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TERRESTRIAL HABITAT SELECTION BY POLAR BEARS (*Ursus maritimus* Phipps) IN THE WESTERN HUDSON BAY LOWLANDS.

BY

DOUGLAS CLARK ©

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfilment of the requirements for the degree of Master of Science.

Department of Zoology

Edmonton, Alberta
Spring 1996

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ISBN 0-612-10699-3

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DEGREE: Master of Science

YEAR THIS DEGREE GRANTED: 1996

150 Barkley Terrace
Victoria, B.C.
V8S-2J6

11 Mar, 1996

UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommended to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled TERRESTRIAL HABITAT SELECTION BY POLAR BEARS (*Ursus maritimus* Phipps) IN THE WESTERN HUDSON BAY LOWLANDS submitted by DOUGLAS ANDREW CLARK in partial fulfillment of the requirements for the degree MASTER OF SCIENCE .

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Abstract

Polar bears (*Ursus maritimus*) in western Hudson Bay are forced ashore from late July to early November each year by melting sea ice. During this ice-free period, bears segregate by age and sex. I investigated habitat selection by different age and sex classes of bears during the ice-free period using both capture data from 1966 to 1994 and relocations from PTT collared adult females in 1991 and 1992. I compared capture and telemetry locations with habitat types classified from scanned LANDSAT TM images, and examined habitat descriptions noted at capture locations. I examined factors which might affect habitat preferences such as berry production, avoidance of conspecifics, and denning opportunities. Avoidance of adult males and the distribution of suitable denning habitat appear to influence habitat selection by female bears, whereas berry production does not. Subadult bears do not appear to select different habitat types than those used by other bears.

Polar bears in the Hudson Bay Lowlands dig different types of structures in permafrost, which they use throughout the on-shore season. Dens consist of entrance tunnels with an inner chamber, and resemble maternity dens dug in snow by polar bears. Shallow pits seem to be temporary resting places, and the function of shallow dens, or pit-dens, is unclear. Pits and pit-dens are primarily occupied by lone, presumably pregnant females, while pits are generally occupied by adult males and used more during summer than autumn. I speculate that these structures each play a role in thermoregulation.

Acknowledgements

I thank my supervisor Dr. Ian Stirling for giving me the opportunity work with an exceptional group of people, and to be part of an investigation into the ecology of a fascinating animal. I am particularly grateful for the guidance and constructive criticism he gave, and for his patience with me. Wendy Calvert provided a tremendous amount of help in the field and the laboratory. Dennis Andriashek provided welcome technical assistance and sound advice on a broad range of topics. My co-supervisor, Dr. Stan Boutin, and committee members Dr. Mark Dale and Dr. Jan Murie provided constructive criticism and direction throughout this study.

Dr. Peter Scott spent an entire week of his 1992 field season sharing his knowledge of northern ecosystems and the Churchill area with me, and has been a constant source of intriguing ideas. Dr. Andrew Derocher (B.C. Ministry of Forests) and Dr. Nick Lunn (University of Alberta) both provided constructive comments and assistance. Dr. Peter Crown, Tim Martin, Deborah Klita and their Spatial Information Systems Lab (University of Alberta, Dept. of Renewable Resources) were unstinting in their help. Our pilot Steve Miller gave exceptional service in the field. Dr. Malcolm Ramsay (University of Saskatchewan) provided information on bears handled during the course of his research. The members of the Federal/ Provincial Polar Bear Technical Advisory Committee provided welcome advice. Sam Barry (Canadian Wildlife Service) provided valuable assistance with statistical analyses. Many people were extremely generous with their time and expertise on specific topics: John Nishi (Gov't. of the NWT, Renewable Resources), Colin Young, Al Veitch (Gov't. of the NWT, Renewable Resources), Ellen Neary (Environment Canada), Dr. Ron Hall

(Forestry Canada), Dr. Richard Moses (University of Alberta), Dr. Steve Zoltai (Forestry Canada) and past and present members of the Stan Clan. The Warden Service of Pacific Rim National Park Reserve supported my efforts and allowed me time to complete this work.

I thank my parents, Drs. Patricia & Peter Clark for believing in me and giving me so many opportunities to learn and discover as I grew up; and my sisters Catherine and Heather for reminding me not take myself too seriously! My grandfather John Clark encouraged my early interest in natural history, and I fondly remember our walks along beaches and trips on the *Sylva Queen*.

Throughout this process, the support and companionship of good friends was always welcome, especially from Corey Bradshaw, Yves Pinsonneault, Kathy Linnaker, Scott Cole, Laurel McKellar & Tyson Cole/McKellar, Tammy Steeves, Mike Wride, Catherine Fear, Hilary Jones, Lisa McDonald, Clint Johnson, Tamara Stewart, Jessica Roberts, and David and Cathrine Cowen.

Support, both financial and logistic, was provided by the Canadian Wildlife Service, the Zoology Department of the University of Alberta, the Canadian Circumpolar Institute (Northern Scientific Training Program), the Manitoba Department of Natural Resources, the Churchill Northern Studies Centre and the Natural Sciences and Engineering Research Council (operating grant to I. Stirling).

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1. INTRODUCTION

1.1 Background

Polar bears (*Ursus maritimus* Phipps) are distributed throughout the circumpolar Arctic. In North America their range extends from the multi-year pack ice on the northern edge of the High Arctic islands south to the Labrador coast and James Bay (DeMaster and Stirling 1981). Their seasonal movements and distribution are largely determined by I.) the presence of suitable sea ice conditions for hunting ringed seals (*Phoca hispida*) and bearded seals (*Erignathus barbatus*) (Lønø 1970; Smith and Stirling 1975) and ii.) the annual break-up and freeze-up of sea ice. Generally they prefer floe edge or active pack ice, with open water leads where seals are more abundant and accessible (Stirling 1974; Stirling et al. 1977, 1993). They also use stable ice with pressure ridges where snow drifts accumulate in which ringed seals build birth lairs (Smith and Stirling 1975; Smith 1980). Although solitary, polar bears do not have exclusive home ranges, presumably because the dynamic nature of sea ice precludes any benefit from defending fixed territories (Ramsay and Stirling 1986). Mating takes place on the sea ice from March to May (Lønø 1970; Ramsay and Stirling 1986) and implantation between mid- September and mid- October (Derocher et al. 1992.) Females have from one to three cubs, usually at intervals of three or more years intervals except in Hudson Bay where breeding intervals of two years are common (Ramsay and Stirling 1986). Female bears with cubs tend to segregate themselves from other bears, possibly to reduce the risk of cub predation by conspecifics (Taylor et al. 1985; Stirling et al. 1993). Females normally den in snow drifts on land (Harington 1968; Lønø 1970) but maternity denning has been documented on the multi-year ice of the polar basin as well (Amstrup and Garner 1994).

Where possible, polar bears remain on the sea ice year-round. In several areas the annual ice melts completely, forcing the resident populations to spend variable amounts of time ashore. Discrete populations of polar bears have been identified throughout their range and though they are geographically distinct, immigration and emigration does occur (Lentfer 1972; Stirling et al. 1975, 1977; Taylor and Lee 1995). In Hudson Bay and James Bay, two populations have been identified: James Bay and eastern Hudson Bay and western Hudson Bay (Taylor and Lee 1995). These populations are subjected to longer periods of open water than are populations further north. They are forced ashore from late July until early November each year by complete melting of the sea ice (Stirling et al. 1977). They cannot hunt seals during this period and little feeding occurs on shore (Russell 1975; Knudsen 1978; Lunn and Stirling 1985; Ramsay and Hobson 1991; Derocher et al. 1993). The bears are mostly inactive and subsist on fat reserves (Nelson et al. 1983; Derocher et al. 1990; Ramsay et al. 1991, 1992), accumulated primarily during late spring and summer just prior to ice break-up (Derocher and Stirling 1990). Pregnant females face much greater energetic demands than other bears because after freeze-up, when the rest of the population returns to the sea ice to hunt, they remain ashore in dens to give birth and do not return to the ice until March (Stirling et al. 1977; Ramsay and Stirling 1986, 1988).

During the summer, bears normally segregate by age and sex. Generally, males remain on the coast, pregnant females and family groups move inland to an area dominated by open tundra, and subadults of both sexes are found throughout. Pregnant females dig earth dens and remain in or near them during this season. Lone, apparently non-pregnant females remain on the coast (Derocher and Stirling 1990). Although the reasons for this segregation is unknown, it has been suggested that the most dominant bears, adult males, travel as little as possible to conserve energy; while females may be motivated by one or more different influences: to feed on berries (Derocher et al. 1993), to reduce the risk of infanticide by avoiding adult males (Taylor et al. 1985), to familiarize female cubs with the location of suitable habitat for denning (Derocher and Stirling 1990), or for pregnant females to keep cool and avoid biting insects by digging earth dens in the permafrost (Derocher and Stirling 1990).

The objective of this study is to examine terrestrial habitat selection by polar bears in western Hudson Bay. In Chapter Two various hypotheses to explain habitat selection by polar bears are tested. Chapter Three describes the distribution and characteristics of earth dens and other structures in relation to the behaviour and patterns of habitat use by bears. Chapter Four summarizes the main findings of this work. Habitat descriptions and the techniques used to classify and map habitat types are presented in Appendix A.

1.2 Study area

The study area is part of the Hudson Bay Lowland physiographic region, located on the western coast of Hudson Bay from latitude 57°00'N to 58°50'N and from longitude 92°40'W to 94°00'W. Approximately 7800 BP the Keewatin ice sheet retreated to the northwest, the Hudson ice sheet disintegrated and the region was inundated by the Tyrrell Sea (Dredge and Nixon 1992). The area has since been subject to isostatic uplift- rebounding from the relieved weight of the ice sheet. The uplift rate seems to have remained relatively constant at 40 cm/century in the vicinity of Churchill (Dredge and Nixon 1992). This resulted in significant recession of the Tyrrell Sea and subsequently Hudson and James Bays.

This region is a gently sloping plain, heavily influenced by isostatic uplift, extensive permafrost and poor drainage (Dredge and Nixon 1992). Glacial till, overlain by marine deposits underlies most of the area: exposed bedrock is limited, found only in the vicinity of Churchill (ibid.). Peat covers approximately 75% of the Hudson Bay Lowlands (ibid.). The thickness of the peat deposit depends directly on time since emergence from the sea: there is little peat development at the coast, and greater thicknesses farther inland. The region is within the zone of continuous permafrost. Because of the extensive permafrost and the level terrain, drainage is poor, and drainage patterns seem quite variable among years. Wetlands are extensive, with marshes and fens near the coast, and bogs and fens inland (Sjörs 1959). In near-coastal areas, isostatic uplift is implicated in vegetational succession (Hik et al. 1992). The forest-tundra transition zone is a prominent characteristic of the study area (Scott et al. 1987).

The climate is dominated by the presence of Hudson Bay: long cold winters and short, cool, wet summers are typical (Thompson 1968). Though warming starts in May, snow remains on the ground for some time following, and the bay remains frozen. Summers usually last from July to September, and average monthly temperatures are 12°, 12° and 6 ° (Stirling et al. 1977) with occasional highs greater than 25°C. Autumn is brief, with cold northwesterly winds common from October onwards (ibid.).

Sea ice in Hudson Bay is both spatially and temporally variable (Larnder 1968). Break-up typically occurs in late July, but its timing varies more than freeze-up, which happens in November. Two features are of particular importance to the polar bear population in western Hudson Bay- a large persistent lead to the northeast of Churchill where these bears may hunt seals, and the tendency for the large ice pans to break up last along the Manitoba and Ontario coasts. This may account for the fidelity of polar bears to this area of Hudson Bay and the adjoining coast.

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2. HABITAT SELECTION BY POLAR BEARS IN THE HUDSON BAY LOWLANDS.

2.1 Introduction

Polar bears inhabiting western Hudson Bay are forced ashore from July until November each year by complete melting of the sea ice (Stirling et al. 1977). They cannot hunt seals during this period and little feeding occurs on shore (Russell 1975; Knudsen 1978; Lunn and Stirling 1985; Ramsay and Hobson 1991; Derocher et al. 1993). They come ashore after feeding on ringed seal (*Phoca hispida*) pups from March/April through mid-July (Derocher and Stirling 1990a, Stirling & Øritsland 1995). Generally adult males remain on the coast, pregnant females and family groups move inland, and subadults of both sexes are found throughout the area. Pregnant females dig earth dens and remain in or near them during late summer and fall. Pregnant females face much greater energetic demands than other bears because they remain ashore in dens to give birth, nurse their cubs for several months and do not return to the ice to feed until the following spring (Stirling et al. 1977). Lone, apparently non-pregnant, females remain on the coast (Derocher and Stirling 1990a). Mating takes place in April and May on the sea ice (Ramsay and Stirling 1988).

This segregation of bears by age and sex, as well as the lack of feeding on shore, suggests that several factors may influence their distribution. If conserving fat reserves was the sole influence, bears should move as little as possible, and one would predict they could all remain on the coast until freeze-up. Only adult male bears do so. Males are significantly larger than females, so their body size might be a constraint which forces them to be sedentary. It has been suggested that cooling from on-shore winds is the reason why adult males remain on the coast (Derocher and Stirling 1990a). Wind speed increases convective heat loss in polar bears (Øritsland 1970; Best 1982) and the regular north-easterly winds off Hudson Bay may make coastal areas preferable to those inland. In terms of total proportional load on the skeletal system, pregnant adult females would be at least as great as adult males. Thus, if cooling alone was the determining factor, pregnant females might be expected to remain on the coast, at least during summer, but they do not.

Taylor et al. (1985) proposed that females with young avoid adult males to decrease the risk of infanticide. If this were so, one would predict that only family groups and weaned subadult bears which had learned this habit would move inland, but one would not expect them to move farther than necessary to avoid adult males. (Derocher and Stirling 1990a) found that family groups travel farther inland (September average= 29 km) than adult males, which travel on average 8km from the coast. Subadult distribution is similar to adult males (September average=13km for females, 9km for males), however subadults have never been observed to prey on cubs (Taylor et al. 1985). There would be no such incentive for pregnant females to move inland since they have no cubs at risk.

Feeding opportunities might influence terrestrial habitat selection by bears. During time on shore, polar bears survive on stored fat (Nelson et al. 1983; Derocher et al. 1990; Ramsay et al. 1991). While bears ashore fast, they have been documented feeding on berries and graminoids, and occasionally on garbage and smaller fauna

(Russell 1975; Lunn and Stirling 1985; Derocher et al. 1993). Although such feeding is not felt to be significant in the overall diet (Lunn and Stirling 1985; Ramsay and Hobson 1991), it might assist bears to conserve their fat reserves. This could be beneficial if it permitted females to lactate longer or allowed them to return to the ice in better condition, and would be critical for animals that came ashore with insufficient reserves to fast until freeze-up. The weight of bears coming ashore varies among years and Derocher et al. (1993) documented an increase in the incidence of terrestrial feeding during 1987 to 1991. During that period, body weights of female bears coming ashore decreased significantly (Derocher and Stirling, 1992). This suggests that in years when bears come ashore in poorer condition, or must spend more time ashore because of the timing of break-up or ice formation, supplemental food might become more important.

