, or frequency of observed Arctic ground squirrel predation. Other unexamined meat sources may be driving stable isotope values in Mackenzie Delta brown bears. My results provide prey-specific support for evidence from stable isotope analysis by Edwards et al. (2010) of intrapopulation variability in foraging behaviour among Mackenzie Delta brown bears.

In Chapter 4, Use of Broad Whitefish by Brown Bears in the Mackenzie Delta Region, NWT, I described predation and caching of broad whitefish by a Mackenzie Delta brown bear, and provided evidence for broad whitefish predation by other GPS-collared bears. Broad whitefish are regionally abundant, undergo seasonal migration and spawning runs, and are comparable in nutritional value to other salmonids (Reist and Chang-Kue 1997, Treble and Tallman 1997, Scott and Crossman 1998, Tallman et al. 2002). Broad whitefish are vulnerable to bear predation when undergoing migrations or spawning runs in small rivers and streams (Reist et al. 1987). While conducting site investigations for evidence of Arctic ground squirrel predation, I encountered a GPS-collared female brown bear that had been capturing, caching and consuming large numbers of broad whitefish at Pete's Creek, a small tributary of the Mackenzie River. A consequent examination of GPS-collar location from this bear, as well as other bears whose home ranges encompassed Pete's Creek, revealed that some bears spent a great deal of time within 200 m of Pete's Creek in autumn, coincident with the period of downstream migration of large juvenile broad whitefish (Bond and Erickson 1985, Reist and Chang-Kue 1997). While this is the first report of bears eating whitefish in the academic literature, a review of traditional knowledge for the Mackenzie Delta region shows that local people have been aware of this behaviour for some time (Fehr et al. 1997, MGP/ISR 2006). Migrating broad whitefish represent a concentrated, high-quality food source which may be important late summer and autumn forage for some Mackenzie Delta brown bears. Spatially-concentrated food sources are particularly vulnerable to disturbance, such that even a small-scale disruption of brown bear foraging behaviour in the vicinity of a fishing location could have implications for bears that depend on those fish for food (Reinhart and Mattson 1980, Chi and Gilbert 1999, Rode et al. 2007). While predation of broad whitefish by brown bears has only been reported in the Mackenzie Delta region, it may also occur in other areas where these two species coexist, namely Arctic Ocean watersheds on mainland North America and Asia from western Nunavut to eastern Siberia.

5.2 Applications of my research

In the face of a changing Arctic climate and increasing anthropogenic development, understanding the ecology of Arctic species and ecosystems will allow us to predict, and in some cases mitigate, the ecological effects of these changes. The Mackenzie Delta region faces both the effects of climate change (Hassol 2004, Prowse et al. 2009) and the development of extensive petroleum extraction and transportation infrastructure (Imperial Oil et al. 2007, Voutier et al. 2008). Knowledge about the identity and spatiotemporal distribution of resources that are important to brown bears (and Arctic ground squirrels) can inform development decisions. Identifying which component of a population uses a resource also allows for predictions about which individuals or groups would be most affected by changes to that resource's availability. I have identified two specific resources used by Mackenzie Delta brown bears, examined which components of the population use them, and demonstrated seasonal variability in their use. This information provides a basis for informing decisions concerning land use planning, environmental impact review, wildlife management, and anthropogenic development in the Mackenzie Delta region. Likewise, this understanding can be used to predict and anticipate the effects of continuing Arctic warming and attendant ecological changes in the Mackenzie Delta region.

Beyond the Mackenzie Delta, the results of my thesis provide both insight and contrast to brown bears' foraging ecology in other Arctic environments. Of particular note are insights into the foraging ecology and predator-prey relationships of Mackenzie Delta bears in a tundra environment with rare or absent caribou. Where caribou are common, they form a large part of brown bears' diet (Young and McCabe 1997, Gau et al. 2002, Collins et al. 2005, Mowat and Heard 2006). Caribou, however, are uncommon or absent from the Mackenzie Delta region during bears' active period (Nagy et al. 2005, Nagy and Johnson 2006, M. Branigan, Government of NWT, *pers. comm*.), though bears in the area may prey occasionally on a semi-domestic reindeer herd (Nagy et al. 1983). The majority of caribou and reindeer herds throughout the circumpolar north are experiencing population declines (Vors and Boyce 2009). In the face of caribou and reindeer declines, examinations of the foraging ecology of northern bear populations with limited access to caribou, particularly those concerning alternate meat sources, provide valuable insight into the subsequent ecology of northern brown bear populations.

