

**PREDICTING WATERFOWL DISTRIBUTION IN THE CENTRAL CANADIAN
ARCTIC USING REMOTELY SENSED HABITAT DATA**

A Thesis

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By

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ABSTRACT

Knowledge of a species' habitat-use patterns, as well as an understanding of the distribution and spatial arrangement of preferred habitat, is essential for developing comprehensive management or conservation plans. This information is absent for many species, especially so for those living or breeding in remote areas. Habitat-use models can assist in delineating specific habitat requirements or preferences of a species. Often coupled with geographic information system (GIS) technology, such models are frequently used to identify important habitats and to better define species' distributions.

Recent and persistent warming, widespread contaminant accumulation, and intensifying land use in the arctic heighten the urgent need for better information about spatial distributions and key habitats for northern wildlife. Here, I used aerial survey and corresponding digital land cover data to investigate breeding-ground distributions and landscape-level habitat associations of greater white-fronted geese (*Anser albifrons frontalis*), small Canada geese (*Branta canadensis hutchinsii*), tundra swans (*Cygnus columbianus*), king eiders (*Somateria spectabilis*), and long-tailed ducks (*Clangula hyemalis*) in the Queen Maud Gulf Migratory Bird Sanctuary and the Rasmussen Lowlands, Nunavut, Canada.

First, I addressed the sensitivity of inferences about predicting waterfowl presence on the basis of the amounts and configurations of arctic habitat sampled at four scales. Detection and direction of relationships of focal species with land cover covariates often varied when land cover data were analysed at different scales, suggesting that patterns of habitat use for a given species at one spatial scale may not necessarily be predicted from patterns arising from measurements taken at other scales. Inference based on species-habitat patterns from some scales may therefore lead to inaccurate depictions of how habitat influences species. Potential variation in species-environment relationships relative to spatial scale needs to be acknowledged by wildlife managers to avoid inappropriate management decisions.

Second, I used bird presence determined during aerial surveys and classified satellite imagery to develop species-habitat models for describing breeding-ground distributions and habitat associations of each focal species. Logistic regression models identified lowland land cover types to be particularly important for the species considered. I used the Receiver Operating Characteristic (ROC) technique and the area under the curve (AUC) metric to evaluate

the precision of models, where the AUC is equal to the probability that two randomly selected encounter and non-encounter survey segments will be discriminated as such by the model. In the Queen Maud Gulf, AUC values indicated reasonable model discrimination for white-fronted geese, Canada geese, and tundra swans (i.e, $AUC > 0.7$). Precision of species-habitat models for king eiders and long-tailed ducks was lower than other species considered, but predict encounters and non-encounters significantly better than the null model. For all species, precision of species-habitat models was lower in the Rasmussen Lowlands than in the Queen Maud Gulf, although discrimination ability remained significantly better than the null model for three of five species (king eider and long-tailed duck models performed no better than the null model here).

Finally, I simulated anticipated environmental change (i.e., climate warming) in the arctic by applying species-habitat models to manipulated land cover data, and then predicted distributional responses of focal species. All species considered in this research exhibited some association to lowland cover types; white-fronted geese, Canada geese, and tundra swans in particular demonstrated strong affinity toward these habitats. Others authors predict lowland cover types to be most affected by warming. Reductions of wet sedge, hummock, and tussock graminoid cover predicted in this simulation, predominantly along the coast of the Queen Maud Gulf study area and in central areas of the Rasmussen Lowlands, suggest that distributions of species dependant on these lowland habitats will be significantly reduced, if predictions about warming and habitat loss prove to be correct.

Research presented here provides evidence that modeling of species' distributions using landscape-level habitat data is a tractable method to identify habitat associations, to determine key habitats and regions, and to forecast species' responses to environmental changes.

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DEDICATION

This thesis is dedicated to my father, Greg Conkin. Your appreciation of the natural world has taken me to some amazing places, thank you.

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CHAPTER 1 GENERAL INTRODUCTION

1.1 BACKGROUND

Defining the spatial distribution of organisms and understanding factors that influence it are among the fundamental endeavours of ecology (Buckland and Elston 1993, Ormerod and Watkinson 2000). Distribution may be a product of environmental history of an area, evolutionary history of a species, population dynamics (including birth, death, and migration rates), intra and interspecific interactions, and resource requirements and physiological constraints of individuals (Bergon et al. 1990, Gaston et al. 2000). However, due to the complexity and interaction of these factors, and the range of spatial and temporal scales at which such factors operate, distributional research has been difficult beyond a theoretical framework (Gaston et al. 2000).

It is generally accepted that individuals of a species distribute themselves within their geographic range primarily in response to habitat features (Levin 1968) as nearly all subsequent decisions made by individual animals are affected by their selection of habitat (Orians and Wittenberger 1991). The selection of breeding grounds particularly is a choice that would have been influenced strongly by natural selection (Cody 1981). Habitat choices can be influenced by numerous environmental cues operating on various spatial and temporal scales. Animals have the opportunity to collect information about their surroundings as they move and birds especially have the mobility to distribute themselves across the landscape in response to the 'qualities' of the habitats that they observe (Kristan III 2007). While it must not be overlooked that other factors are involved in distinguishing where individuals may or may not occur (e.g., competition, perceived threat of predation, past experience, migration rates), habitat features are generally investigated first in explanatory research of distribution (Deppe and Rotenberry 2008).