Berries are an important food source for other species of bears prior to hibernation, and the distribution of berry-producing plants is a major determinant of habitat use (Pearson 1975; Hamer and Herrero 1983; Martin 1983). One would predict that if berries were an important food source for the population as a whole, then all bears would actively feed; as is the case with other bear species. This prediction does not hold: Derocher et al. (1993) found that only 31-34% of adult females alone or with cubs and 26% of all males fed on berries. Lactating females and their young did not feed at a significantly higher frequency than females without cubs, or subadults of either sex. However, adult males fed on vegetation significantly less frequently than did bears of other age and sex classes. It is possible that segregation of polar bears occurs because energy demands are greater for some classes of bears, such as females with young, and that they consequently select berry producing habitat more strongly than those classes with lesser demands. Segregation by reproductive status has been documented for red deer (*Cervus elaphus*): Clutton-Brock et al. (1982) found that lactating hinds selected higher quality grazing habitat than those without calves. The differences between red deer and polar bears are significant, but the principle of differential habitat selection is unlikely to be limited to red deer alone. To date, there is insufficient information to dismiss terrestrial feeding as a factor in habitat selection by polar bears. Derocher et al. (1993) do not indicate the frequency or quantity of feeding by individual animals, nor the energy gained. Without this information, the importance of terrestrial feeding cannot be determined.

Derocher and Stirling (1990a) noted that adult females with and without cubs go inland to the denning area during the summer. They suggested that this behaviour may assist female offspring to learn about the location of the denning area, to which they will return in subsequent years to give birth. While this may be so, it seems unlikely to be the primary reason for females to go inland.

Territoriality is another mechanism which might influence habitat selection. However, polar bears on the sea ice do not establish or defend territories, when competition over food might be expected (Ramsay and Stirling 1986). Additionally, female polar bears often den in close proximity to one another in the study area (Ramsay and Stirling 1990), on the Svalbard Archipelago (Hansson and Thomassen 1983), and on Wrangel Island (Belikov 1980) with little, if any, antagonistic interaction. Conversely, no evidence of cooperative parenting behaviour has been observed, though Lunn (1986) documented one apparent instance of this at the garbage dump at Churchill, Manitoba.

Pregnant females use earth dens while inland, prior to establishing maternity dens in snowdrifts, which do not seem to form until November or December (Ramsay and Stirling 1990). One would thus expect dens to be found in habitat types which are amenable to the formation of deep snow drifts in winter, and only pregnant females to use that habitat unless it had some value to other bears. Solitary, and presumed non-pregnant females are more common on the coast throughout the on-shore season. Dens are only found inland, in the large area dominated by lichen tundra, on thermokarst lakes and river banks (Jonkel et al. 1972, Ramsay and Stirling 1990). This area is underlain by continuous permafrost in a deep deposit of peat: in coastal regions of Hudson Bay this combination of vegetation, relief and permafrost are unique to this area (Dredge and Nixon 1992).

Examining a combination of mechanisms and recognizing the constraints on certain classes of bears may provide the most satisfactory explanation of the observed distribution of bears in the Hudson Bay Lowlands. Possible reasons for habitat selection may be summarized in several hypotheses which are not mutually exclusive. Despite this drawback, the following hypotheses and predictions provide a framework for interpreting observations on the terrestrial habitat in which polar bears of different age and sex classes are found.

1. <u>Avoidance of Males Hypothesis</u>: Adult male polar bears are cannibalistic. Though

the frequency of infanticide appears to be low, harassment and the threat of infanticide may be sufficient to influence female bears with young to move inland where they would be less likely to encounter adult males, which prefer coastal areas, and not because selection of any inland habitat type confers an advantage to them.

Prediction: Female bears with young will use habitat types in inverse proportion to their use by adult males.

2. Avoidance by Subadults Hypothesis: Subadult bears are subordinate to all other bears, and attempt to avoid bears of all other age and sex classes at all times.

Prediction: Subadult bears will select habitat types where they are less likely to encounter other bears, such as wetland.

3. Berry Feeding Hypothesis: Supplemental feeding permits bears to decrease their rate of weight loss while on shore. Females with young have the greatest energy demands when lactating, so they would have the greatest need for food to supplement their fat reserves during this period, and provide the most sensitive test for this hypothesis.

Prediction 1: Females with young will select more strongly than other classes those habitat types with the greatest berry production.

Prediction 2: Females with young will exhibit stronger selection of berry producing habitats during years of high berry production than during years of low berry production.

Prediction 3: If bears are foraging, the activity levels of telemetry-collared bears should be higher during years of high berry production (1991) than during years of low berry production (1992 and 1993) as bears move among berry-producing habitat patches.

4. Energy Conservation Hypothesis: If females with young inland are not foraging they should be conserving energy to maintain lactation.

Prediction: Female bears should move little, and even if constrained from doing that by active cubs, should select habitats and features which help them thermoregulate, further reducing energy expenditure. Forest, hummocks and banks allow this, and are widely available throughout the inland area; but bears should select open habitat types for maximum wind cooling early in the season when ambient temperatures are high, and then move to forested areas for shelter as ambient temperature falls in October-November.

5. Den Hypothesis: Pregnant female bears must minimize energy expenditure as much as possible. Since they must move inland eventually to establish a maternity den, they should find a suitable location as soon as possible and then remain there until den entry.

Prediction: Pregnant females will select rivers and lake edges in the large inland area of lichen tundra where treed peat banks permit digging dens.

2.2 Methods

2.2.1 Study area

The study area is on the western coast of Hudson Bay near Churchill, Manitoba from latitude 57°00' to 58°50'N and from longitude 92°40' to 94°00'W. The entire area is at less than 200m elevation and has little relief. It contains numerous lakes, rivers and creeks and is underlain by continuous permafrost. This region is a transition zone between boreal forest and low arctic tundra (Ritchie 1962).

2.2.2 Habitat classification and mapping

Classification of plant species abundance scores from 158 sites examined in 1992 and 1993 with TWINSPAN (Hill 1979) indicated the presence of six broad habitat types: intertidal flats, beach ridges, unvegetated (including alluvial deposits, inland beach ridges, rock outcrop, developed areas), wetlands (including fen, string bog, sedge meadow), lichen tundra and closed-canopy spruce forest (Appendix A). We performed a supervised classification on two mosaiced, scanned LANDSAT TM images to map the extent of these habitat types (Figure A.7).

2.2.3 Berry production among habitats

During the 1992 field season I established 75 permanent 1m^2 plots on 10 sites located opportunistically on berry patches, with 5-10 plots in each patch. All berries on each plot were harvested with a commercial hand held berry scoop. On these plots I measured weight and number of ripe and unripe berries of *Empetrum nigrum* and *Vaccinium uliginosum*. *Vaccinium vitis-idaea* and *Oxycoccus microcarpus* were present, but do not seem to be eaten by bears. Berries were weighed as soon as was practical after picking: either fresh that day or stored frozen, and weighed within ten days.

2.2.4 Habitat selection tests

Polar bears were captured between 1966 and 1994 during both spring and fall, using chemical immobilization techniques (Stirling et al. 1989): each animal was marked using eartags and lip tattoos. The capture data were stored in a central database maintained by the Canadian Wildlife Service. Prior to 1992, locations were determined to the nearest minute from 1: 250 000 NTS topographic maps: since then, capture locations have been determined with a GPS receiver (Garmin Corp., Lenexa KS). To reduce possible bias from bears seeking human food and garbage in the town of Churchill, captures that were northwest of 58°44'N, 94°00'W were excluded. Few bears have been observed or captured northwest of the Churchill townsite, so it is unlikely that this exclusion biased the test results.

In the spring of 1991-1992, adult female polar bears were fitted with Platform Telemetry Transmitter (PTT) collars (Telonics Inc., Mesa AZ). Seven bears were collared in 1991, nine in 1992 and five in 1993. These collars transmitted data for eight hours every five days: the duty cycle. Only relocation points with location-classes one to three were used in analyses, corresponding to average position accuracy levels with one standard deviation equal to 150m (location class one), 350m (location class two) and 1km (location class three) (Anonymous 1989). The first relocation in each duty cycle was selected unless it was clearly anomalous. Visual examination of the plotted relocation points revealed that once on land most bears moved inland within five to ten days. They remained in a limited area for most of the on-shore period and then returned to the ice within five to ten days. To minimize bias from including relocations while bears were travelling and which might have been independent of habitat type, I excluded all relocations before 10 days after the mean date ashore for collared bears (cutoff dates were August 2, 1991 and August 25, 1992) and after October 31 each year, and also excluded bears for which fewer than 5 relocation points were obtained for this period. This left a sample of three bears in 1991 and six bears in 1992. This sample contained only one bear without young on shore during the study periods.

Activity was measured with a tip switch inside the PTT collar, oriented along the longitudinal axis of the animal. During each duty cycle a sensor transmitted a count of the number of seconds in the previous 24 hours in which the switch was activated. I refer to this number converted to a percentage as "percent-day active". The number of locations of each class of bear in each habitat type was determined with the *sites occurrence* tool of the geographic information system GRASS 4.1 (Anonymous 1993) on an IBM RS6000 workstation. I used two different habitat selection tests, necessitated by the nature of the two different sources of data; capture and PTT. Since each captured bear contributed only one location per year, use per individual cannot be determined from those data. The Bonferroni-χ^2 method of Neu et al. (1974) was applied to capture data. I performed this test for each age and sex class of bear: lone adult females, adult females with young (family groups), adult males, subadult males and subadult females, with capture data broken down by month.

I calculated Manly's Alpha (α) for each habitat type for the individual bears (Manly 1974; Chesson 1983). This measure of preference has two forms: we have used the form which assumes that resources (the area of the different habitat types) are not significantly depleted by use (occupancy by female polar bears). This is defined as:

$$\alpha = \frac{r_i / n_i}{\Sigma^{m}_{j=1} r_j / n_j}$$

where r_i = the relative use of habitat *i*, n_i = the relative availability of habitat *i*, r_j = the relative use of habitat *j*, n_j = the relative availability of habitat *j*, and *m* = the number of habitat types present. Possible values of α range between zero and one, all α values sum to one, and each α is compared to the reciprocal of *m* for interpretation. If $\alpha > 1/m$, that habitat is selected for, if $\alpha < 1/m$, that habitat is selected against, and if $\alpha = 1/m$, that habitat is used in proportion to availability.

The α values are normally distributed, so hypotheses involving the α's may be tested with standard statistical tests (Chesson 1983). However, the set of α values for each habitat type for each individual is a vector, and since the elements of the α vector are linearly dependent, a matrix transformation of the α vector is required. This involves multiplying the α vector by an m x m-1 contrast matrix, yielding an α' vector of length m-1 (Chesson 1983; Schooley 1994). Preliminary examination of the results of the Bonferroni-X^2 tests suggested that selection results varied by geographic scale: the entire study area versus inland and coastal regions. To test for the effects of both year and scale on selection by adult female bears, I transformed the α values for each PTT collared bear in 1991 and 1992 as described and performed a MANOVA with two main effects: year and scale, plus year x scale interaction.

2.2.5 Sensitivity analysis

Accuracy assessment of the habitat map indicated significant misclassifications (Appendix A) so I examined the sensitivity of the selection tests to this type of error. From a sample of ground-truthed pixels I estimated relative bias of each habitat type by subtracting the proportion of pixels of other classes which were incorrectly called that habitat type from the proportion of pixels of that type which were classed as other types. I multiplied this quantity by the proportional availability of each habitat type, and re-tested use versus this bias-adjusted availability.

2.2.6 Determination of habitat use from capture records

The habitat a bear is in when first sighted is recorded on capture forms. The habitat types used were: tundra, coastal tundra, beach ridge, tidal flat, willow thicket, wetlands, hummock, spruce forest (excluding strips or clumps associated with rivers and creeks), burns, riparian strips and lake edges. These categories are often defined by features too small to show on the satellite images, and so do not correspond directly to the mapped habitat classes. I summarized the number of bears of each age and sex class found in each habitat between August 15 and October 15 inclusive, when the bears were most likely to be remaining in a small area, rather than travelling to and from the coast. I selected only the most recent 200 records, starting in 1994 and going back, and assigned each independent capture to commonly noted habitat categories. If there were fewer than 200 records for a particular class, all records were used.

2.3 Results

2.3.1 Berry production

In 1993, I found that seven of the 10 sites had been extensively fed on by Canada geese (*Branta canadensis*). Because of this, I analysed only 1992 berry production. The average berry production per site in lichen tundra was 14.0 g/m^2 (SD=27.0, n=6), in spruce forest it was 56.7 g/m^2 (SD=67.0, n=2) and in wetland it was 3.5 g/m^2 (SD=7.3, n=2). Both ripe and unripe berries were included. Analysis of variance indicated that mean berry production differed among habitat types ($F_{.05,(1)2,71}=10.11$, $p<.0002$).

2.3.2 Habitat selection by lone females

Lone females appeared to select stream banks (63/200 captures) and lakeshores (57/200) which border lichen tundra more than tundra itself (33/200). They appear to select lichen tundra during September and October, and avoid it during other months (Table 2.1). Spruce forest was consistently avoided by all age and sex classes (Table 2.1).

2.3.3 Habitat selection by females with young

Females with cubs-of-the-year (COYs) select lichen tundra (Table 2.1) (33/200) and make extensive use of riparian strips (40/200) and lakeshores (37/200).

Females with yearling and subadult cubs show a similar distribution to females with COYs (Figure 2.1); 28% were captured in lichen tundra (41/149), 26% on lakeshores (38/149) and 21% in riparian strips (31/149).

Interpretation of habitat selection from Manly's α values are made by comparing each α to the reciprocal of *m*, the number of habitat types. In Table 2.2, $m=3$, so that if $\alpha > 1/3$, that habitat is selected for, if $\alpha < 1/3$, that habitat is selected against, and if $\alpha = 1/3$, that habitat is used in proportion to availability. Lichen tundra was only the habitat type selected for in either year by PTT-collared female bears, and both spruce forest and wetland were selected against in both years. The MANOVA indicated that there was a highly significant scale effect ($F=8.817$, $df=1$, $P=0.005$) but the year effect was not significant ($F= .065$, $df=1$, $P=0.800$), nor was there significant year/scale interaction ($F=.170$, $df=1$, $P=0.682$). Analysis of variance indicated that mean activity was significantly greater in 1991 (average 6.8%,SD 6.7%) than in 1992 (average 4.7%, SD 4.5%) ($F=3.90$, $df=1,157$ $p=0.018$).

2.3.4 Habitat selection by adult males

Adult males showed strong selection for dry coastal habitat types (Table 2.1): 40% were captured on beach ridges (79/200). They also seemed to make relatively more use of lakeshore than rivers (39/200 and 13/200 captures respectively) and were captured in willow thickets more often than other bears (25/200) (Figure 2.1).

2.3.5 Habitat selection by subadults

Beach ridges, tidal flats and unvegetated areas seem to be preferred (Table 2.1). Inland, spruce forest and in fewer months lichen tundra seem to be selected against (Table 2.1). The numbers of bears captured in each region, and observations from capture locations indicate that subadult females have a different distribution than subadult males. Twenty-five percent of female subadults were captured in lichen tundra (47/186), 13% on lakeshores (25/186) and 13% on beach ridges (24/186). Twenty-one percent of male subadults were captured on beach ridges (41/196), 16% on lakeshores (31/196) and 13%in willows (26/196) (Figure 2.1). Proportionately more females than males were captured in the tundra region in September (females 57%, males 35%) and October (females 25%, males 6%) (Table 2.1).

2.3.6 Sensitivity of selection testing to classification error

The percent cover of each mapped habitat type is: water 21%, beach ridge 1%, intertidal <1%, unvegetated <1%, spruce forest 26%, wetland 28% and lichen tundra 23%. Bias for each habitat type is: water 60%, beach ridge -5%, intertidal 0, unvegetated 40%, spruce forest -26%, wetland 5% and lichen tundra -10%. Positive values are overestimations, negative are underestimations. Testing use versus adjusted availability resulted in few differences from testing against unadjusted availability. Females with COYs used wetland in July and intertidal in August in proportion to their availability. Previously, both types had been considered selected for during those months. During August, September and October, adult male use of the wetland class changed from used in proportion to availability to selected against.