5.3 Directions for future research

My research sheds light on the use of Arctic ground squirrels and broad whitefish as sources of dietary meat for Mackenzie Delta brown bears. Our knowledge of brown bear prey in the Mackenzie Delta, however, remains incomplete. Only a small component of the population shows evidence of predation on Arctic ground squirrels, and a comparison of bears' foraging behaviour to their stable isotope values indicates that prey species other than Arctic ground squirrels may be more important to the Mackenzie Delta bears as a population. Broad whitefish in Pete's Creek appear to be an important resource for a small number of bears, but we lack knowledge about broad whitefish runs in other creeks and rivers, and the extent to which bears use them. Edwards et al. (2010) used carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) values of hair and claw material to identify foraging profiles for Mackenzie Delta brown bears; for 38 of 52 bears (73%), plant materials were predicted to contribute to <49% of their diet. While Arctic ground squirrels and broad whitefish contribute to the meat consumed by

Mackenzie Delta brown bears, what other meat sources are these bears eating, and how can we investigate them?

Direct observation offers continuous detail of food searching, handling and consumption by focal animals (Litvaitis 2000). Direct observation of Mackenzie Delta brown bears, over a sufficiently long period, would answer many questions concerning their diet and foraging behaviour. The nature of tundra environments, and the brown bears that inhabit them, pose many challenges to direct observation. Long sightlines and lack of cover mean that brown bears in tundra environments must often be observed from great distances to avoid disturbing them, hampering identification of their foraging behaviour (MacHutchon 2001, MacHutchon and Wellwood 2003). Brown bears that are aware of observers may change their foraging behaviour, flee, or act defensively. Transportation to remote study sites is also very costly. Despite these challenges, incorporating direct observation into investigations of Mackenzie Delta brown bear foraging ecology would provide a level of detail lacking in previous studies.

A bank of accumulated observation data may be available in the form of traditional ecological knowledge. Though details of broad whitefish predation by brown bears were first reported in the peer-reviewed literature by Barker and Derocher (2009), traditional knowledge of this phenomenon had existed for some time (Fehr et al. 1997, MGP/ISR 2006). Traditional knowledge can provide a culturally-transmitted, multi-generational account of relationships within an ecosystem (Berkes et al. 2000). The synthesis of traditional and scientific knowledge, however, faces significant challenges. Attempts at incorporating traditional knowledge into ecological research and decision making have encountered communication barriers, issues with the origin, specificity, scale and value of knowledge, misunderstanding about the role of metaphor and myth in describing ecological relationships, and the poorly-defined role of intellectual property rights in traditional knowledge collection and dissemination (Nadasdy 1999, Usher 2000, Ellis 2005). Overcoming these pitfalls is necessary for transparent and equitable transfer of traditional and scientific knowledge. Of particular note are differences in approaches to understanding complex ecological processes; the Western positivist approach to understanding ecological phenomena involves a paring away of excess complexity, whereas the conceptual models of ecological processes composing traditional ecological knowledge are adapted to embracing this complexity (Peloquin and Berkes 2009). For scientific ecologists, the level of complexity presented by many traditional knowledge accounts of ecological phenomena is difficult to incorporate into research programs and resource management decisions. As a starting point for ecological inquiry, however, traditional ecological knowledge can (and should) play an important role. Along with literature review, and consultation with other researchers familiar with the study area, accumulation and review of local traditional ecological knowledge should play a part in the development of field research programs. Traditional knowledge stems from accumulated and culturally transformed observation of local ecology, and can provide a broader perspective on ecological processes that is not available from other sources (Berkes et al. 2000, Ellis 2005). A potent source of information about organisms and processes within the Mackenzie Delta, Inuvialuit and Gwich'in traditional knowledge warrants consideration in the design and interpretation of research into the foraging ecology of Mackenzie Delta brown bears.