For wildlife ecologists, defining the spatial distribution of a species is a necessary prerequisite to proper management (Williams et al. 2002), while knowledge of preferred habitats is often vital for its conservation (Gibson et al. 2004). Despite this, such information is often absent; particularly so for species with extensive ranges or those that inhabit remote areas. Contemporary methods of collecting distributional data needed to delineate species' ranges or to identify species-habitat preferences require intensive survey efforts. Yet, cost and logistic factors generally mean that intensive surveys are often limited in their spatial extent and temporal replication (Verlinden and Masogo 1997, Osborne et al. 2001).

In North America, populations and distributions of breeding waterfowl are monitored annually by systematic aerial surveys conducted through cooperative efforts of the U.S. Fish and Wildlife Service, Canadian Wildlife Service, state and provincial agencies, and non-governmental organizations (USFWS 2009). However, many important breeding areas of waterfowl and other waterbirds occur outside of the scope these surveys (USFWS 2006, Conant et al. 2007). In particular, portions of Canada's western and central arctic have been identified as significant for these birds, yet survey coverage in these areas has not been consistent. In some regions, surveys have not been conducted at all (Conant et al. 2007). Current inadequacies to our knowledge on species' distributions in this region signify a major information deficiency and limits managers to construct proper conservation plans for these species.

Correlative methods have commonly been applied to discern bird-habitat associations and are increasingly extended to map distributions at local scales. Using existing survey data, species encounters may be linked to available environmental information to ascertain preferred habitats and potentially model distributions where survey coverage has been poor (Buckland and Elston 1993). Many studies (e.g., Lyon 1983, Avery and Haines-Young 1990, Austin et al. 1996, Suárez-Seoane et al. 2002) have related bird distributions to habitats using remotely sensed data such as Advanced Very High Resolution Radiometer or Landsat satellite imagery. Until recently, high cost and limited availability has restricted the use of this type of data on regional scales. However, satellite imagery has become ever more accessible and at a reasonable expense (Osborne et al. 2001). The use of geographic information systems (GIS) has further allowed a substantial step forward in terms of the quality and quantity of environmental data that can be analysed (Wheatley et al. 2005).

The ability to model species' distributions based on habitat data signifies an important step in the management and conservation of wild bird populations (Guisan and Zimmermann 2000). Early work on green woodpeckers (*Picus viridis*) and common redstarts (*Phoenicurus phoenicurus*) by Buckland and Elston (1993), buzzards (*Buteo buteo*) by Austin and others (1996), and Himalayan river birds by Manel et al. (1999) helped to advance predictive distribution modeling techniques using bird-habitat relationships. In recent years, several authors have extended such methods to improve bird inventories, establish avian conservation priorities (e.g., Milsom et al. 2000, Gibson et al. 2004), and estimate responses of bird populations to environmental change (e.g., Bayne et al. 2005). In arctic regions, identification of

habitat correlates of species' distributions and the use of modeling techniques may contribute valuable information about key habitats and help to better delineate distributions of birds in this region.

1.2 THESIS ORGANIZATION AND STUDY OBJECTIVES

I have organized my thesis into an introductory chapter, two data chapters, and a synthesis. To reduce redundancy in the data chapters, I have included a General Methods section (Chapter 2) where I identify study areas, focal species, and data collection and quantification procedures common to both data chapters. Methodologies specific to each data chapter are found therein.

My first thesis objective was to address the role of spatial scale as it relates to habitat selection and to highlight the need for scale to be applied appropriately in studies of species-environment relationships (Chapter 3). I used Mann-Whitney U-tests to illustrate variability in species-habitat patterns when land cover features are analysed at different spatial scales. For each focal species, results are discussed with respect to how factors guiding habitat selection differ with spatial scale. Common deficiencies with the application of scale in research of species-environment relationships are examined.

My second and main thesis objective (Chapter 4) was to incorporate land cover data analysed at multiple spatial scales to model landscape-level distributions of waterfowl species breeding in arctic Canada. Models were used to predict distributions and were validated with independent data. Results have been extended to gain inference of species' distributions in areas not covered by survey efforts. Applications of modeling approaches are discussed, specifically for their use in identifying key habitats and their potential to forecast species' responses with environmental change. I concluded the thesis (Chapter 5) with a synthesis of major findings, implications for research of species' distributions and habitat selection, and potential contributions toward species and habitat management and conservation.

CHAPTER 2 STUDY AREAS, FOCAL SPECIES, AND GENERAL METHODS

2.1 STUDY AREAS

This study was conducted at two mainland sites in Canada's central arctic: the Queen Maud Gulf Migratory Bird Sanctuary and the Rasmussen Lowlands, Nunavut (hereafter, QMGMBBS and RL) (Figure 2.1). Both locations have been recognized within Canada as Important Bird Areas (IBA Canada 2004) and internationally as Ramsar sites (Wetlands of International Importance) (Ramsar 2005). Brief descriptions of each study area, including location relative to major topographic features, significant geological and ecological characteristics, and biological importance are given in sections 2.1.1 and 2.1.2.