2.4 Discussion

2.4.1 Assessment of methods

This investigation revealed some limitations to the technique of conducting a supervised classification on scanned LANDSAT TM images. The bias estimation indicated that selection tests are reasonably robust against misclassification of habitat types, but the discrepancies between those results and the capture observations suggest otherwise. The bias estimates alone provide an optimistic measure of error: unrelated errors of omission and commission may partially cancel out when subtracted from each other, so the bias estimates indicate only how much over- or underestimation of each class may have occurred. They give no information on how those errors are distributed among habitat types, which may be an alternative explanation of why the use versus bias-adjusted availability tests differed little from the first tests. This may also indicate that the effects of habitat type misclassification errors on selection tests cannot be easily detected with this type of comparison.

The distribution of bears indicated by capture-site observations differs from that suggested by the map-based selection tests. The map-based approach based on broad habitat types is not sensitive enough to represent features such as hummocks, willows, shorelines or narrow strips of riparian vegetation in which bears are often found. The habitat descriptions on the capture data forms identified features finer than the resolution of the habitat map or which were qualitatively different from identified habitat types. Shorelines and rivers are linear features, and are not well represented by a raster-format habitat map. Bears captured on shorelines would have frequently been plotted in the cover class water, and thus excluded from selection tests. Most treed river corridors are narrower than the 155m resolution of the map, and they were not adequately represented. Imprecision in the plotted location of bears is also a possible source of error, which I have not tested. Observations at capture locations indicate a strong association with riparian strips and lakeshores. On the habitat map less than 4% of the tundra region is more than one km from water, and less than 1% of the same region is more than one km from spruce forest. Buffer zones of any width, representing a measure of proximity to lakeshores and larger rivers, would have included most of the study area and would not have accurately identified these habitat elements. Few capture locations were associated with the wetland yet in many cases this was significantly selected for. This probably results from use of willow thickets, hummocks and lakeshores within larger areas of wetland, and not of the extensive sedge meadows or string bogs.

The apparent effect of scale of analysis on habitat selection is intriguing. This likely results from the proportional availability of the different habitat types changing at different scales. Porter and Church (1987) demonstrated that scale-dependent results could be artifacts from the spatial arrangement of different habitat types. They showed that where habitat types are distributed regularly, results are likely to be robust, and where habitat types are aggregated, test results could be misleading. Since different habitat types are generally limited to specific regions of the study area, and the entire study area is accessible to bears, the spatial arrangement of habitat types is probably less important to polar bears than their qualities, such as denning suitability or exposure to cooling winds.

Examining capture-location habitat data highlights an important point about selection tests: the results are only relative statements about use and availability, and still need to be viewed in an ecological context. Statistically significant preference or avoidance may be meaningless if it results from a few individuals using a very rare habitat type, or from a landscape made up of one or a few common habitat types and several rare types- in that case the common type may not be selected for even if it is the most used (McLellan 1986). Beach ridge, intertidal and unvegetated habitat types are often selected for, but the number of most classes of bear captured there appears low: statistical significance may be simply due to their limited extent ($< 1\%$ cover) in the study area. A small number of bears located in such a scarce habitat type would give such a result. Most age and sex classes seem to select beach ridges and other dry coastal habitat types (Table 2.1) but only adult males are found in large numbers on beach ridges, except during November when most bears are returning to the coast prior to freeze-up.

2.4.1 Habitat selection by adult males

Adult males showed strong selection for beach ridges- a habitat type found along most of the coastline of the study area. Derocher and Stirling (1990a) postulated that most adult males remained near the coast to reduce energy expenditure from travelling. There is likely little potential energetic benefit to moving inland for berry feeding relative to the cost of travel. Adult males do not seem to make significant use of other supplemental foods, such as human garbage, during the on-shore period (Lunn & Stirling 1985), likely because as a group they are less nutritionally stressed than other bears.

On the coast, adult males commonly form groups of up to 14 animals. Derocher and Stirling (1990b) suggested that by becoming familiar with conspecifics, adult males may derive social benefits from aggregating. These results support their idea that aggregations might form partially because of habitat selection by dominant animals. The distribution of aggregations corresponds with beach ridges, the most commonly selected habitat; both are more extensive in the northern portion of the study area than in the south. Beach ridges would provide a cool, open area where bears in an aggregation could easily observe each other at various distances. Also, in fall their testosterone levels are the lowest in the year which would help to reduce the overall level of agonistic behaviour (Palmer et al. 1988).

2.4.2 Avoidance by subadults

Subadult male bears seem to select the same habitat as adult males: beach ridges. Subadult females are more widely distributed among inland habitats; they have a strong association with lichen tundra and lakeshore, and males have some association with willow thickets in both the coastal and inland regions. These distributions more closely resemble those of adults of each sex than they do each other. If subadults actively avoid other bears, it is probably on an individual encounter basis; they do not seem to select different habitats as an avoidance tactic. Derocher and Stirling (1990a) suggested that subadults may not regard adult males as a threat on shore, since visibility is great, and competition for resources apparently nonexistent. Stirling (1974) suggested that yearling cubs and subadults can outrun adult males, and may not be at risk from them. Latour (1981) found that subadult females tended to separate themselves from both subadult and adult males in an area of overall high concentration of bears; moving inland would achieve this. This distribution is also consistent with the supposition that bears' knowledge of the denning area is reinforced by repeated visits (Derocher and Stirling 1990a). If female bears learned this as cubs they might attempt the trip on their own, even before they were mature and seeking their own dens.

2.4.3 Selection of berry producing habitat

Although the greatest apparent berry production is in the spruce forest habitat type, it should be noted that there were only two sites located in spruce forest, and one of those sites was unusual: a dry riverbed with large white spruce (*Picea glauca*) and heavy willow cover. I initially located these sites opportunistically, and was only able to place two sites in spruce forest, in contrast to six in lichen tundra, suggesting that although berry production may be less per unit area than spruce forest, berries may be more widely distributed, and hence available to polar bears, in lichen tundra. Studies on a related species, *Vaccinium globulare*, indicate that berry production is reduced by shading from a tree canopy (Martin, 1983), as might occur in the spruce forest habitat type. It is possible that the majority of the berry crop in the inland area is produced in the lichen tundra habitat type simply because of it's greater extent than spruce forest.

There is weak support at best for the hypothesis that berry feeding opportunities influence the distribution of family groups. Lichen tundra is selected for by both females with COYs and yearlings in September, and by females with COYs in October. These are the months in which Derocher et al. (1993) documented the highest incidence of feeding. However, both females with COYs and females with yearlings also make significant use of riparian strips and lakeshores rather than just the adjacent tundra (Figure 2.1).

The MANOVA results show that average selection was not significantly different between 1991 and 1992. However, lichen tundra was more strongly selected for in 1991, a relatively better crop year, than 1992, a poor crop year. This effect could have been obscured by the similarities among years: selection of inland habitats over coastal habitats. This might indicate that berry feeding is a less of a priority overall than that which governs selection of the inland area in the first place. At a local scale, opportunistic feeding may influence choice of habitat by females with COYs. Once they are in the same general area that they occupy every year, if berries are present they could search for berry-producing patches. The costs of doing so would be small compared to movements made to and from feeding areas on the sea ice, therefore the benefits from berry feeding would not need to be large for this strategy to persist. This would be an efficient strategy if, as was the case between 1991 and 1992/1993, the productivity of berry crops fluctuates among years. Moving inland specifically for berries would entail the risk that the trip would be of no benefit, and less energy might have been expended if they had stayed in one place. Also, the potential benefit from berry feeding alone is insufficient to draw many adult males inland. If the berry crop was a significant seasonal food source for the population, adult males would be expected to use it as well as females.

Collared bears were generally inactive throughout the on-shore season in both years. The activity levels in 1991, when berries were more abundant, were significantly higher than in 1992, when they were relatively less abundant. However, activity levels in both years were still low, and variance was high, so this may not represent a biologically significant difference. Thus it is possible, if not conclusive, that a higher level of activity in 1991 could reflect a greater amount of feeding on berries. Typically, berries become the dominant food item in both black bear (*Ursus americanus*) and grizzly bear (*Ursus arctos*) scats in a short period of time, suggesting that they are used as soon as they become available (Pearson 1975; Eagle and Pelton 1983; Hamer and Herrero 1983; Nagy et al. 1983a, b). If polar bears fed on berries to the same extent, one would expect to see a sharp increase in activity when berries ripen. Recognizing that not all bears feed on berries and that this is a relatively small sample, no such change was detected. Only one collared bear handled in the on-shore season in 1991 showed signs of berry feeding; it is not known how many of the PTT-collared bears may have been feeding in either year because not all of them were handled. It is also possible that if berries were plentiful, activity would be low since bears would not have to travel far between feeding sites. For example, Hamer and

Herrero (1983) noted that when food is widely distributed and abundant, grizzly bears from the same population in Alberta range extensively, feeding en route, and feed intensively in localized areas. However, the data from PTT-collared female bears indicate only localized movements after bears reached their inland destinations. Similarly, Knudsen (1978) and Latour (1981) reported that most polar bears on shore in the Hudson Bay Lowlands moved little, and spent much of their time resting.

The maximum yields of berries in the study plots are much lower than published estimates of berry production in other areas. Translated into kg/ha for comparison, the maximum yield on a single (spruce forest) site in 1992 (0.48 kg/ha, primarily *E. nigrum*) is much lower than several published yields of *Vaccinium* sp.: 270 kg/ha in a black spruce stand in Alaska (Hatler 1967), Noyce and Coy's (1990) yield of 9 kg/ha in black spruce, Cherkasov's (1974) 33-188 kg/ha and Kolupaeva's (1980) 160-296 kg/ha. In those studies, *Vaccinium* sp. berries were important to black bears in Hatler's study area, but not in Noyce and Coy's. Shevtsova et al. (1995) documented significant annual variation in berry production by *V. vitis-idaea* and *E. nigrum* in northern Finland. They suggested that berry production by those species in their area was generally low and highly variable. It seems unlikely that berry crops in this study area could contribute significantly to the energy balance of this population of polar bears. However, the amount of annual variation in berry crops in this study area is unknown and our estimates were obtained during qualitatively poor years.

2.4.4 Energy conservation

Adult male bears, as well as PTT collared females were generally inactive, but there is no evidence that family groups, or any bears select open areas early in the season then move to forested areas for shelter. No class of bear selected or used spruce forest at any time. Observations at capture locations suggest that females with young are found closely associated with lakeshores and spruce-bordered creeks and riverbeds, which could afford them shade and wind shelter. Bears of all age and sex classes are found on small hummocks and peat mounds, though not in high numbers. Such microsites are widespread and may be more useful to bears for comfort and thermoregulation than extensive areas of different habitats, since using such areas would mean travelling long distances between patches of different habitat.

2.4.5 Selection of denning habitat

The hypothesis that suitable denning locations influence the distribution of adult females cannot be rejected. Table 2.1 likely combines habitat selection for two groups of bears: pregnant and non-pregnant. Lone non-pregnant females tend to remain on the coast, selecting beach ridges, while pregnant females go inland. Lone pregnant females selected riparian strips and lakeshores in lichen tundra, on the edges of which dens are found. Once lone females arrive at particular locations in the denning area they are relatively inactive (Derocher and Stirling 1990a). Once females have established dens they remain in the vicinity, and some bears enter dens for at least part of the time by late August to early September.

2.4.6 Summary

The pattern of segregation of age and sex classes of polar bears on shore during the ice-free period mirrors that observed on sea ice (Stirling et al. 1993) although the habitat types are obviously different and the bears' distribution among sea ice types is largely influenced by the availability of seals. Since bears on shore feed little in comparison to their behaviour on the ice, this suggests that their terrestrial distribution is unlikely to be significantly based on energetic concerns.

The hypothesis of adult male avoidance cannot be disproved, though different avoidance strategies may be employed by different age and sex classes. Subadult polar bears do not appear to select habitat which is used little by other bears: this suggests that if they do seek to avoid other bears, they do so through other behaviours. Subadult males do not appear to choose different habitats than adult males, whereas subadult females and adult females with young do, though probably not for this reason alone. It is possible that subadult females and males are following the patterns of adults of their respective sexes in preparation for maturity; familiarizing themselves with denning areas and aggregation points, respectively. The location of suitable denning habitat seems to most strongly influence lone adult female bears.

I am unable to assess fully the influence of terrestrial feeding, but the lack of use of berry-producing habitats by male bears, the lack of interannual differences in selection and the low activity of PTT collared bears suggest that any effect is not strong. Berry feeding does not appear to have the same ecological significance here as it does for other bear species which must hibernate through winter. I have not adequately tested the hypothesis that energy conservation influences habitat selection by family groups, or other classes of bear. To do so, the costs of travel, terrestrial feeding and thermoregulation in these conditions need to be more completely understood, and the use of microsites needs to be quantified.

These results suggest that habitat selection by polar bears may be governed by different mechanisms for different portions of this population. Both social and energetic concerns seem to be involved, in different ways, for different age and sex classes of bears.

Table 2.1. Proportional use of habitat types by bears of different age and sex classes by month, obtained by plotting capture locations on the habitat map. Values for habitat classes which were significantly selected for are boldfaced, values for types significantly selected against are italicized, $\alpha = .05$.

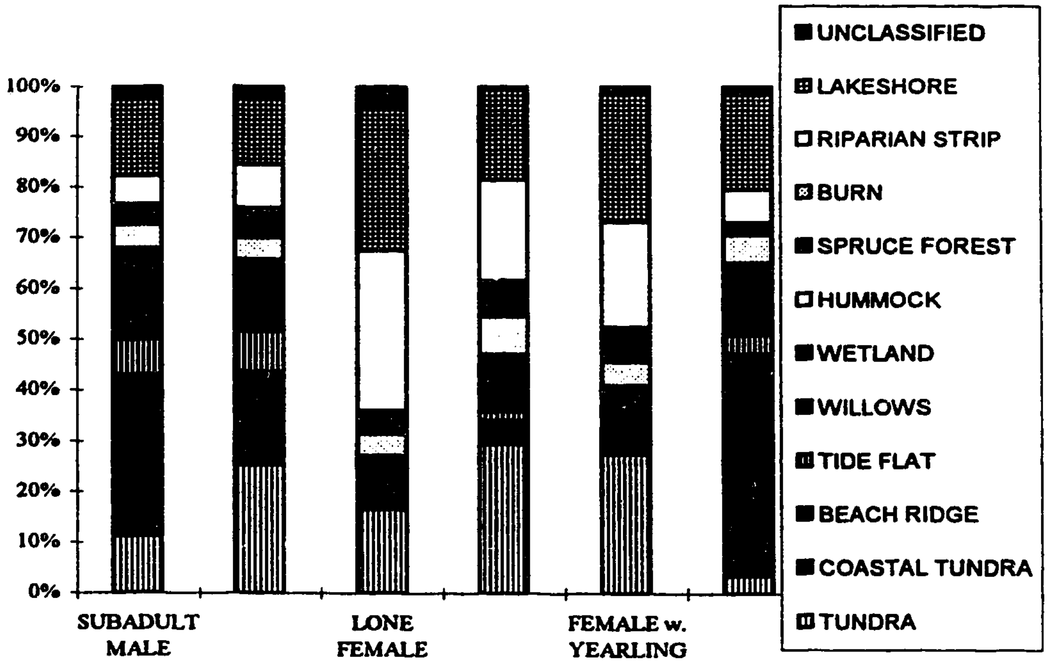
Bear Class	Habitat Type	JULY	AUG	SEPT	OCT	NOV	Σ
lone females	beach ridge	0.00	**0.14**	0.02	**0.07**	**0.19**	**0.06**
	intertidal	0.00	**0.09**	0.00	0.00	0.04	0.01
	unvegetated	0.00	0.07	0.00	0.01	0.08	0.02
	spruce forest	0.00	*0.05*	*0.24*	*0.16*	*0.12*	*0.19*
	wetland	1.00	**0.49**	*0.24*	0.40	0.38	*0.33*
	lichen tundra	0.00	*0.16*	**0.49**	**0.36**	*0.19*	**0.39**
n		5	43	192	70	26	336
females with COY	beach ridge	0.17	**0.12**	0.02	0.00	**0.20**	**0.05**
	intertidal	**0.33**	**0.05**	0.01	0.00	0.05	0.03
	unvegetated	0.00	**0.09**	0.01	0.01	**0.25**	**0.05**
	spruce forest	0.00	*0.07*	*0.12*	*0.09*	0.00	*0.09*
	wetland	**0.50**	**0.46**	**0.43**	**0.50**	0.30	**0.44**
	lichen tundra	0.00	*0.20*	**0.41**	**0.40**	0.20	**0.34**
n		6	74	152	68	20	320
females with Yrlgs.	beach ridge	**0.50**	0.07	0.00	0.06	**0.50**	**0.05**
	intertidal	0.00	0.07	0.01	0.00	0.00	0.02
	unvegetated	0.00	0.07	0.00	0.00	0.00	0.01
	spruce forest	0.00	*0.11*	*0.10*	0.15	0.00	*0.11*
	wetland	0.50	**0.57**	**0.42**	0.50	0.25	**0.47**
	lichen tundra	0.00	*0.11*	**0.46**	0.29	0.25	**0.33**
n		2	28	67	34	4	135