A more in-depth examination of diet using indirect methods also holds promise. For organisms that use many different food sources, such as bears, stable isotope analysis is better suited to providing estimates of trophic position, rather than the contribution of specific food items to their diet (Phillips and Gregg 2003, Phillips et al. 2005). For examination into the contributions of specific food items to bear diet, fatty acid signature analysis appears promising (Iverson et al. 2001, Iverson et al. 2004, Thiemann 2008). Identification of food sources incorporated into bears' diet requires fatty acid collection from both bears and potential food sources, and sufficient diversity of fatty acid signatures among food sources that their contributions to bears' fatty acid signatures are discernable (Thiemann et al. 2007, Thiemann 2008, Thiemann et al. 2008). An examination of fatty acid signatures of potential food sources for Mackenzie Delta brown bears should reveal which species possess unique fatty acid biomarkers, which can be identified within the fatty acid signatures of bears that feed on them. Fatty acid signatures among marine species are particularly diverse (Iverson et al. 2001), and incorporation of potential marine food items (beluga; *Delphinapterus leucas*, ringed seal; *Pusa hispida*, bearded seal; *Erignathus barbatus*) into the archive of potential food sources would identify the marine component of Mackenzie Delta bears' diet. With further research into the metabolism, incorporation and *de novo* synthesis of fatty acids in brown bears, analysis of the quantitative contribution of various food sources to brown bear diets may be possible (Iverson et al. 2004, Thiemann 2008).

Analysis of scat contents is another indirect method of gaining information about an organism's diet, and is often less invasive than stable isotope and fatty acid sample collection. Fecal residues, however, do not give a straightforward representation of diet, and must be corrected for digestibility, ratio of digestible to indigestible parts, selective consumption of different carcass or plant parts, and bias in scat collection and analysis (Floyd et al. 1978, Greenwood 1979, Hewitt and Robbins 1996, Litvaitis 2000, Spaulding et al. 2000). Determining species occurrence in scat samples, however, is less contentious than determining percent composition of ingested items (Litvaitis 2000). Nagy et al. (1983) collected and analyzed scat from Mackenzie Delta brown bears during the 1970s; resumed collection and analysis of bear scat would allow a comparison with contemporary bear diet, and provide direction to further study of food sources used by Mackenzie Delta brown bears.

Finally, the wishes of the Inuvik and Tuktoyaktuk Hunters and Trappers Associations to limit GPS-collaring of male brown bears, whose harvested hides are a valuable source of income, meant that very few GPS-collar data were available for male bears. With such a small sample of male bears, my ability to draw conclusions about male-specific foraging ecology was limited. This was particularly apparent during the latter years of the Mackenzie Delta brown bear project, when few or no GPS-collared male bears were available for site investigations into Arctic ground squirrel and broad whitefish predation. Brown bears are a sexually dimorphic species (Stirling and Derocher 1990, Hilderbrand et al. 1999b), and differences in morphology between sexes are often linked to differences in foraging ecology (Isaac 2005, Rode et al. 2006). Male bears' lack of dependent young also influences their behaviour and diet (Weilgus and Bunnell 1995, Ben-David et al. 2004, Rode et al. 2006). Male brown bears in the Mackenzie Delta region are likely to demonstrate different foraging strategies than female bears. The use of radio- and GPS-collars is culturally unacceptable to many First Nations and Inuit communities in northern Canada, particularly when their use has implications for the subsistence and monetary value of the animal in question (Byers 1999). The development and use of more culturally-acceptable research methods, such as direct observation, scat analysis, and biopsy dart sampling of bear tissues, may allow for further insight into the foraging ecology of male brown bears.

5.4 Final Conclusions

Accurate information about both the diet content and behavioural component of a species' foraging ecology is essential for understanding the abundance and distribution of species, and their role within their ecosystem

(Andrewartha and Birch 1954, Stephens et al. 2007, Krebs 2008). For brown bears, a wide-ranging omnivore with many potential food sources (Pasitschniak-Arts 1993), questions concerning diet and foraging behaviour are complex. Despite an ability to subsist on plants, brown bears have the digestive morphology of a carnivore (Bunnell and Hamilton 1983, Pritchard and Robbins 1990, Stirling and Derocher 1990), and consumption of meat by brown bears has been linked to increased population density, higher fecundity, faster growth, and larger body size (Hilderbrand et al. 1999a,b, Rode and Robbins 2000, Felicetti et al. 2003). My thesis provides insight into the use of meat sources by brown bears in the Mackenzie Delta region. I describe patterns of use of Arctic ground squirrels, a small mammal food source thought to be important to northern brown bear populations. I also identify a novel meat source for brown bears, broad whitefish, and describe its observed and potential use by Mackenzie Delta brown bears. Brown bears in the Mackenzie Delta region are a sensitive population in a difficult environment, and face challenges of climate change and impending petroleum development. By increasing our understanding of components of their diet, and the behaviours related to obtaining them, my research will aid in managing and conserving Mackenzie Delta brown bears and the environment they live in.

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