2.1.1 Queen Maud Gulf Migratory Bird Sanctuary

The QMGMBBS (centered at 67°00'N, 100°30'W) is located approximately 85 km east of Bathurst Inlet and 75 km south of the community of Cambridge Bay (Ikaluktutiak). Bordered in the north by the Queen Maud Gulf, the sanctuary extends inland approximately 135 km. It is characterized by extensive lowlands consisting of glacial till and marine sediments of postglacial emergence atop Precambrian bedrock (Latour et al. 2008). Major drainages include the Ellice, Perry, Armark, Simpson, and Kaleet rivers. Relief features consist of Precambrian outcrops and boulder fields, as well as glacio-fluvial remnants such as eskers, drumlins, and raised beaches (McCormick et al. 1984).

The QMGMBBS sustains a considerable population of muskoxen and the calving grounds of the Ahiak caribou herd lie within its borders (Latour et al. 2008). The area is recognized for its importance to a vast array of bird species; most notably as a key breeding and moulting site for large numbers of waterfowl (Alisauskas 1992). In 1961, the area was designated as a Migratory Bird Sanctuary under the Migratory Bird Convention Act of 1917 to formally protect nesting birds.

The QMG study area (that covered by aerial surveys and included in land cover analyses) follows the coast along the entire east-west extent of the sanctuary, reaching inland to distances ranging from 44 to 120 km (Figure 2.2), covering a total area of 30,857 km².

Excluding marine environments, lowland and upland habitats cover roughly equal portions of the study area (Figure 2.3). Most lowland covers (wet sedge meadow, hummock

graminoid tundra, tussock graminoid tundra, and low shrub tundra) are relatively equal in proportion, with the exception of the shrub thicket cover, which occurs rarely.

Lowlands consist of vast wetland complexes of tundra ponds and sedge meadows, interspersed with hummock and tussock graminoid communities. Uplands are composed of lichen, moss, and heath vegetation often with exposed sand, gravel, and cobbles (Ryder 1969, Didiuk and Ferguson 2005).

2.1.2 Rasmussen Lowlands

The RL study area (68°40'N, 93°00'W) lies east of Rae Strait and the Rasmussen Basin, approximately 55 km south of Spence Bay (Taloyoak), and is situated on the boundary of two major Ecozones: the warmer and well-vegetated southern arctic and the colder and barer northern arctic (Ecological Stratification Working Group 1996). Similar to the QMG study area, the RL are characterized by vast lowlands, particularly between the Inglis and Murchison River drainages and along the area's southern extent. Again, lowlands consist of marine sediments reflecting postglacial emergence, but underlying bedrock is of Palaeozoic origin rather than Precambrian (Latour et al. 2008). Beyond the 'true' lowlands, the study area extends north to include glacial moraines forming the Ross Hills and west across Shepherd Bay to the Saatuq Peninsula. The escarpment of the Wager Highlands runs along the eastern boundary of the area (Figure 2.4).

Like the QMGMB, the RL provide habitat for significant populations of migratory birds (Latour et al. 2008). Particularly renowned for its high richness in shorebird species (Johnston et al. 2000), the RL are also recognized as the most important nesting area in the eastern arctic for tundra swans (Hines et al. 2003). Despite calls for its designation as a National Wildlife Area (Hines et al. 2003, Johnston et al. 2000), the RL remain without formal protection.

The RL study area covers 10,487 km², including both marine and terrestrial environments. Lowland habitats comprise the majority of non-marine areas (Figure 2.3), and are dominated by wet sedge meadow communities (Latour et al. 2008, this document). Upland habitats are significantly less common than they are in the QMG study area, as is freshwater, covering 11% and 12%, respectively, of the study area.

2.2 FOCAL SPECIES

Distributions of five waterfowl species, from three guilds, were examined in this study. Specifically, (A) tundra swans (*Cygnus columbianus*), (B) arctic-nesting geese including greater white-fronted (*Anser albifrons frontalis*) and small Canada geese (*Branta canadensis hutchinsii*), and (C) sea ducks including king eiders (*Somateria spectabilis*) and long-tailed ducks (*Clangula hyemalis*), were considered.

Focal species include both declining and expanding populations. While king eiders and long-tailed ducks have shown significant apparent declines (Sea Duck Joint Venture 2003), populations of tundra swans, white-fronted and Canada geese have increased across much of the central arctic (Serie et al. 2002, Hines et al. 2003). Because the main intention of the thesis was to illuminate species' distribution patterns in relation to land cover attributes, I chose to exclude highly colonial species from the study. Distributions of colonial organisms are largely influenced by interactions with conspecifics (Wolf and Trillmich 2007) and it was decided that relationships between species' distribution and land cover may be less evident than in non-colonial species.

2.3 DATA COLLECTION – AERIAL SURVEYS OF FOCAL SPECIES

Aerial surveys were conducted for the QMG (22-26 June, 2002 and 13-19 June, 2003) and RL (22-24 June, 2006) study areas as part of an ongoing initiative by the Arctic Goose Joint Venture under the North American Waterfowl Management Plan to map distributions and gather baseline population estimates of waterfowl and other wildlife in unsurveyed areas of Nunavut. Surveys were timed to coincide with the nesting phase for most waterfowl species in arctic Canada (Smith 1995, Hines and Wiebe 2004); as such, most birds were widely dispersed as breeding or territorial pairs (Hines et al. 2003). All surveys were conducted using a Bell 206b helicopter flying at an above-ground altitude of approximately 50 m and at speeds of 100-150 km/h.