adult	beach ridge	**0.44**	**0.26**	**0.20**	**0.38**	**0.44**	**0.29**
males	intertidal	**0.37**	**0.18**	**0.09**	**0.15**	**0.11**	**0.14**
	unvegetated	0.07	**0.20**	**0.20**	**0.11**	**0.17**	**0.17**
	spruce forest	0.00	*0.01*	*0.06*	*0.02*	*0.02*	0.03
	wetland	*0.11*	0.30	0.30	0.27	*0.24*	*0.28*
	lichen tundra	0.00	*0.05*	*0.15*	*0.06*	*0.02*	*0.09*
n		27	206	366	219	96	914
subadult	beach ridge	**0.75**	**0.14**	**0.09**	**0.42**	**0.36**	**0.25**
females	intertidal	**0.25**	0.07	**0.07**	0.06	**0.12**	**0.08**
	unvegetated	0.00	**0.16**	0.00	**0.08**	**0.12**	**0.07**
	spruce forest	0.00	*0.02*	*0.08*	*0.01*	0.03	*0.04*
	wetland	0.00	0.39	**0.46**	0.34	0.30	**0.38**
	lichen tundra	0.00	0.23	0.30	*0.08*	*0.06*	*0.18*
n		4	44	100	85	33	266
subadult	beach ridge	0.00	**0.26**	**0.18**	**0.43**	**0.48**	**0.34**
males	intertidal	**0.25**	0.06	**0.09**	**0.14**	**0.10**	**0.11**
	unvegetated	**0.25**	0.06	**0.12**	**0.10**	0.08	**0.10**
	spruce forest	0.00	0.00	*0.05*	*0.01*	0.00	*0.02*
	wetland	0.50	**0.46**	0.38	0.30	0.35	0.35
	lichen tundra	0.00	0.16	*0.17*	*0.03*	0.00	*0.09*
n		4	50	98	135	52	339

Table 2.2. Manly's alpha for PTT-collared female polar bears in 1991 (n=3 bears) and 1992 (n=6 bears), obtained by plotting relocations on the habitat map (standard deviations in parentheses).

Habitat Type	1991	1992
spruce forest	0.18 (0.08)	0.21 (0.21)
wetland	0.21 (0.07)	0.32 (0.29)
lichen tundra	0.61 (0.13)	0.47 (0.22)

Figure 2.1. Percent of each age and sex class of polar bear captured in different habitat types, described from the most recent 200 capture records for each class.



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3. DISTRIBUTION, CHARACTERISTICS AND USE OF POLAR BEAR EARTH DENS AND RELATED STRUCTURES.

3.1 Introduction

Polar bears (*Ursus maritimus*) inhabiting western Hudson Bay are forced ashore from late July until early November each year by the complete melting of sea ice (Stirling et al. 1977). Once bears are on shore in the Hudson Bay Lowlands they segregate by age and sex class: in general, adult males remain along the coast, and adult females with and without cubs move inland, commonly 30-50 km (Derocher and Stirling 1990). Subadults are found throughout the coastal and inland areas. Because they cannot hunt seals during this period and little feeding occurs on shore (Russell 1975; Knudsen 1978; Lunn and Stirling 1985; Ramsay and Hobson 1991; Derocher et al. 1993), bears are mostly inactive and subsist on their stored fat reserves (Nelson et al. 1983; Derocher et al. 1990; Ramsay et al. 1991, 1992). While they fast, bears have been reported occupying both earth dens and simple shallow pits (Jonkel et al. 1972; Stirling et al. 1977).

The objectives of this chapter are to describe the types of structures dug, quantify the age and sex classes of bears using them, and evaluate possible hypotheses to explain their function. Jonkel et al. (1972) speculated these structures were used by adult bears for temporary resting and cooling through shade and direct contact with permafrost during the relatively warm ice-free season. Other possible explanations for this behaviour include maternity denning and escape from insect harassment.

3.2 Materials and methods

Active (occupied by a bear) and inactive (not occupied) dens were located opportunistically throughout the study area in August and September of 1992 and 1993 while searching for polar bears by helicopter as part of a long-term population study. Search effort was spread over the entire study area (Chapter 1) and in all habitats. Some bears in dens were located by radio-telemetry. Often, when inactive dens were found close to active dens; I investigated these nearby structures as well. I also examined several areas where a number of den sites were seen in order to survey as many dens as possible. In this way, both active and inactive dens were surveyed in a non-random but non-selective manner.

In the field I recognized three different types of structures used by polar bears. These were classified as: 1.) shallow round to oblong pits on the tops of banks or beach ridges, 2.) earth dens in peat banks, with an elliptical entrance and a long, narrow entrance tunnel, often parallel to the bank, leading to a larger inner chamber and 3.) possibly intermediate structures consisting of simple shallow, semicircular excavations into peat banks which lacked an entrance tunnel. I treat each of these types separately, and refer to them as pits, dens and pit-dens, respectively.

I measured the length, width and depth of pits and the dimensions of dens and pit-dens, as shown in Figure 3.1 and Figure 3.2 respectively, to the nearest 10 cm with a steel tape. I measured permafrost depths adjacent to and within dens with a steel probe graduated at 10 cm intervals. I did not measure the slopes of banks containing dens since they were abrupt and many were rounded from slumping, and the open den entrance was often a large portion of the bank's height. I made simultaneous temperature measurements inside and outside dens with an alcohol thermometer. Vegetation and physical features above, adjacent to and in front of dens were qualitatively described at each site. I obtained latitude and longitude of dens with a Garmin GPS-100 global positioning system receiver. The identification of polar bear habitat types was described in Chapter Two. Aspect measurements were tested for significance with Rayleigh's test and Watson and Williams' test (Zar 1984) with $\alpha=0.05$. All statistical tests were performed on Microsoft Excel 5.0.

Use of dens or pits was recorded for polar bears captured during population studies between 1966 and 1994 and stored in a central database maintained by the Canadian Wildlife Service. I extracted age, sex and reproductive status of all polar bears using earth dens or pits. In years prior to this study, pit-dens were generally recorded only as dens so I was not able to identify a large sample of them. Females with young were divided into two groups; those with cubs-of-the-year (COYs) and those with yearling cubs.

3.3 Results

Figure 3.3 illustrates the distribution of 41 dens, 43 pit-dens and 48 pits I examined in the study area. Of 18 fresh dens, 15 (83%) were occupied: none of 23 old dens were occupied. Of 33 fresh pit-dens, 19 (58%) were occupied, and none of the seven old pit-dens were occupied. Twenty-two of 32 (69%) fresh pits were occupied, and only one of 15 (7%) old pits was occupied. Fresh dens were defined by the presence of digging during the current field season, judged by the dryness of excavated peat and the condition of vegetation in and adjacent to the den or pit. Three pit-dens and one pit which I was unable to determine the age of were excluded from analyses of den measurements, but included in other analyses.

3.3.1 Characteristics

Dens have round entrances which typically lead into a larger inner chamber (Figures 3.1 and 3.3). Thirty-five dens had a single chamber and six had two or more. Eleven dens and their entrances were perpendicular to the bank, 17 curved to the left parallel to the bank, eight curved to the right and two extended in both directions. The dimensions of both fresh and old dens are presented in Table 3.1. Mean aspect of the dens was 119° (circular SD 150°, $r=0.033$, $p>0.50$, $n=41$), and was not significantly different from a random distribution.

A typical pit-den is shown in figure 3.4. Pit-dens are simpler structures than dens, typically being just semicircular excavations. Of those measured, 22 were symmetrical, four curved to the right, and six curved to the left. Eleven were either collapsing or were too shallow to determine if they were curved or straight. Table 3.2 shows the average dimensions of measured pit-dens. Mean aspect of pit-dens was 135° (circular SD 89°, $r=0.299$, $0.2<p<0.5$, $n=43$), significantly different than random. The mean aspects of dens and pit-dens were significantly different ($F=13.446$, $p<0.001$).

A typical pit is shown in Figure 3.5. Depth in this case refers to maximum vertical depth below the rim of the pit. Table 3.3 shows the average dimensions of pits examined. Mean aspect of the landforms which pits were situated on was 52° (circular SD 102°, $r=0.207$, $0.1<p<0.2$, $n=48$), not significantly different than random.

Mean depth to permafrost inside fresh structures (24 dens, 35 pit-dens and 15 pits) was 12.4 cm (SD=12.5 cm), and mean depth outside was 38.8 cm (SD=18.9 cm): a significant difference ($F=70.457$, $p<0.0001$). Depth to permafrost outside dens, pit-dens and pits was not significantly different ($F=1.335$, $p=0.270$), nor was depth to permafrost inside ($F=0.055$, $p=0.946$).

The average temperature inside and outside 36 dens was 7.5°C (SD 1.9°C) and 9.2°C (SD 2.8°C) respectively, a difference that was statistically significant ($t=3.73$, $p=0.0007$, $df=35$). Temperature variance was also significantly less inside than outside ($F=2.17$, $p=0.013$, $df=35$).

Thirty-three of 41 dens had spruce (mainly *Picea mariana*) on the top of the bank above them, 32 of 40 pit-dens had spruce above them, and five of 26 inland pits had spruce above them. Tree heights in relation to the different types of structure did not appear to vary much: estimated mean tree height above all types was 2.1m (SD 1.0m, $n=70$).

In or immediately in front of nine structures I noted dry vegetation apparently cut by bears which I interpreted to be bedding material. This included *Carex* sp. (4), *Elymus arenaruius* (3) *Sphagnum* sp. (2), *Ledum groenlandicum* (2), *Potentilla palustris* (1) and *Salix* sp. (1).

3.3.2 Distribution among habitat types

Table 3.4 shows the distribution of dens, pit-dens and pits in relation to habitat type. Dens and pit-dens were typically found on banks with lichen tundra above and water or wetland below. In contrast, pits were found in all habitat types except spruce forest and unvegetated areas. These structures were often located on banks and beach ridges, which have different habitat types above and below them, so it would be misleading to view them as associated with a single habitat type. The heights of banks and ridges on which dens (n=41), pit-dens (n=40) and pits (n=47) were located were significantly different (p=0.0009, F=7.421, df=124): average heights were 2.5m, 3.0m and 1.8m respectively. Average heights of dens pit-dens and pits above the bases of banks were not significantly different, and were 1.5m, 1.8m, and 1.5m respectively.

Twenty five dens (61%) were on lakeshores, 4 (10%) were on river and creek banks, and 12 (29%) were not obviously associated with water. Similarly, 21 (50%) pit dens were on lakeshores, 11(26%) were along river and creek banks, and 10 (24%) were not near water. Pits had a somewhat different distribution: 19 (40%) were on lakeshores, one (2%) was on a riverbank, 22 (46%) were just above or nearly at high-tide line and six (12%) were not associated with water. The average distance from water, if the structure appeared to be located on a shoreline, for all types of structure was 10.2m (SD 12.6m) and was not significantly different among structures (F=0.175, p=0.840).

3.3.3 Use by polar bears

Of 14 bears that were occupying dens when captured during 1992 and 1993, 11 (79%) were lone females, two (14%) were subadult males and one (7%) was an adult male. Seventeen bears were occupying pit-dens: 15 (88%) were lone females, one (6%) was a subadult male and one (6%) was an adult male. Of 15 bears occupying pits, two (13%) were lone females, two were females with cubs of the year, one was a subadult male (7%), and ten were adult males (67%). Tables 3.5 and 3.6 show the age and sex classes of bears captured in each month, in dens and pits respectively. Pit-dens were distinguished from dens in only six cases in the capture database: these were one adult male in July, two lone females and one subadult female in September, one female with yearlings in October and one subadult female in November.

3.4 Discussion

3.4.1 Characteristics

My observations on the structure of earth dens are similar to those of Jonkel et al. (1972). As well, dens found in this study are similar in conformation and size to maternity dens dug in snow by adult female polar bears, described from other areas (Harington 1968; Lentfer and Hensel 1980). Harington (1968) made a distinction between maternity dens in snow, which resemble earth dens, and temporary dens in snow, which resemble pit-dens. Temporary snow dens were also recognized by Uspenski and Kistchinski (1972), Belikov (1980), Hansson and Thomassen (1983) and Lutsyuk (1978). Snow dens used during the summer by polar bears in the High Arctic (Schweinsburg 1979) were also similar in size and shape.

Harding (1976) and Nagy et al. (1983a, b) found dens made by grizzly bears (*Ursus arctos*) along the western Arctic coast similar in shape and size to the dens I have described. References to structures similar in size and shape to the pits I have described often refer to them as daybeds (Craighead and Craighead 1972; Mysterud 1983; Mollohan 1987). Black bears (*Ursus americanus*) inhabiting the arctic tundra in Labrador excavate dens in mineral soil as well as using natural rock shelters, but are not known to dig into permafrost (A. Veitch, pers. comm.).

It is unclear exactly whether or not dens and pit-dens have different roles during the summer. They are found in the same habitat types and locations, bears appear to rest in both, and both seem to be used predominantly by adult female bears. Belikov (1980) observed that temporary dens were typically used for only a few days, after emergence from maternity dens. Pit-dens may be shallower than dens because they are used only temporarily during the ice-free season.

Alternatively, pit-dens may be partially completed or abandoned efforts to build dens. If pit-dens were the beginnings of dens, one would expect to see a continuum of depths, from shallow to deep, however this is not the case. Dens and pit-dens have quite different average depths (204cm and 112cm respectively for fresh structures) and intermediate structures have not been observed (Tables 3.1 and 3.2). It is improbable that every attempt to dig a den is successful, and abandonment of denning attempts has been documented for other animal species in the Arctic. Cheesemore (1969) found partially completed arctic fox (*Alopex lagopus*) dens which had been abandoned once they reached permafrost. Harington (1968) interpreted claw marks in a snowbank adjacent to a den to be an abandoned attempt by a polar bear to dig there. It is possible that permafrost is a hindrance for polar bears. Nagy et al. (1983a, b) found only two out of 137 grizzly bear dens in the Western Arctic dug into peat banks: the remainder of the excavated dens were in talus slopes or unfrozen alluvium. Grizzly bears have longer claws than other bear species- considered to be an adaptation for digging (Stirling and Derocher 1990). That grizzlies appear to select substrates other than frozen peat when a choice is available could indicate either that it is less stable or that it is more difficult to excavate. However, seasonal differences in the timing of den excavation might explain this discrepancy. Grizzlies in most areas feed actively through summer and autumn and so apparently dig dens later in the season than polar bears do (Craighead and Craighead 1972; Pearson 1975; Nagy et al. 1983a, b). If so, grizzly bears would be able to choose from a broader range of sites, since more areas would be frozen and possibly better able to support a den.

The depth perpendicular to the bank face of dens and pit-dens is similar and roughly corresponds to the depth of unfrozen peat on the bank faces (P. Scott pers. comm.), suggesting that the permafrost may at least limit how deep a den may be excavated in a single year. Entrance tunnels turn at approximately the same depth from the bank surface, and Servheen and Klaver (1983) described grizzly bear dens of similar dimensions in Montana which also had abrupt turns when the entrance tunnels reached obstructions, in their cases, rock slabs. Judging by the presence of both freshly dug and older, dry peat outside established dens, polar bears appear to re-excavate old dens during their own tenancy. Over successive years a pit-den might be extended deeper during thawing periods. However since polar bears exhibit fidelity only to general areas inland and apparently not to specific den sites (Derocher and Stirling 1990; Ramsay and Stirling 1990) it is unlikely this represents investment over successive years by the same bears.

The generally southeast orientation and high variation in den aspect is similar to other studies in this area (Jonkel et al. 1972; Ramsay and Stirling 1990), though the lack of statistical significance is curious. One might predict a preference for south-facing banks might be preferred because they are sheltered from prevailing northeast winds and are more exposed to the sun. These observations might simply reflect the flat nature of the study area: any relief, no matter what its exposure, may be adequate. Since pit-dens are shallower, orientation might be more important for obtaining wind shelter in them than in deeper dens: their significantly different, less variable and more southerly aspect than dens is consistent with this. The mean aspect of pits, 52°, and the open nature of areas where they are found, would position them to take advantage of onshore winds for cooling.

Spruce trees grew along the upper edges of banks over a large portion of dens. Several authors (Craighead and Craighead 1972; Jonkel et al. 1972; Harding 1976) suggest that tree roots are important to stabilize bear den ceilings. I frequently observed banks slumping in the study area; however several pit-dens were located beneath overhanging peat slumps so support may only be a limitation for deeper dens. That dens do survive from year-to-year in the thermally dynamic active layer of peat suggests that tree roots may be involved. Spruce trees are typically found in narrow bands on the tops of banks, and dens might curve parallel to banks in order to remain underneath the protective root matrix. There would be obvious benefit to avoiding den collapse: Clarkson and Irish (1991) documented a family group of polar bears apparently killed by the collapse of a snow den in the Western Arctic.

Craighead and Craighead (1972) noted that every grizzly bear they observed did some additional digging immediately prior to entering a den, which they suggested was a stereotypic behaviour. They also found bedding material in every occupied grizzly bear den they examined. Dens with polar bears in them exhibited signs of fresh digging, although the presence of bedding was not frequent. This may indicate that close contact with permafrost is desired for cooling, at least during the summer months. In dens examined in the study area, the bedding material was either in the den entrance or in a pit in front of the den. Pits in front of dens were typically dug into newly excavated, unfrozen peat, suggesting that they are not made for permafrost contact, but perhaps for sunning. On cool dry days female bears were often sighted on these peat mounds, just outside their dens. Both Craighead and Craighead (ibid.) and Harding (1976) documented grizzly bears incorporating bedding materials into day-beds where they rest near dens immediately after emergence in the spring. Female polar bears are typically lethargic and remain in or very near dens during autumn, so despite the seasonal difference a similar use of bedding material is possible.

3.4.2 Distribution

The distribution of dens and pits located during these surveys was consistent with that described by Stirling et al. (1977) and Derocher and Stirling (1990). Dens on lakeshores predominate in the sample: however these dens may be more visible than dens along the more heavily-vegetated riverbanks, so this difference may not reflect a preference for lakes over rivers and creeks. The distribution of dens, pit-dens and pits among habitat types reveals clear associations. Pits were found in all habitat types except spruce forest and unvegetated areas, suggesting that habitat type may be less important than other characteristics such as relief, exposure or proximity to water. For example, three pits I found occupied by two adult males were located in the intertidal zone on a bed of wave-deposited kelp approximately 0.5m thick. Such a location could only be intermittently occupied. This is consistent with a hypothesis of Schweinsburg (1979), who described bear tracks in the high Arctic leading to pits dug in snow, and suggested that the pits were temporary resting sites during travel. In contrast, dens and pit-dens were typically found on banks with lichen tundra above and water or wetland below. Doutt (1967) and Jonkel et al. (1972) reported earth denning in sand and gravel ridges, as well as in peatlands. In the study area, peat banks and coastal beach ridges are the only relief, and bears exhibited a definite tendency to dig in such areas. I found only pits associated with beach ridges. This may be because beach ridges in the study area have no shrubs or trees which could reinforce the ceiling with roots, unlike the sites described by Doutt (1967) on South Twin Island in James Bay. Published photographs indicate that those dens have some willow cover above them. Inland beach ridges in the study area do not appear to be used for denning. These sites are characterized by Dredge and Nixon (1992) as being unsorted deposits 1-2m deep and underlain by clay. The area is forested and much of these deposits are overlain by peat (ibid.), which may be present in too shallow a layer to dig a den in. Investigation of this area, and comparison of tree cover, soil characteristics and permafrost depth with known denning areas would be useful. There are large alluvial deposits along the Knife River north of Churchill, where bears have rarely been observed, and have never been reported to den. Dredge and Nixon (1992) describe this area as similar to the deposits along the Owl and Broad Rivers, both of which are heavily used for denning. This suggests that female bears could find a den and avoid males by going north of the study area as well as they would inland. Bears are usually deposited on shore in the study area by melting sea ice (Stirling et al. 1977), and by travelling directly inland females may encounter fewer bears than if they were to travel north along the coast. However, some bears come ashore south of the study area and subsequently move northwards along the coast so such a trip is possible.

South of the study area permafrost is discontinuous; the permafrost features that provide relief in the study area: banks, ice-pushes and palsas, become scarcer. Bears in Southern Hudson Bay and James Bay travel farther inland and are more dispersed than in the study area (Jonkel et al. 1976, Prevett and Kolenosky 1983, Stirling et al. 1977), suggesting that they may select permafrost features for denning in those areas as well. In these areas pit-dens appear to be the most common structures (Jonkel et al. 1976). Although this could indicate that polar bears denning east of the Nelson River have different requirements for a den, that is unlikely since bears do move between this area and the main denning area. More probably this reflects a difference in the availability or suitability of substrate for excavating and maintaining deep dens.

The nature of permafrost may explain why pregnant females bears move inland in the summer rather than remaining on the coast and waiting for cooler temperatures to travel. Digging is energetically expensive, and it would be much easier to dig into the thawing peat of the thermally active surface layer than to start later in the autumn when it is frozen solid. Craighead and Craighead (1972) found that grizzly bears digging in unfrozen soil took at least three to seven days to excavate a den of a similar size to those I observed, which indicates that a significant effort must be involved in digging these dens. I observed few unoccupied fresh dens and comparatively more unoccupied fresh pits & pit-dens. This suggests that these three types of excavation probably involve different levels of investment, with dens having the greatest and pits the least. Maximum thaw depth is typically encountered during late August (Dredge and Nixon 1992). Any weakness in the den structure would be most evident when it is thawed, and this could give adequate time to dig another den at minimal cost should it be required. Once the den has been dug, it would offer cooling from shade and permafrost contact during the summer, and wind shelter during the autumn when temperatures drop, but snow has yet to accumulate.

3.4.3 Use of dens,pit-dens and pits by polar bears

Bears of all age and sex classes used earth dens and pits. Subadult males and females with COYs did not use pit dens. The great majority of bears using pit-dens and dens were lone adult females. The incidence of females with young, subadults and adult males is roughly equal, and minor in comparison, suggesting that den use by these other classes may be simply opportunistic. Most bears using pits were adult males. Since males tend to occupy coastal areas without permafrost, digging dens is not an option, and pits in such areas appear to be in sites that provide adequate cooling through wind exposure.

There was a difference in the timing of peak use of dens and pits: 55% of bears using pits were captured in August, and 65% of bears using dens were captured during September. This may reflect temporary use of pits while initially travelling inland, but data on the movements of these bears is unavailable. This may be an indication of the importance of pits for resting and thermoregulation. On average, the warmest months of the year are July and August, and most bears are only just returning to shore in late July. Use of pits seems to decline sharply after September, when the weather becomes colder and windier. One possible bias in these data arises from the timing of the field seasons. Typically, mark and recapture studies have been conducted between late August and early October, and so more captures of bears in dens, pits or pit-dens would be recorded for this period, possibly over-estimating occupancy then, and underestimating occupancy earlier and later in the season. Nevertheless, it appears that the greatest use of pits occurs prior to that of dens.

Earth dens may also provide some security from predators: conspecifics, humans and wolves (*Canis lupus*) (Ramsay and Stirling, 1984). Bears would be more difficult to detect in dens than in the typically open landscape of the study area, and defence would be easier from inside a den. On several occasions during each field season, some lone adult females could not be induced to leave their dens.

3.4.4 Conclusions

The physical layout of these dens is not unique to this population of polar bears, nor even the species, though the timing and location of denning is. This suggests that earth denning is only a slight modification of an extant energy conservation strategy, brought on by seasonal environmental conditions. Dens, pit-dens and pits probably have a role in thermoregulation. Dens offer shade, wind shelter and contact with permafrost. Earth dens were significantly cooler than ambient temperatures and exhibited less temperature variation than was measured externally: the relatively cool, stable environment inside earth dens probably helps bears thermoregulate more efficiently and so conserve energy. Pit-dens also appear to provide these opportunities. Pits are used most during the warmer early portion of the on-shore season, apparently as cool resting sites. Dens provide escape from biting insects: inland pits and pit-dens do not. These benefits would apply equally to females with young, yet they rarely use dens. They may be constrained from doing so by the typically high activity level of cubs, and there may be more benefit to the cubs by allowing them to move and learn about the area, rather than be kept in a den.

Many of the benefits of denning described so far have been based on observations made during the summer and early autumn, yet earth dens seem to be occupied by female bears into the winter as well. Progesterone levels recorded by Derocher et al. (1992) suggest that implantation occurs between mid- September and mid- October, with parturition taking place between mid- November and mid- December. Early in winter and possibly in years of light snowfall, earth dens might represent the only shelter for neonate cubs, which could be critical to their survival (Blix and Lentfer 1979). If this is the case, the role of earth dens as maternity dens could be more important than simply for thermoregulatory or any other benefits gained during the summer and autumn.

Table 3.1. Average dimensions of earth dens (cm) (standard deviations are in parentheses).

Age	Entrance Length	Entrance Width	Entrance Height	Chamber Length	Chamber Width	Chamber Depth	Chamber Height
Fresh	124 (56)	96 (21)	66 (15)	130 (15)	141 (31)	204 (80)	89 (13)
n	6	16	16	4	17	17	17
Old	215(124)	148 (75)	56 (10)	183(176)	155 (55)	298(149)	84 (21)
n	4	14	7	6	20	19	17

Table 3.2. Average dimensions of pit-dens (cm) (standard deviations are in parentheses).

Age	Entrance Width	Entrance Height	Back Width	Depth	Back Height
Fresh	104 (24)	80 (22)	139 (52)	112 (47)	89 (24)
n	19	19	33	29	30
Old	121 (37)	78 (15)	90 (30)	118 (67)	66 (14)
n	4	4	7	7	6

Table 3.3. Average dimensions of pits (cm) (standard deviations are in parentheses).

Age	Length	Width	Depth
Fresh	156 (77)	140 (65)	16 (20)
n	32	32	32
Old	125 (50)	121 (46)	35 (27)
n	15	15	15

Table 3.4. Distribution of habitat types associated with dens, pit-den and pits.

	Association	Beach Ridge	Intertidal	Wetland	Lichen Tundra
Den	Above	0	0	5	36
	Below	0	0	36	4
Pit-Den	Above	0	0	9	31
	Below	0	0	37	1
Pit	Surrounding	19	3	6	12
	Below	0	0	16	1

Table 3.5. Age, sex and reproductive status of polar bears in dens for each month.

Month	Lone Female	Female w. COY	Female w. Yrlg	Female w.Unk. Young	Subadult Female	Adult Male	Subadult Male	Σ
July	0	0	0	0	0	0	0	0
August	7	0	0	2	1	3	1	14
Sept.	85	2	1	15	3	16	5	127
Oct.	36	2	1	0	3	1	0	43
Nov.	8	0	0	1	2	0	0	11
Σ	136	4	2	18	9	20	6	195

Table 3.6. Age, sex and reproductive status of polar bears in pits for each month.

Month	Lone Female	Female w. COY	Female w. Yrlg	Subadult Female	Adult Male	Subadult Male	Σ
July	1	0	0	2	9	0	12
August	3	5	1	2	20	4	35
Sept.	0	2	0	1	10	0	13
Oct.	0	0	0	0	3	0	3
Nov.	0	0	0	0	1	0	1
Σ	4	7	1	5	43	4	64

Figure 3.1. Schematic diagram of a typical earth den (top view), showing the location of horizontal measurements taken.

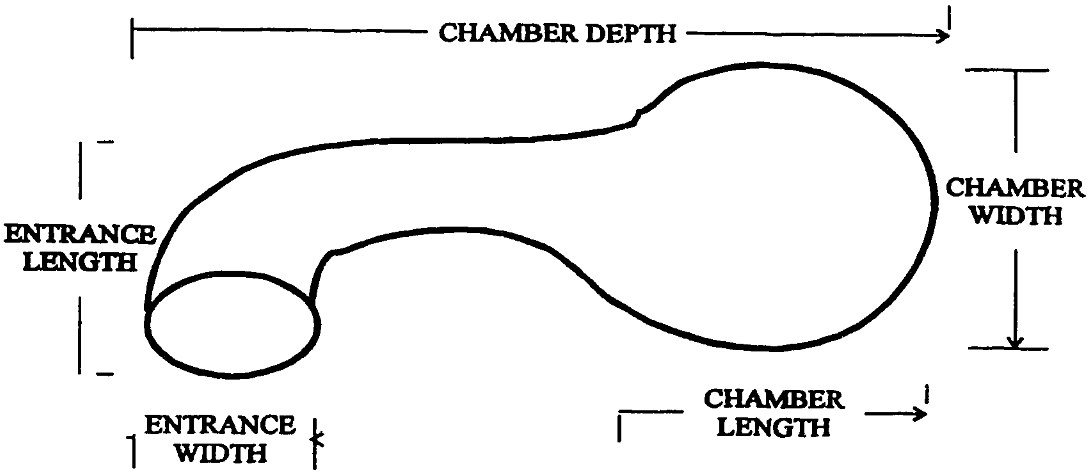

Figure 3.2. Schematic diagram of a typical pit-den in three dimensions, showing the location of measurements taken.