Surveys followed linear transects oriented at roughly right angles to the coastline of each study area (Figures 2.2, 2.4). Transects varied in length and were separated by an interval of 10 km. Transects were subdivided into segments 2 km in length and 400 m in width (200 m on either side of the flight line). Number of each species counted per segment was recorded by two observers, one in the front left seat and the other in the rear right seat (equipped with a bubble

window for better viewing), and were entered on a per segment basis. The centroid of each segment was used for geo-reference for all observations within that segment.

In the QMG study area (2234 segments), the number of segments where focal species were detected were 997 with white-fronted geese, 1212 with Canada geese, 404 with tundra swans, 378 with king eiders, and 573 with long-tailed ducks (Table 2.1). In the RL study area (363 segments), white-fronted geese were detected in 120 segments, Canada geese in 93, tundra swans in 87, king eiders in 43, and long-tailed ducks in 25 segments.

2.4 QUANTIFICATION OF LAND COVER AND GEOGRAPHIC COVARIATES

I assembled a GIS database of land cover variables for the QMG and RL study areas (Table 2.2). Two sources of land cover data were used during the project: (1) digital topographic data, and (2) classified satellite imagery. Topographic data (at a scale of 1:50 000) were obtained from the National Topographic Database (NTDB, Natural Resources Canada 2006). Source data for the NTDB include aerial photographs, SPOT and LANDSAT satellite imagery, and reproduction material (Geomatics Canada 1996). Relevant land cover themes were incorporated into analyses in relation to distributions of the focal species.

Classified land cover data of the QMGMS were acquired from Didiuk and Ferguson (2005). This classification was based on Landsat Thematic Mapper (TM) satellite imagery which was recorded at a spatial resolution of 30 m². Using available cloud-free imagery for the summer months between 1986 and 1992, Didiuk and Ferguson identified 10 terrestrial land cover classes and 3 water land cover classes. Accuracy of their classification was assessed through aerial inspections and ground visits following ground-truth sampling protocols outlined by Story and Congalton (1986). Descriptions of each land cover class are included in Appendix A.

A considerable time lag exists between dates that images were captured by satellite and dates of aerial surveys for the QMG study area (10-17 years). While sizeable conversions of an area from one land cover type to another can occur during such a time period (e.g., via ‘catastrophic’ lake drainage), I feel that these changes are on such a scale that species-land cover relationships identified in this project were not significantly affected (along the western arctic coastline, Mackay (1992) estimated the drainage of one to two lakes per year over the last few millennia). Other natural disturbance agents (frost action, wind, herbivory) tend to be slow-acting or occur on fine scales such that structural and functional changes to land cover are

relatively minor over short time spans (Walker and Walker 1991). However, recent and persistent climatic changes in the arctic are expected to result in substantial changes to habitat, primarily due to a deeper thaw of the active layer and loss of permafrost (Hinzman et al. 2005). As the frequency interval of the arctic disturbance regime changes, similar investigations of species-land cover relations will likely require that species encounter data and land cover data be collected within a shorter time span.

The scheme of 13 land cover classes used by Didiuk and Ferguson (2005) was retained for all analyses of satellite data for my research, with the exception of one additional class being identified. Because most sea water was frozen at the time of all surveys, water pixels occurring in marine environments (typically included in the moderately turbid water class (H₂OMT) by Didiuk and Ferguson) were reclassified as marine ice (ICE) for my analyses.

Data about land cover comparable to the QMG were unavailable for the RL so I obtained satellite images of that area and used a supervised classification method in PCI Geomatics (2007) to assign land cover types. This method allows matching of spectral signatures of a group of pixels for a known cover type (so-called ‘training sites’) with similar signatures to classify unknown pixels (Tso and Mather 2001). First, unclassified orthorectified Landsat Enhanced Thematic Mapper (ETM) images for the RL study area, and a subset of images from the QMG area, were downloaded from GeoGratis (Natural Resources Canada 2007). From available images, I selected those whose capture day/month most closely matched dates of imagery used by Didiuk and Ferguson (2005). The RL study area image was taken on 03 September, 2000; the QMG study area images were taken on 10 August, 2000 and 07 July, 2001.

The RL and QMG images were appended to form a single image. I then established multiple training sites for each of the 13 land cover classes in the QMG section of the appended image based on known cover types from the Didiuk and Ferguson (2005) classification. To capture variability in spectral values within a land cover class, 30 or more training sites were identified for each class, with the exception of exposed peat (EP) which was relatively rare in the QMG area (only 15 training sites selected). The image was then processed using the maximum-likelihood classification algorithm and all pixels in the appended image were assigned cover types based on the training site values.

Because I was unable to revisit the RL study area to verify the accuracy of the classification, I used the percentages of training site pixels in each land cover class that were

correctly classified as a quality measure for the overall classification (Table 2.3). Because only values of training site pixels are considered during the classification process (i.e., actual locations of areas used as training sites are not taken into account), a post-hoc assessment of pixels used as training sites that have been correctly classified provides a “confidence-based quality assessment” of the overall classification (Strahler et al. 2006). Assuming that the training set was extensive and well-selected, the set will tend to follow the true accuracy of the entire classification (McIver and Friedl 2001).

Land cover and geo-referenced waterfowl data were imported into the GIS so that relationships between bird encounters and land cover could be estimated. For each transect segment, the percentage of each land cover type was summarized at four spatial scales (Figure 2.5): for the original linear 2 km x 0.4 km segments, and then for circular areas with radii of 1, 2.5, and 10 km (from the segment centre).

In addition to land cover covariates, basic geographic covariates (latitude, longitude, distance to the coast, and elevation) were calculated in the GIS so they could also be investigated in relation to species encounters. Elevations were derived from elevation contour layers from the NTDB (Natural Resources Canada 2006). As with waterfowl data, geographic variables were assessed at the centre of each segment.

2.5 TABLES

Table 2.1 Number of segments where focal species were detected during aerial surveys of the Queen Maud Gulf study area (22-26 June, 2002 and 13-19 June, 2003) and Rasmussen Lowlands study area (22-24 June, 2006).

Study Area	No. of Segments	No. of segments where focal species were detected				
		white-fronted goose	Canada goose	tundra swan	king eider	long-tailed duck
Queen Maud Gulf	2234	997	1212	404	378	573
Rasmussen Lowlands	363	120	93	87	43	25
Total	2597	1117	1305	494	421	598

Table 2.2 Environmental and geographic covariates considered in correlative analyses to explain distributions of focal species in the Queen Maud Gulf study area (22-26 June, 2002 and 13-19 June, 2003) and Rasmussen Lowlands study area (22-24 June, 2006).

Variable	Code	Dataset ^a	Description
Elevation	ELEV	NTDB	elevation at segment centre
Esker	ESKER	NTDB	% segment area covered by eskers
Sand	SAND	NTDB	% segment area covered by sand
Tundra polygon	POLY	NTDB	% segment area covered by tundra polygons
Tundra pond	POND	NTDB	% segment area covered by tundra ponds
Watercourse	RIVER	NTDB	% segment area covered by watercourses
Wetland	WETLAND	NTDB	% segment area covered by eskers
Waterbody, discrete	WAT_D	NTDB	% segment area covered by waterbodies not connected to watercourses
Waterbody, tapped	WAT_T	NTDB	% segment area covered by waterbodies connected to watercourses
Water, clear	H ₂ OCLR	LANDSAT	% segment area covered by clear water
Water, moderately turbid	H ₂ OMT	LANDSAT	% segment area covered by moderately turbid water
Water, turbid	H ₂ OTUR	LANDSAT	% segment area covered by turbid water
Active deposits	AD	LANDSAT	% segment area covered by active deposits
Wet sedge meadow	WSM	LANDSAT	% segment area covered by wet sedge habitat
Hummock graminoid tundra	HGT	LANDSAT	% segment area covered by hummock graminoid tundra habitat
Tussock graminoid tundra	TGT	LANDSAT	% segment area covered by tussock graminoid tundra habitat
Low shrub tundra	LST	LANDSAT	% segment area covered by low shrub tundra habitat
Shrub thicket	ST	LANDSAT	% segment area covered by shrub thicket habitat
Moss-lichen tundra	MLT	LANDSAT	% segment area covered by moss-lichen tundra habitat
Lichen-heath tundra	LHT	LANDSAT	% segment area covered by lichen-heath tundra habitat
Bedrock and boulder field	BBF	LANDSAT	% segment area covered by bedrock and boulder fields
Exposed peat	EP	LANDSAT	% segment area covered by exposed peat
Marine ice	ICE	NTDB/LANDSAT	% segment area covered by marine ice
Latitude	LAT	Geographic	latitude at segment centre
Longitude	LON	Geographic	longitude at segment centre
Coast distance	CSTDIST	Geographic	Euclidean distance from segment centre to nearest coastline

^a Abbreviations used: NTDB = National Topographic Database; LANDSAT = Classified Satellite Imagery

Table 2.3 Distribution of pixels classified in land cover training sites for the Queen Maud Gulf study area during the image classification procedure used to attribute land cover types to the Rasmussen Lowlands study area.

	Pixels	Actual land cover ^a													% correct		
		H ₂ OCLR	H ₂ OMT	H ₂ OTUR	AD	WSM	HGT	TGT	LST	ST	MLT	LHT	BBF	EP			
Intended land cover	H ₂ OCLR	30336	26640	3696													87.8
	H ₂ OMT	45520	2168	43232	48	64		8									95.0
	H ₂ OTUR	9448		720	8728												92.4
	AD	8720				8376	56					160		128			96.1
	WSM	10280					10120		144		16						98.4
	HGT	1864				24		1728		72	32	8					92.7
	TGT	2568						64	2232	120	64	24	40	24			86.9
	LST	4008						280	128	3464	96		40				86.4
	ST	2168					16	32	40	392	1680		88				77.5
	MLT	4696					8	64		48	32	4544					96.8
	LHT	5768						64			176	32	4248	1040	208		73.6
	BBF	2584									32		416	2048	88		79.3
	EP	122					2	1	3				21	2		93	76.2

Overall accuracy = 87.6

a Abbreviations used: H₂OCLR = water, clear; H₂OMT = water, moderately turbid; H₂OTUR = water, turbid; AD = active deposits; WSM = wet sedge meadow; HGT = hummock graminoid tundra; TGT = tussock graminoid tundra; LST = low shrub tundra; ST = shrub thicket; MLT = moss-lichen tundra; LHT = lichen-heath tundra; BBF = bedrock and boulder field; EP = exposed peat.