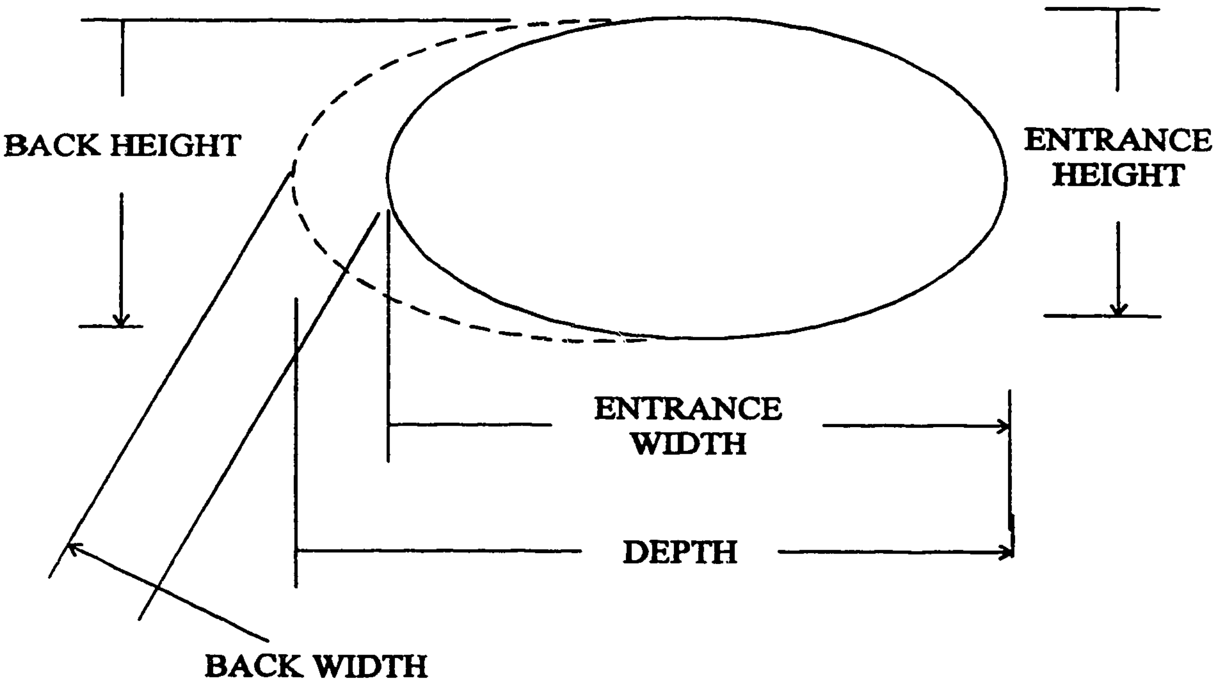

Figure 3.3. Map of study area, showing location of 41 surveyed dens, 43 pit-dens and 48 pits.

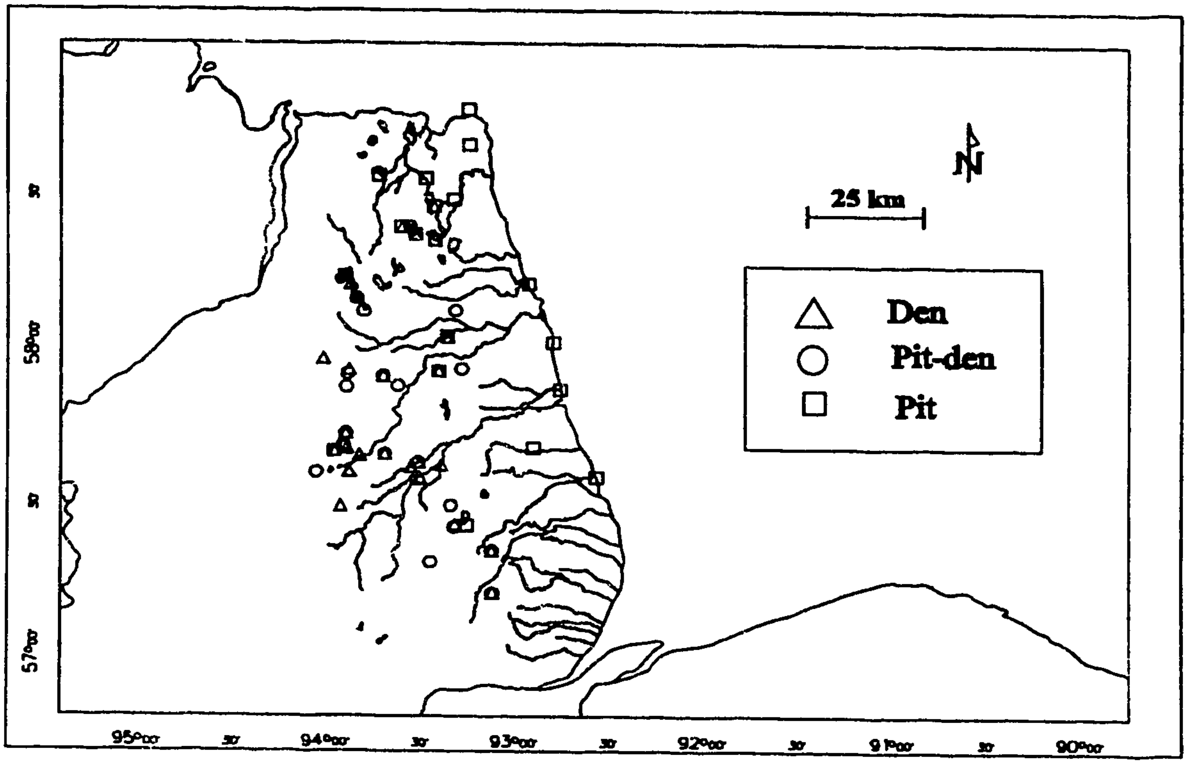

Figure 3.4. A typical earth den.

Figure 3.5. A typical pit-den.

Figure 3.6. A typical pit.

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4. SUMMARY

4.1 Some limitations of habitat selection tests

Determining an animal's preference for a resource such as habitat by testing the animal's use versus the habitat's proportional availability has limitations, several of which have been discussed in Chapter 2. An additional criticism of the level of understanding which may be gained is that such studies do not address the mechanisms driving habitat selection. Asking this different and logically subsequent question is necessary to gain more than a correlation between animal locations and habitat types (Hobbs and Hanley 1990; Schooley 1994). Most studies assume that habitat types identified *a priori* have ecological relevance to the study animal, and that location in a habitat type, or in association with a feature infers a causal relationship (Aspinall and Veitch 1993). Often this assumption is addressed implicitly, since habitat types defined by vegetation often incorporate differences in food quantity or quality. Hutto (1985) cited numerous examples supporting the fundamental relationship between food distribution and the use of space by animals. Studies should explicitly test the relationship between an individual, population or species and its chosen habitat. In this investigation it is apparent that there are more factors than food availability to consider.

The terms "selection" and "use" are often used interchangeably in investigations of animals' use of space and resources, and both have unfortunate connotations. Selection implies a conscious choice by individuals: something difficult to establish (Hutto 1985). Use can refer either to consumption of a resource or to the occupation of space in an environment. Avoidance, defined as selection against a habitat type can be difficult to separate from unavailability or indifference. No investigator can be sure that he or she has accurately described how much and of which habitat types the animal perceives to be available. Only in some cases is this obvious, such as where territories are clearly defined, or where certain areas are devoid of needed resources or geographically separated. Johnson (1980), McLellan (1986) and Porter and Church (1987) have demonstrated the importance of correctly determining availability: the denominator of the selection equation. Availability of a habitat type may vary with the spatial scale of the investigation, and this can alter whether or not a habitat type is considered to be selected for, against, or not at all (a random distribution). An animal may select an area with a predominance of one habitat type because of the abundance of that habitat type at that particular location, and still not show use of that type significantly greater than availability within that area. Simultaneous analysis on a broader scale would reveal this important distinction. This also emphasizes the point that both use and availability of habitats are only relative quantities, and any conclusion from their comparison may not be correct at a different scale (Porter and Church 1987; Thomas and Taylor 1990; Aebischer et al. 1993): as seems to be the case in this study.

4.2 Summary

Overall, different age and sex classes of polar bears show distinct differences in their habitat preferences. Generally, adult males, lone and presumably non-pregnant adult females, and subadults of both sexes select dry coastal habitats such as beach ridges. Inland, adult females with and without young select riverbeds and lakeshores within an area dominated by lichen tundra. A greater proportion of subadult males than females remain on the coast, where they select beach ridges. Those subadults that travel inland, primarily females, select lichen tundra and lakeshores, but are found in all habitat types.

The distribution of bears on shore seems to be influenced by the same social constraints that operate during the rest of the year, mainly avoiding dominant conspecifics which are most often adult males. Most female polar bears travel farther inland than is necessary to avoid adult males, but a lesser distance than they travel while hunting on the sea ice (Derocher and Stirling 1990). This investment in travel could have several benefits: it puts lone female bears in an area where earth dens are already available or may be constructed for thermoregulating, permits opportunistic feeding on berries, and further reduces the likelihood of encountering any bears except other females.

Mattson (1990) proposed that female bears of several species share the common strategy of using unoccupied and often less productive habitat to increase the security of their young. Nonetheless, Wielgus and Bunnell (1994) observed that the greatest overlap between male and female grizzly bear (*Ursus arctos*) ranges occurred during the berry season, when that resource would be important to both sexes. It seems unlikely that the small berry crops measured in the study area could contribute significantly to the energy balance of this population of polar bears. Food production does not appear to be a measure of habitat quality for any age or sex class of polar bears in the Hudson Bay Lowlands. Sampling over more years should be undertaken since annual variability in berry crops could indicate otherwise, at least during some years.

Nutritional factors other than the availability of terrestrial foods could also influence habitat selection. There can be significant year-to-year variation in the date when bears come ashore: the longer they remain on the sea ice, the more opportunities they will have to hunt seals. Every seal represents a significant nutritional gain (Stirling and McEwan 1975); consequently, bears may have less need of supplemental food while on shore if they have greater hunting success beforehand. Conversely, reduced hunting success, or less time available to hunt might demand that bears forage to survive the onshore season.

Selection of habitats for thermoregulatory reasons, e.g willow thickets or spruce clumps for wind shelter may occur, but I have been unable to address this adequately due to the limitations of my mapping techniques. However, pregnant females bears strongly select riverbeds, creeks and lakeshores inland, habitats that provide suitable denning sites. The use of dens and related structures seems to be at least partially for thermoregulation. Earth dens and pit-dens are primarily occupied by pregnant females, but are not used for parturition. Both structures offer shade, wind shelter and contact with permafrost, all of which would help a bear thermoregulate and conserve energy. Dens would also provide relief from biting insects and security from predators. Additionally, in years of light snowfall, earth dens would be the only shelter available for neonate cubs. Pits are generally occupied by adult males and used more during summer than autumn, most likely as temporary resting places in exposed locations.

Dens, pit-dens and pits dug by polar bears resemble structures created by other bear species, but how similar the functions are among species is not known. For instance, pit-like structures made by black bears are not located in exposed places (Mollohan 1987), so wind exposure may not be desirable, whereas it appears to be for polar bears resting in pits. The function of polar bear earth-dens requires further clarification before interspecific comparisons could be anything but speculative. These structures seem to result from an adaptation of a highly conserved behaviour, digging dens of a specific shape, to the uncharacteristic, but locally abundant, frozen peat substrate. Quantifying the energy conservation potential of dens, pit-dens and pits would provide more conclusive information on the ecological roles of these structures.

The patterns of habitat selection which I have described pose interesting questions, and suggest some directions for further study. Foremost, habitat selection by polar bears inland needs to be examined at a finer geographic scale and a longer temporal scale to reliably test several of the hypotheses which I have proposed. Quantifying the benefits of terrestrial feeding is required: specifically, how much nutritional value could be gained from berries by those bears that do feed on shore. An intriguing, though logistically daunting, topic of investigation is the extent and possible benefit of individual variation in habitat selection and behaviour by polar bears. Some individual bears appear to have different patterns of habitat selection than would be expected for their age and sex class and only some bears feed while on shore, indicating that they may employ different energy conservation strategies. Examining the variation of strategies among individual animals could provide information on how important energy conservation is to bears during the on-shore season, and how they can best achieve that. Equally challenging, further study of intraspecific interactions inland could clarify the role of conspecific avoidance in polar bear social behaviour. Though infanticide has been proposed as a mechanism for population regulation in bear species, evidence of intraspecific killing is sparse (Taylor et al. 1985). Some adult males are found in the denning area where the majority of females with young are; comparisons of the activity and behaviour of these males with those on the coast could show whether they are resting or actively pursuing other bears. More significantly, examining whether or not these bears affect the distribution of others could demonstrate how much infanticide, or just the perception of the threat of it, influences habitat selection by female bears with young. Though annual variation in sea ice conditions and seal availability in Hudson Bay undoubtedly affects the condition of polar bears coming ashore from year to year, more understanding of these relationships is required. This would increase our understanding of the mechanisms and ecological significance of energy conservation to polar bears while ashore in the Hudson Bay Lowlands.

The study area seemed to offer a situation where alternative hypotheses of habitat selection could be tested by examining each age and sex class of bear separately, and considering the constraints on, and likely motivations of, each class. However, I acknowledge that direct measurements of fitness would ultimately be required for conclusive explanations of habitat selection. Polar bears in the Hudson Bay Lowlands provide an example of an otherwise solitary species occurring at high densities during a season when competition for mates and food is non-existent. This investigation suggests that gaining understanding of habitat selection is a complex process, in which several mechanisms, apparently both social and energetic, may influence different portions of a population of animals in different ways.

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APPENDIX A. CLASSIFICATION AND MAPPING OF TERRESTRIAL HABITAT USED BY POLAR BEARS IN THE HUDSON BAY LOWLANDS .

A.1 Introduction

The objective of this paper is to quantitatively describe and map habitat types available to polar bears during the on-shore period in the Hudson Bay Lowlands. Dredge (1992) and Dredge and Nixon (1980, 1986, 1992) described the physical geography of the study area in detail. Biotic communities in the study area, and similar regions of the Hudson Bay Lowlands are described by Shelford and Twomey (1941), McClure (1943), Ritchie (1957, 1960, 1962), Sjörs (1959), Sims et al. (1979, 1982, 1987), Pala and Boissoneau (1982), Pala and Weischet (1982) and Rewcastle (1983, 1986). The *Studies on lichen-dominated systems* series of papers by K.A. Kershaw and others provides comprehensive details on phytosociology, lichen ecology and succession in the Hudson Bay Lowlands (see for example Neal and Kershaw (1973), Kershaw (1974, 1977a) and Pierce and Kershaw (1976)).

This investigation required identifying the distribution of polar bear habitat types at a finer scale than has been conducted to date. The maps of Ritchie (1962) are 1: 1 000 000 scale, and have a minimum map unit approximately 1.5 km^2. Additionally, his map units are not homogenous habitat types, but illustrate the proportion of different plant communities within them.

Bears seem to be associated with specific vegetation types and features, such as the treed edges of creeks and lakes (Stirling et al. 1977). Because there is less than

100m vertical relief in the study area topography seemed unlikely to influence polar bear distribution, except at the localized scale discussed below. Although bears feed little while ashore, some feeding on berries does occur, especially by females with dependent young (Derocher et al. 1993). I wished to include an assessment of the possible influences of berry production on habitat selection, which necessitated a vegetation-based approach. However, the distribution of polar bear dens was reported to be dependent on the presence of permafrost and specific geographic features- riverbanks, creeks and lakeshores (Jonkel et al. 1972), so landform and soil needed to be considered as well. An integrated system that includes these three elements is a biophysical land classification (Lacate 1969), and several authors have examined the associations between landform, soil and plant community in the Hudson Bay Lowlands (Ritchie 1962; Dredge and Nixon 1986; Sims et al. 1987). Consequently I undertook a habitat classification focusing mainly on vegetation analysis and how that indicates other associated conditions.

A.2 Materials and methods

A.2.1 Habitat classification

Field surveys of plant communities were conducted from August 24 to September 1, 1992 and August 25 to September 14, 1993. I examined 66 sites in 1992 and 92 sites in 1993 throughout the study area (Figure A.1), during polar bear mark-recapture flights which were part of ongoing research by the Canadian Wildlife Service. Although flights were conducted with the primary goal of locating bears, I included sites where bears were not found to reduce bias, and at least five sites were located in each visually distinct plant community. Sites were located with a Garmin GPS-100 receiver (Garmin Corp., Lenexa, KS). Sites were circular, measuring 300m^2 and delineated with a plot cord from a fixed central stake. On each site I recorded modified Domin-scale scores of plant species abundance (Kershaw 1977b) on 16 equidistant 30cm x 30cm quadrats per site. The quadrats were aluminum frames with nylon line strung at 10cm intervals, describing 9 squares. Scores ranged from 0 to 9, corresponding to the number of squares each species occurred. If an individual plant was found in more than one square, it was so counted. Plant species as well as lichens were counted and voucher specimens were collected when necessary for identification. Identifications were made from Johnson (1987) and by comparison with herbarium specimens at the Churchill Northern Studies Centre. *Carex* sp. and other sedges, mosses (except *Sphagnum* sp. and "tuft moss" *Tomentyphthum nitens*), crustose lichen species on rocks, unidentifiable *Salix* sp., and unidentifiable grasses were not separated beyond that description. On each site I recorded aspect, landform type and height, permafrost depth, the presence of water, potential cover for bears, and trees. In 1992 and 1993, I examined 34 sites and 2 sites respectively where species scores were not recorded: sites in homogenous areas were used for identifying training sites for habitat classification.

Scores from each year, and both years together were analysed with TWINSPAN (Hill 1979) to determine differences among plant communities, to describe indicator species and to point out potential year-to year bias in our site selection. TWINSPAN is a FORTRAN program which classifies multivariate data (plant species abundance) into an ordered two-way table (species and site). Five pseudospecies, which permit TWINSPAN to make divisions based on relative abundance levels as well as presence/absence of plant species, were specified in each run and no weighting was applied to any. The divisions of plant communities provided by TWINSPAN, although quantitative, are not absolute, nor do they necessarily correspond directly to habitat types. TWINSPAN yields eigenvalues, which are ratio-scale measures for comparison of the strength of each division. I interpreted habitat types from these divisions with the following criteria:

1. At least five sites had to be present in each division.
2. The maximum number of divisions was set at 15, but only differences observed within the first four divisions were used, since finer divisions were often made on the basis of less than five sites. This satisfied the previous criterion, and since this was a broad scale investigation, it prevented an unwieldy number of possible habitat types from being identified.
3. Habitat types had to be readily recognizable in the field, especially by personnel without a botanical background. TWINSPAN classifications provide indicator species for each division which may be used to identify habitat types in the field.

A.2.2 Habitat mapping

Satellite imagery was the most cost- and time-effective way to map habitat types consistently. LANDSAT TM products, with 7 spectral bands and 30m x 30m resolution have been widely used for habitat mapping (e.g. Craighead and Craighead 1991; Ferguson 1991; Matthews 1991; Aspinall and Veitch 1993; Stoms et al. 1993). Each spectral band of an image is a duplicate of the same scene, and is composed of relative reflected radiance values measured from a different portion of the electromagnetic spectrum (Simonett et al. 1983). However, the full multispectral data set is expensive and large; approximately 300MB of disk space would have been required for the study area. We considered two alternative methods to full multispectral classification: manual digitizing or raster-scanning of aerial photographs or film-format satellite images. Manual digitizing of cover types to the level of detail required would have been prohibitively time consuming. Carstensen and Campbell (1991) evaluated the spatial accuracy and precision of a desktop scanner and felt that it was sufficient for many cartographic applications. Frank and Thorn (1985) demonstrated that scanned data could be used to map alpine vegetation accurately. They scanned a portion of a 1:50 000 colour infrared aerial photograph to map approximately 3 km^2 of mountainous terrain. Given the size of our study area, approximately 150 km by 100 km, we postulated that we could obtain acceptable resolution and accuracy from scanning film-format LANDSAT TM images. These scanned images would not only be less expensive, but, we hoped, would also yield smaller data sets which could be manipulated more readily with the computing resources available.

Cover types can be identified on a digital image through classification. Image classification involves algorithms which group the pixels that make up an image into discrete classes. Each class represents a different cover type (habitat type) and is subsequently shown in a thematic map by a single colour value or theme. Many classifications can be improved through image enhancement prior to classification (ibid.). An unsupervised classification based on radiance values alone is objective, but often inaccurate when compared to field survey results. A supervised classification, in which the algorithm incorporates information about what actually exists at surveyed locations, or training sites, will usually be more accurate (Schowengerdt 1983). To be used with any degree of confidence, classifications require an accuracy assessment to be done *a posteriori* (Story and Congalton 1986).

I obtained 1: 1000 000 scale colour composite film copies of two sequential cloud-free geocoded and radiometrically corrected (CAL 2) LANDSAT Thematic Mapper 5 (TM) frames in bands 3,5,4 (Radarsat Int., Richmond, B.C.) dated 11 July, 1990. I chose this band combination for it's resemblance to colour infrared aerial photography, commonly used for vegetation discrimination. I scanned the relevant portions of these images at 300 dpi in a Hewlett-Packard Scanjet II with no enhancement, and saved them as 24-bit colour uncompressed TIFF 5.0 format files.

Image processing and classifications were done using PCI-Works (PCI Inc., Richmond Hill, ON) on an IBM RS6000 workstation. I merged the two images with three common ground control points and colour balanced them. I geographically referenced the composite image with a first-order transformation and nearest-neighbour interpolation derived from five ground control points that had been previously located by GPS. For the classification, I chose training sites that were located within homogenous patches and larger than 500m across. The area and number of training sites in each habitat type is given in Table A.1.

I applied a maximum likelihood classification to the image, with a hand-digitized mask removing most of the ocean in the image from classification. I merged rock and urban classes because of the small sample of training sites and called this class "unvegetated" due to the relatively low abundance of vegetation compared to the highly visible substrates- bedrock, developed areas and gravel.

Initially, class separation was poor between spruce forest and wetland, lichen tundra and beach ridge, intertidal and unvegetated, and water and wetland. To improve class separation I masked the coastal and inland areas of the image, and the same classification applied to each separately. The landscapes in the two areas differ significantly: coastal areas have no peat deposits, and the few beach ridges inland are heavily forested, not bare. The shape of lakes differs: round thermokarst lakes are only present inland on peat, lakes in the coastal areas form between beach ridges and are mostly linear. I used these criteria to locate the mask line. I then merged the two classified images to create a single map. Incongruities across the coastal/inland mask line were noted. In the field I never observed patches of lichen tundra abutting patches of unvegetated/beach ridge- as was shown on the classified image, and several known areas of spruce forest were misclassified as fen. I adjusted the mask line correspondingly, and repeated the classifications, assigning unclassified pixels to the most likely class.

To assess the accuracy of the supervised classification, I digitized 266 points from a 1:250 000 NTS topographic map which I annotated during flights in 1993. I prepared an error matrix of these reference points of known habitat type against the thematic map using the ERRMAT routine of IDRISI 4.1(Eastman 1992). The ERRMAT routine produces a matrix is a contingency table comparing the classified image to the series of known reference points (Story and Congalton 1986).

A.3 Results

A.3.1 Habitat classification

I observed 103 species of plants and lichens, which are listed in Appendix B. From the TWINSPAN analysis I identified 8 habitat types.

1. Beach Ridge (Figure A.2):

Beach ridges are marine deposits of gravel and sand up to 5m high parallelling the shoreline; they may be several km long. Extensive areas are not vegetated, or sparsely so. Recognizing that beach ridges are extensive inland in the Hudson Bay Lowlands (Neal and Kershaw 1973), I use this term to refer to the habitat type made up of the most recent ridges along the intertidal zone, and dominated by *Elymus arenarius*. Shelford and Twomey (1941) identified this as a distinct plant community. *Hordeum jubatum*, *Honckenya peploides*, *Gentiana propinqua*, and *Stellaria* sp. are common.

2. Coastal Tundra (Figure A.3):

Coastal tundra includes inland beach ridges with developed plant communities, and the highest portions of the alluvial deposits at the mouth of the Broad and Owl Rivers. Bare gravel substrate is widespread. *Dryas integrifolia* is predominant, as was noted by Shelford and Twomey (1941) and Pierce and Kershaw (1976). *Salix reticulata*, *Arctostaphylos rubra* and *A. alpina*, *Bartsia alpina*, *Cetraria* spp., and *Rhododendron laponicum* are common. *Shepherdia canadensis* occurs in sheltered sites.

3. Wetland (Figure A.4):

This habitat type is widespread throughout the study area, and its name is a relative term, as most of the study area is considered to be wetland by Sjörs (1959) and Zoltai et al. (1988). Here, it refers primarily to fens, and also to extensive sedge meadows among peat polygons, which are acidic, nutrient-poor bogs. In fens, standing water is extensive and mineral-rich, and peat is shallow or non-existent. *Larix laricina*, and *Scirpus caespitosus* predominate. Ribbed fen, or string and flark features (Sjörs 1959; Seppälä and Koutaniemi 1985) are common, especially in the southeast of the study area.

4. Coastal Wetland (Figure A.5):

This is a species-rich and structurally heterogenous habitat type including all plant communities found in poorly drained areas between beach ridges. Kershaw (1974) described a sequence of succession in such sites, as hummocks form in wet sedge meadows, grow and eventually become colonized by heaths, shrubs and lichens. *Scirpus caespitosus* and *Carex* spp. predominate in meadows, and hummock-colonizing plants included *Myrica gale*, *Petasites sagittata*, *Rumex occidentalis*, *Stellaria* sp., *Pyrola grandiflora* and *P. secunda*. We were able to identify *Salix planifolia*, *S. arctophila*, *S. lanata*, *S. candida*, *S. pedicellaris*, and *S. athabaskensis* in such areas. Willow thickets found inland around lake and river edges are similar to this habitat type, often forming dense thickets up to 2m tall.

More extensive sampling of coastal wetlands in 1993 indicated that brackish intertidal wetlands were quite different from those areas. *Puccinellia phryganodes* dominates. *Salix brachycarpa*, *Potentilla egedii*, *Senecio congestus* and *S. indecorus*, *Carex* spp., *Ranunculus* sp., *Chrysanthemum arcticum*, *Hippuris* sp. and unidentified grasses are also present. In these areas we observed extensive, heavy grazing by lesser snow geese (*Chen caerulcscens caerulescens*)- often all plant material was grazed to less than 1cm height. Vegetation was often sparse, and bare mud common.

5. Lichen Tundra (Figure A.6):

This habitat type is extensive inland, and is dominated by polygonal peat plateaus (Zoltai and Tarnocai 1975). The peat deposits appear thick: thermokarst lakes are common and we typically measured an active (unfrozen surface peat) layer of 30cm. This habitat type has extensive local relief, with peat hummocks: *Ledum groenlandicum*, *Rubus chamaemorus*, *Empetrum nigrum*, *Vaccinium uliginosum*, *V. vitis-idaea* and *Tomentyphthum nitens* are common on the top and sides of the hummocks. Lichens, mainly *Cladina stellaris*, *C. mitis*, *C. rangiferina*, *Alectoria ochroleuca*, and *Cetraria nivalis* are also conspicuous. *Scirpus caespitosus*, *Carex* spp., *Sphagnum fuscum* and other mosses, *Salix* spp., *Betula glandulosa*, *Oxycoccus microcarpus* and *Andromeda polifolia* are found in the intervening wet depressions.

6. Spruce Forest (Figure A.7):

Stands of *Picea mariana* are found along river and creek beds and inland of most of the lichen tundra. Smaller patches and individual trees of *Picea mariana* and *P. glauca* are widespread on peat and on alluvial deposits (also *P. glauca*) on the Churchill, Broad and Owl Rivers and on the Twin Lakes and Marantz Lake kames and Norton Lake esker. Tree canopy closure varies considerably, from near closure in some riverbeds and on glacial kame deposits to open woodland on peat polygons.

A lichen understory, predominantly *Cladina* spp., was common in upland stands similar to that described by (Kershaw 1977a), moss understory was found along rivers. *Ledum groenlandicum* and *Vaccinium vitis-idaea* are also found in the understory.

7. Rock Outcrop:

Bare rock is found in a limited area to the east of the Churchill townsite. These outcrops support a varied plant community, as observed by Rewcastle (1983), reflecting opportunistic colonization of small sheltered microhaitats in rock crevices. A clear division of this plant community was only seen in the classification of 1992 data, and then only at 2 sites. I included it, despite this, because of the high visibility of the rock substrate in the field and on the LANDSAT images. Crustose lichens are common, and in crevices, *Picea glauca*, *Salix* species, *Cladina* species, *Alectoria ochroleuca*, *Empetrum nigrum*, *Arctostaphylos rubra*, *A. alpinum*, *Vaccinium uliginosum*, *V. vitis idaea*, *Rubus chamaemorus*, *Carex* sp. and mosses may be found.

A.3.2 Habitat mapping

The thematic map of classified habitat types is presented as Figure 2.1. The resolution of the final classified image had a pixel size of 155m x 155m. The average RMS error (calculated by PCI-Works), an estimate of average spatial precision, was 195m. The area of each habitat class in the study area map is presented in Table A.1.

The LANDSAT imagery purchased did not include a small portion of the southwest corner of the study area which field reconnaissance revealed was largely an open fen wetland. This area lay outside the path width of the orbit from which our images were taken. Few bears use the area (I. Stirling pers. comm.); therefore I felt that its inclusion would not be particularly informative, nor cost-effective.

In the initial image classification, only 5.6% of pixels were unclassified, and were subsequently assigned to the nearest class. This indicates that the identified classes and their spectral signatures were comprehensive. However, the results of the error assessment on the final classified image suggest that there was still significant error. The proportion of pixels correctly classified was 48%. Table A.2 presents the results of the error assessment on the classification.

A.4 Discussion

The TWINSPAN cluster analysis produced weak quantitative divisions between plant communities, however these divisions corresponded strongly to physical elements of the habitat types. Only the division demarcating the *Elymus arenarius*- dominated beach ridges (often pure *E. arenarius*) had eigenvalues consistently greater than 0.5 among years. The next prominent division separated coastal and inland plant associations, corresponding to the divide between colluvial or alluvial surface material and peatlands. This is consistent with Ritchie's (1960) primary division to separate plant communities. The high species count, and lack of typical species associations on rock outcrops prevented this habitat type from being quantitatively distinct. No division with an eigenvalue below 0.2 was used to describe habitat types. Greater sampling emphasis on wetlands in 1993 revealed 34 species which I did not observe in 1992. Consequently, I repeated the 1993 classification with those species omitted, for comparison to the 1992 data. This did not result in any different divisions within the criteria I used for defining habitat types. However, the clear identification of the *Puccinellia*- dominated marshes, surveyed mostly during 1993, indicates that this type of analysis is influenced by sampling effort.

I identified fewer habitat types than the number of plant communities mapped by Ritchie (1962) whose scheme incorporated more information about vegetation structure. The two maps are not directly comparable, since Ritchie's was based on visual interpretation of aerial photographs, and was drawn at a larger scale. However, several habitat types are similar in description and extent: lichen tundra with lichen heath, intertidal with (coastal) sedge meadow, wetland with sedge meadow and larch forest, and spruce forest with shrub and scrub forest. Inland, the habitat types correspond directly to peatland types mapped by Dredge and Nixon (1986): spruce forest- forested peat with thermokarst ponds, lichen tundra- open bog with ice-wedge polygons, wetland- fen and fen meadow with mudboils. It was not possible to quantitatively compare their map with this one, but visually, the similarity in the distribution of habitat types and peatland types is apparent.