2.6 FIGURES

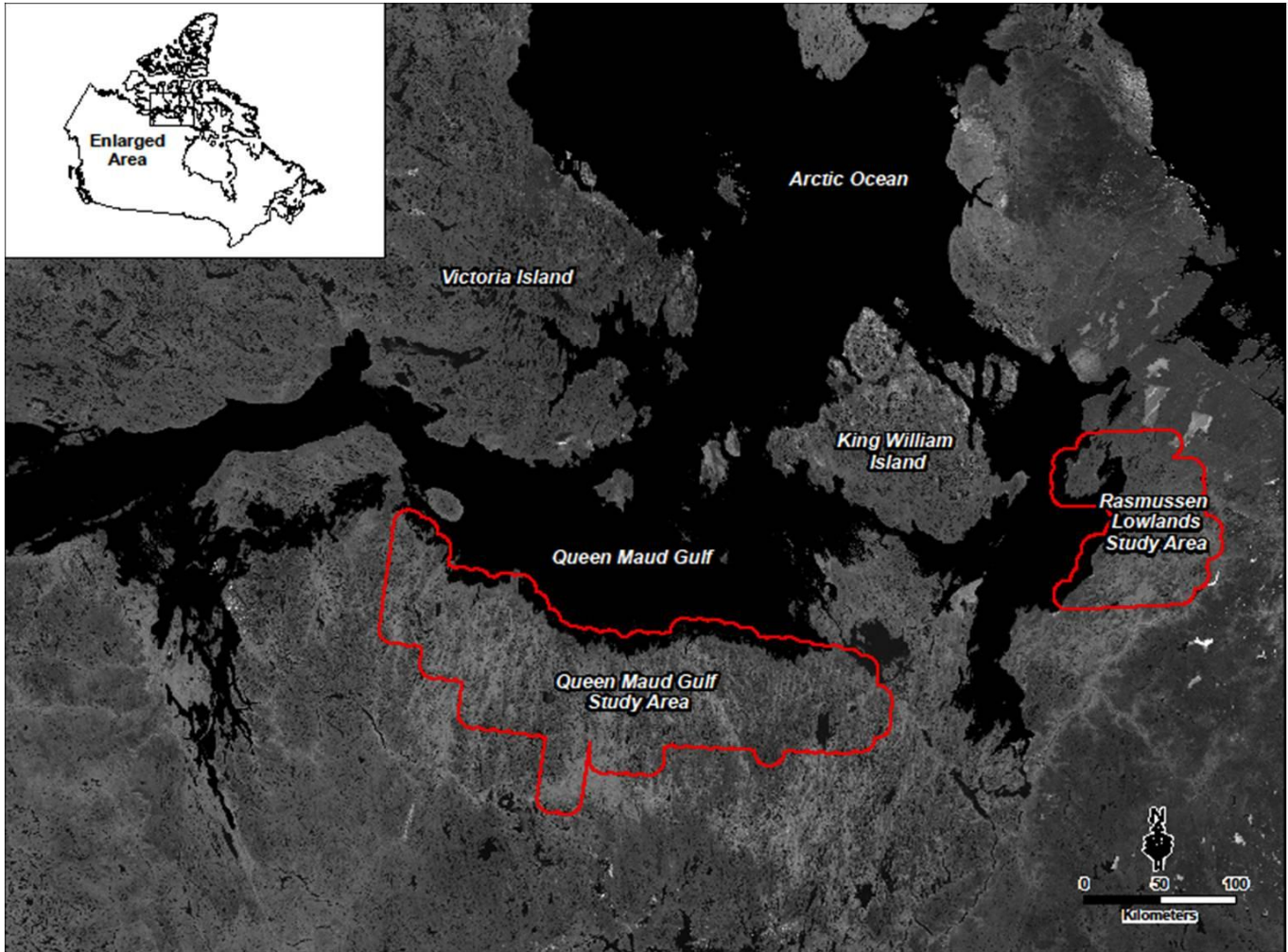


Figure 2.1 Location of the Queen Maud Gulf study area and the Rasmussen Lowlands study area, Nunavut, Canada.