Two components of map accuracy needed to be assessed- spatial precision and thematic or classification accuracy (Janssen and van der Wel 1994). Map resolution should not be any less than the bear location data. Two sorts of location data are used in habitat analyses (Chapter 2), each with different precision. Capture locations are recorded to the nearest minute of latitude and longitude. Individual relocations from satellite telemetry collars are assigned a location quality index by the data vendor Service Argos. I used only location class 1, 2 and 3 relocations: the standard deviation of the distribution of relocations in each class is 1000m, 350m and 150m respectively (Harris et al. 1990). This map's pixel size of 155m x 155m and RMS of 195m is equivalent to or less than any of these, and should be acceptable for such analyses.

Two complementary types of classification error are recognized: misclassification of any given pixel represents not only the of the error of commission, of placing that pixel into an incorrect class, but also the error of omission of the pixel from the correct class (Story and Congalton 1986). Omission error may be measured as the proportion of a sample of points classed as a different habitat type than they actually are. Commission error is the proportion of points of other habitat types classed as the indicated type. Both types of error must be considered in an attempt to reveal the distribution of classification errors and their causes.

Examination of Table A.2 reveals several misclassifications which could affect the interpretation of subsequent analyses of polar bear distribution. The mapped extent of several habitat types is underestimated: in increasing order, beach ridge, lichen tundra, and spruce forest. Conversely, wetland, unvegetated and water (in increasing order) are overestimated on the map. Distinct features such as beach ridges and tide flats are well differentiated. The low accuracy of the beach ridge classification is probably due to spatial, rather than classification error: beach ridges are often narrower than one pixel width. Frank (1988) found that sparse plant communities could not often be distinguished from their substrate. This is likely the case on much of the beach ridge, intertidal and unvegetated areas. However, the gravel or sand contrasts well against surrounding wet areas, and the identification of features such as beach ridges was probably not hindered by this. Good separation between lichen tundra and the other inland habitat classes in the classification algorithms initially suggested that the class was well represented. However, it was mapped less accurately than might have been expected, indicating that habitat types may be intermixed at a very fine scale in this region. Visual examination of the original images and a 1:250 000 TM band 3,5,4 image of a portion of the inland area supports this explanation. In the eastern part of the inland area, closer to the coast, areas of lichen tundra which were not drained by larger creeks or rivers had more small ponds than tundra adjacent to rivers.

This was not detected in the image scanning, and resulted in such areas being classified as wetland, which underestimated tundra and overestimated wetland. It is possible that the representation of several different wetland types by a single class might obscure relationships between bears and specific wetland habitat features, such as willow thickets (Chapter Two). Also, several known areas of 25-35 year old burned forest were classified as wetland, further over-representing this habitat type. The poor classification of spruce forest may have been due to the coarseness of the pixels relative to the typically narrow strips of forest found throughout much of the surveyed portion of the study area. Also, these areas rarely had completely closed tree canopies, and the lichen understory would have appeared similar to adjacent open lichen tundra. Indeed, each of these classes was most often misclassified as the other. This indicates the need for finer resolution to determine more accurately the use of these two habitats by polar bears.

The scanned image did not contain as much information as was in the original TM data set, since it was only a sampling of that image. For the application here, this is the major limitation of the technique, since fewer cover types could be identified from this single-band image than would have been obtained from the original three bands of TM data. For this reason, this mapping technique probably has limited application for identifying any except gross cover types which occur in large, well-defined patches. It would be worthwhile repeating the mapping procedure with a full multispectral digital TM data set. Not only would spatial precision and classification accuracy be improved, but more habitat classes could probably be described. It would be instructive to compare such a classification with the results of this work. This might be most appropriate in a finer scale investigation; perhaps of the inland denning area, and when bear locations could be determined with a corresponding degree of precision.

Table A.1. Area of habitat types in the study area, and number of training sites in each habitat type.

Habitat Type	Area (km$^{2)}$	Number of Training Sites
Unvegetated	225	4
Water	4053	12
Beach Ridge & Coastal Tundra	156	14
Intertidal	166	3
Wetland	5195	9
Lichen Tundra	5672	20
Spruce Forest	4715	12

Table A.2. Error matrix for the supervised classification. Columns represent reference data points, rows represent classified map pixels at the same locations. The bottom row is the proportion of pixels in a habitat type which were correctly assigned to that class (1- error of omission). The last column is the proportion of pixels classified to a habitat type that actually belonged in that class (1- error of commission).

	water	b.	int.	unveg.	spruce	wet.	tundra	*n*	
water	12	2	0	0	13	17	15	59	.20
beach ridge	0	4	1	1	0	5	0	11	.36
inter-tidal	0	1	3	0	0	0	0	4	.75
unveg-etated	0	2	0	4	0	4	0	10	.40
spruce	0	0	0	0	12	0	15	27	.44
wetland	2	4	0	0	19	55	10	90	.61
tundra	1	0	0	0	24	2	38	65	.58
n	15	13	4	5	68	83	78	266	
	.80	.31	.75	.80	.18	.66	.48		

Figure A.1. Map of study area, showing location of plant community survey sites.

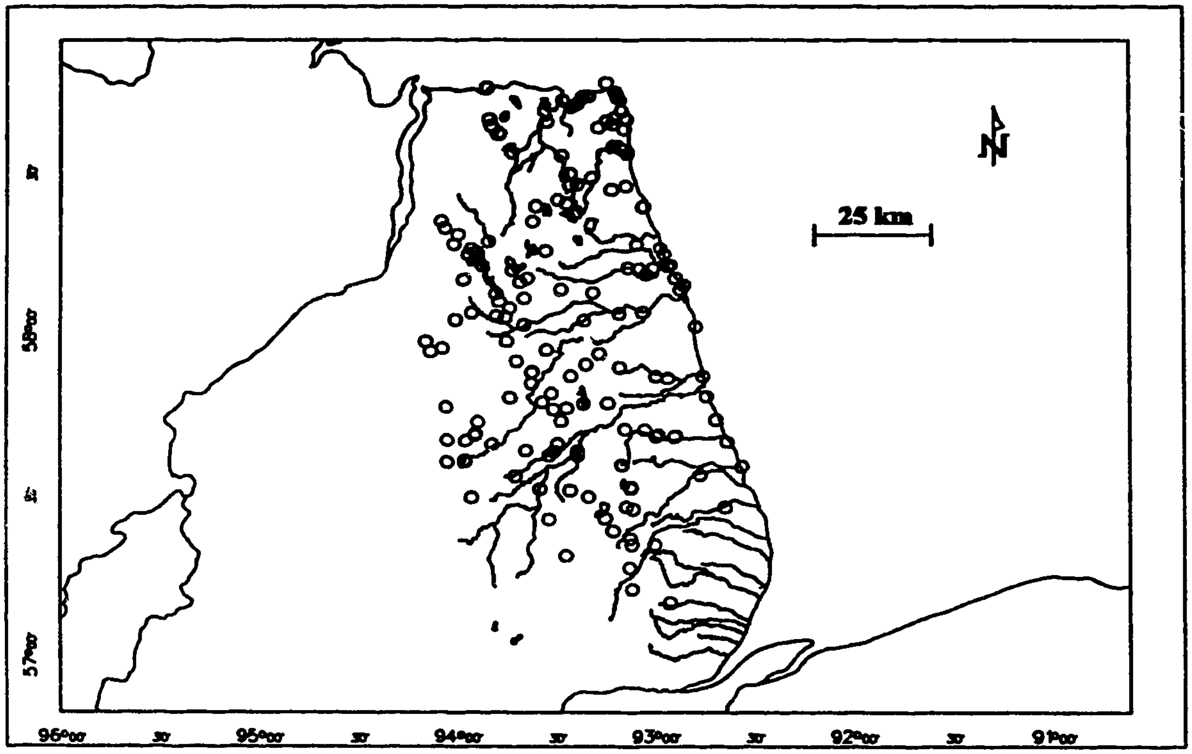

Figure A.2. A coastal beach ridge with intertidal flats visible in the upper right.

Figure A.3. A dry coastal area with alluvial deposits, representative of the unvegetated habitat type.

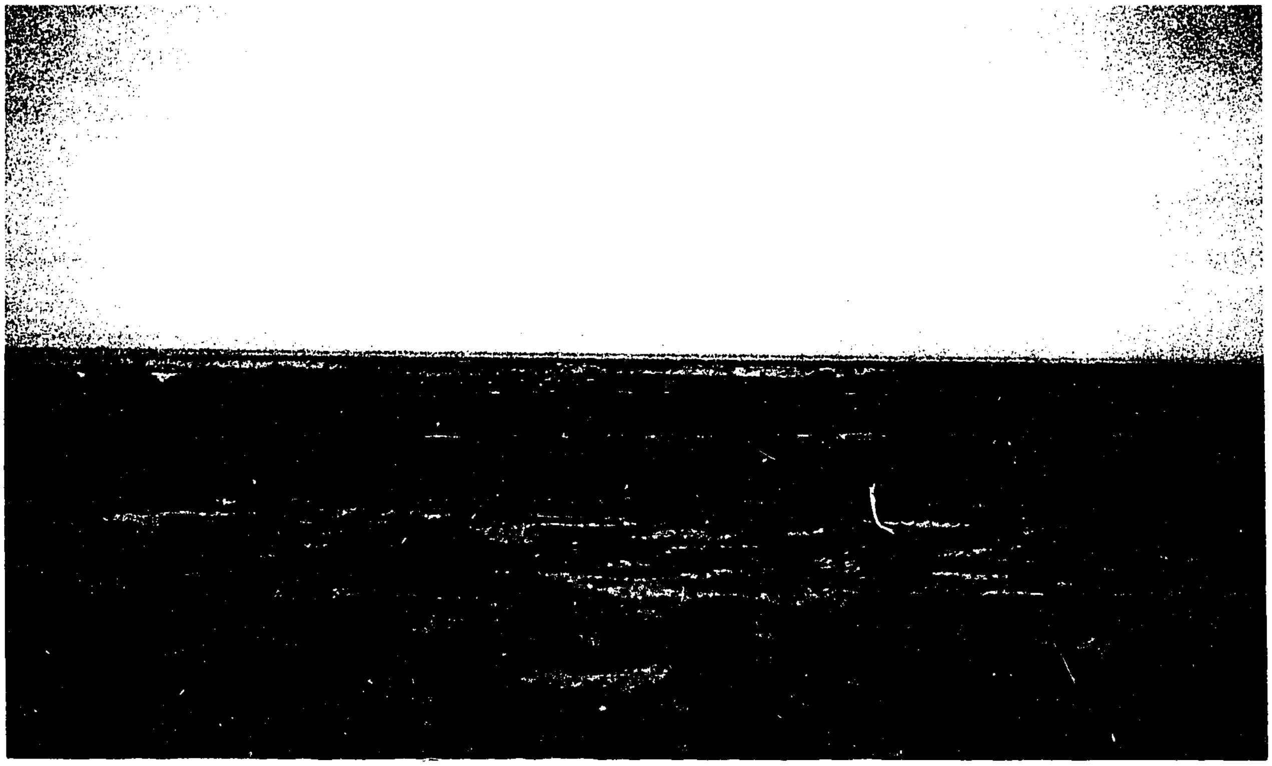

Figure A.4. Inland fen with larch, a common wetland type.

Figure A.5. Spruce forest, note the prominent lichen understory and open canopy.

Figure A.6. The lichen tundra habitat type.

Figure A.7. Habitat types of the study area, classified from scanned LANDSAT TM images.

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APPENDIX B. LICHENS AND PLANTS IDENTIFIED DURING THE 1992 AND 1993 FIELD SEASONS.

Nomenclature for lichens follows Thompson (1984), for bryophytes follows Crum (1983), and for vascular plants follows Porsild and Cody (1980).

Lichens

Alectoria sp. (Ach.)
Cetraria cucullata (Bell.) Ach.
Cetraria laevigata Rass.
Cladina stellaris (Opiz) Pouz. & Vezda
Cladina mitis Standst.
Cladina rangiferina (L.) Wigg.
Peltigera sp. Willd. em. L. Rabenh.
Spherpophorus globosus (Huds.) Vain.

Bryophytes

Sphagnum sp. L.
Tomenthypnum nitens (Hedw.) Loeske

Vascular Plants

Pteridophyta

Botrychium lunaria (L.) Sw.
Equisetum arvense L.
Equisetum variegatum Schliech.

Coniferae

Juniperus communis L.
Larix laricina (DuRoi) Koch
Picea glauca (Moench) Voss
Picea mariana (Mill.) B.S.P.

Monocotyledonae

Calamagrostis sp. Adans
Carex sp. L.

Elymus arenarius L.
Eriophorum sp. L.
Hordeum jubatum L.
Juncus sp. L.
Lycopodium sp. L.
Poa sp. L.
Puccinellia phryganodes Trin.
Scirpus caespitosus L.
Triglochin maritimum L.

Dicotyledonae

Achillea nigrescens (E.Mey.) Rydb.
Alnus crispa (Ait.) Pursh
Andromeda polifolia L.
Anemone multifida Poir *s. lat.*
Arctostaphylos alpina (L.) Spreng.
Arctostaphylos rubra (Rehd. & Wils.) Fern.
* *Artemisia hyperborea* Rydb.
Atriplex glabriuscula Porsild & Cody
Bartsia alpina L.
Betula glandulosa (Michx.)
Castilleja raupii Pennell *s. lat.*
Chrysanthemum arcticum L.
Cornus canadensis L.
Descurainia sophioides (Fisch.) O.E. Schulz
Draba alpina L.
Drosera sp. L.
Dryas integrifolia M. Vahl
Empetrum nigrum L.
Epilobium angustifolium L., *s. lat.*
Galium sp. L.
Gentiana propinqua Richards.
Geocaulon lividum Richards.
Honckenya peploides (L.) Ehrh.
Hippuris sp. L.
Kalmia polifolia Wang.
Ledum decumbens (Ait.) Lodd.
Ledum groenlandicum Oeder
Matricaria ambigua (Ledeb.) Kryl.
Menyanthes trifoliata L.
Moneses uniflora (L.) Gray
Myrica gale L.

Oxycoccus microcarpus Turcz.
Oxytropis campestris (L.) DC.
Parnassia sp. L.
Pedicularis groenlandica Retz.
Petasites sagittatus (Banks) A. Gray
Pinguicula vulgaris L.
Polygonum sp. L.
Potentilla pulchella R.Br.
Potentilla egedii Wormskj.
Potentilla palustris (L.) Scop.
Pyrola grandiflora Radius
Ranunculus sp. L.
Rhododendron lapponicum (L.) Wahlenb.
Rubus acaulis Michx.
Rubus chamaemorus L.
Rumex occidentalis S. Wats.
Salix arctophila Cockerel
Salix athabascensis Raup
Salix brachycarpa Nutt.
Salix candida Flügg
Salix lanata L.
Salix pedicellaris Pursh
Salix planifolia Pursh
Salix reticulata L.
Saxifraga sp. L.
Saxifraga aizoides L.
Saxifraga tricuspidata Rottb.
Senecio indecorus Greene
Senecio congestus (R.Br.) DC.
Shepherdia canadensis (L.) Nutt.
Smilacina trifolia (L.) Desf.
Solidago multiradiata Ait.
Stellaria sp. L.
Tofieldia pusilla (Michx.) Pers.
Vaccinium vitis-idaea L.
Vaccinium uliginosum L. *s. lat.*

Families not identified to species

Cruciferae sp.
Leguminosae sp.
Liliaceae sp.

* Tenative identification by P. Scott and Clark, 1993.

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