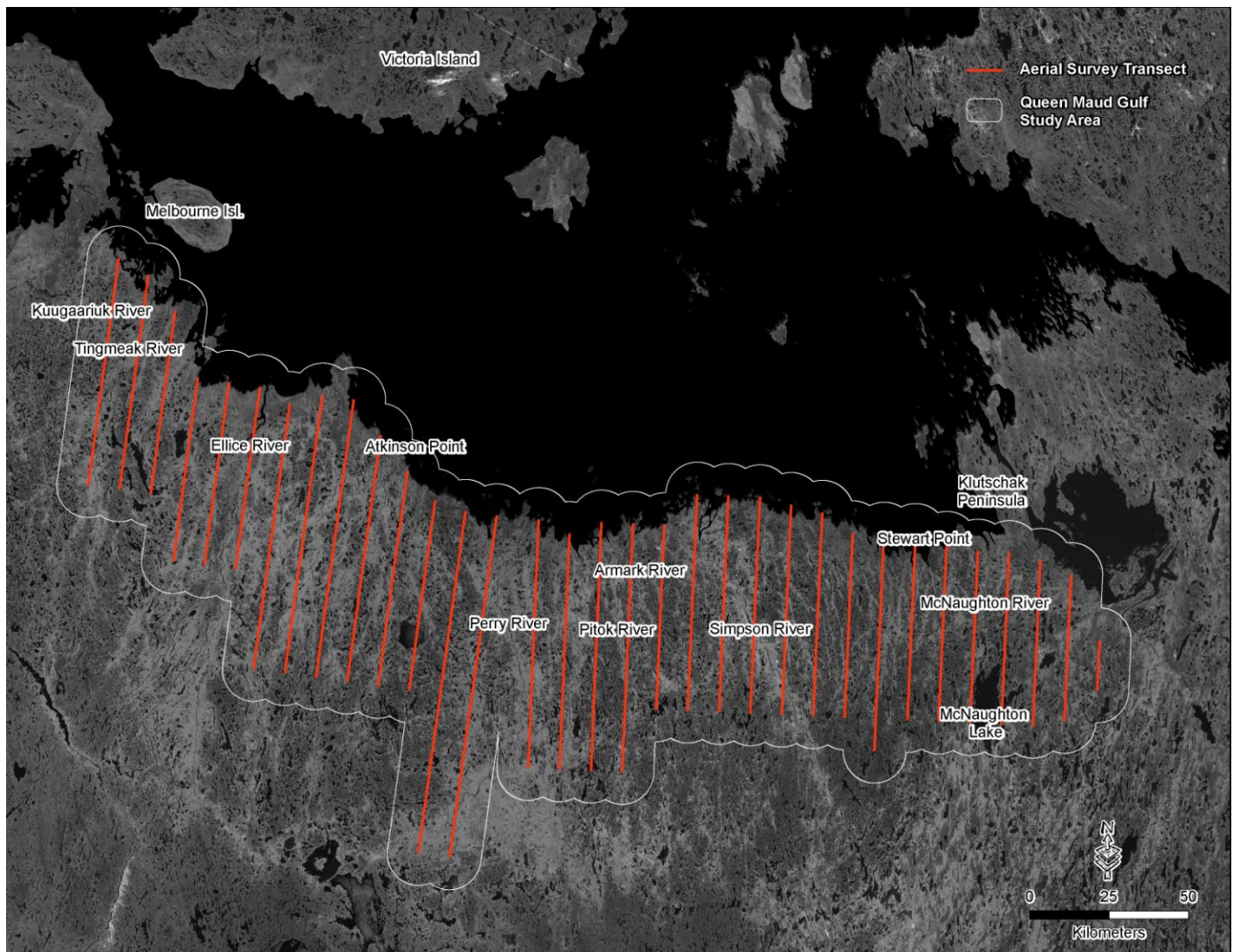


Figure 2.2 Location of aerial survey transects and prominent topographic features within the Queen Maud Gulf study area, Nunavut, Canada. Aerial surveys were conducted 22-26 June, 2002 and 13-19 June, 2003.

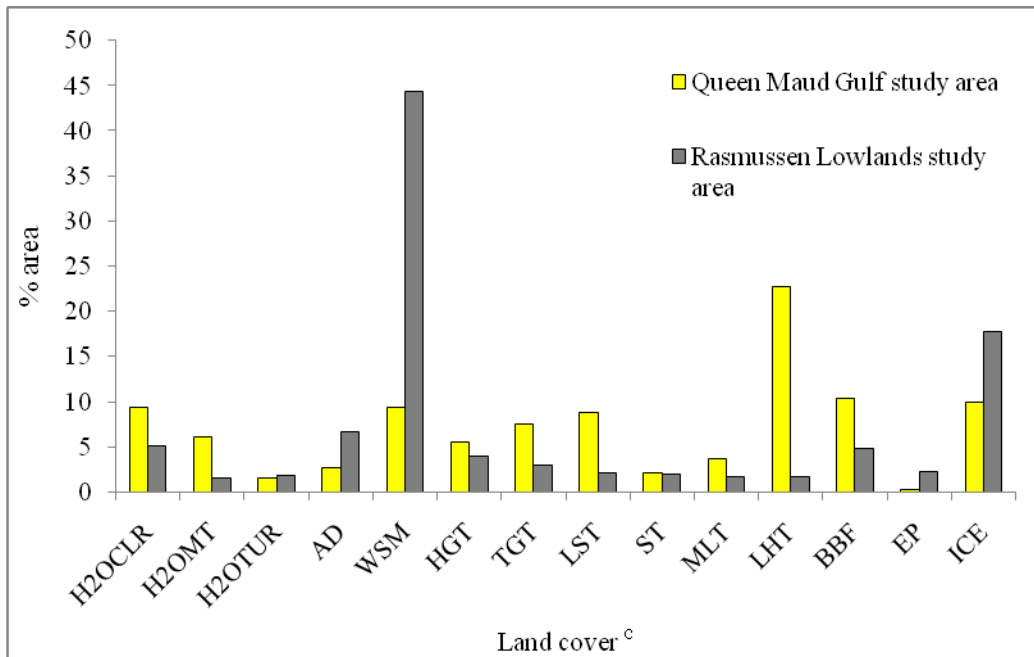


Figure 2.3 Land cover classification of the Queen Maud Gulf study area^a and the Rasmussen Lowlands study area^b.

^a Source: Landsat Thematic Mapper satellite imagery (Didiuk and Ferguson 2005);

^b Source: Landsat Enhanced Thematic Mapper satellite imagery (this document).

^c Abbreviations used: H₂OCLR = water, clear; H₂OMT = water, moderately turbid; H₂OTUR = water, turbid; AD = active deposits; WSM = wet sedge meadow; HGT = hummock graminoid tundra; TGT = tussock graminoid tundra; LST = low shrub tundra; ST = shrub thicket; MLT = moss-lichen tundra; LHT = lichen-heath tundra; BBF = bedrock and boulder field; EP = exposed peat.

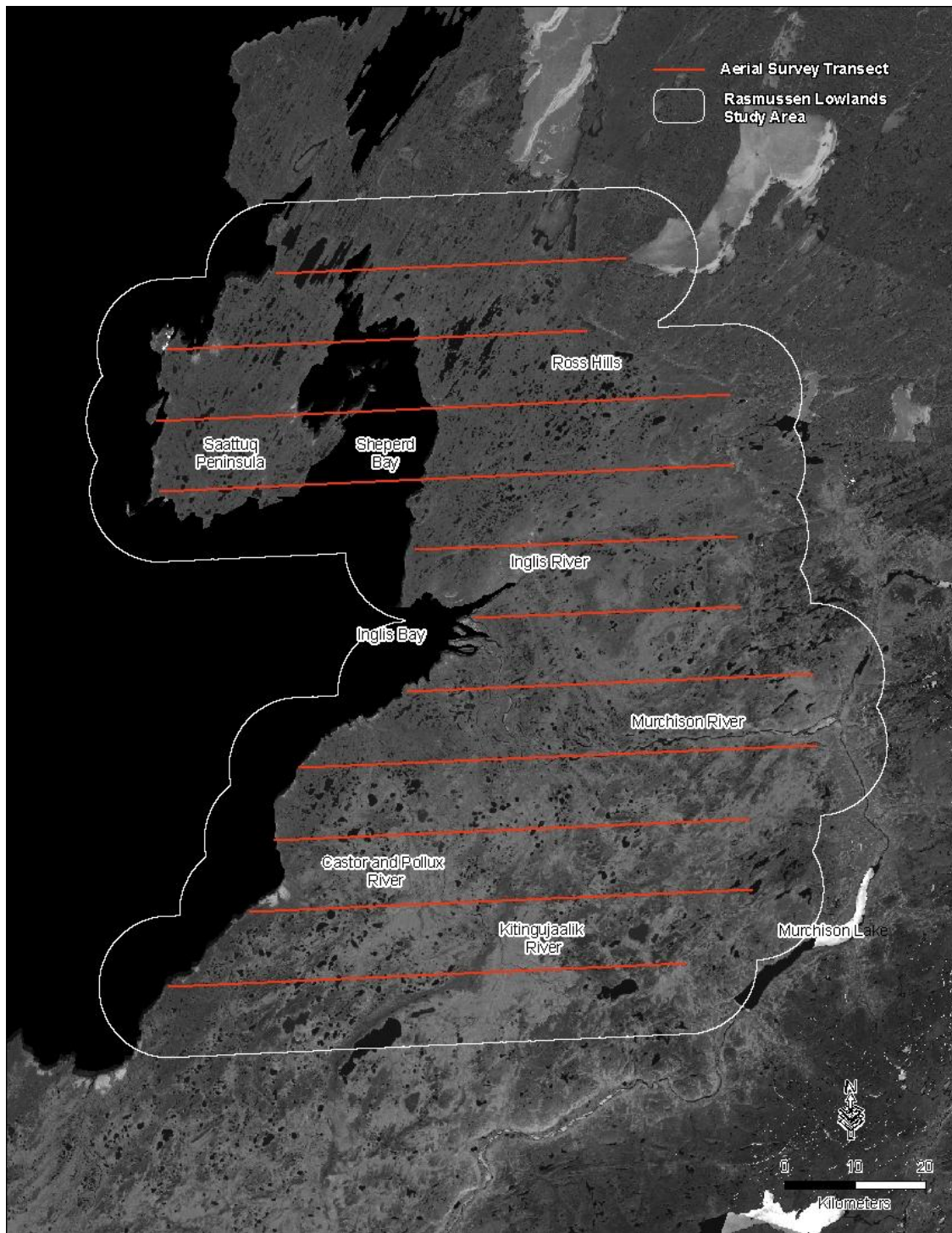


Figure 2.4 Location of aerial survey transects and prominent topographic features within the Rasmussen Lowlands study area, Nunavut, Canada. Aerial surveys were conducted 22-24 June, 2006.

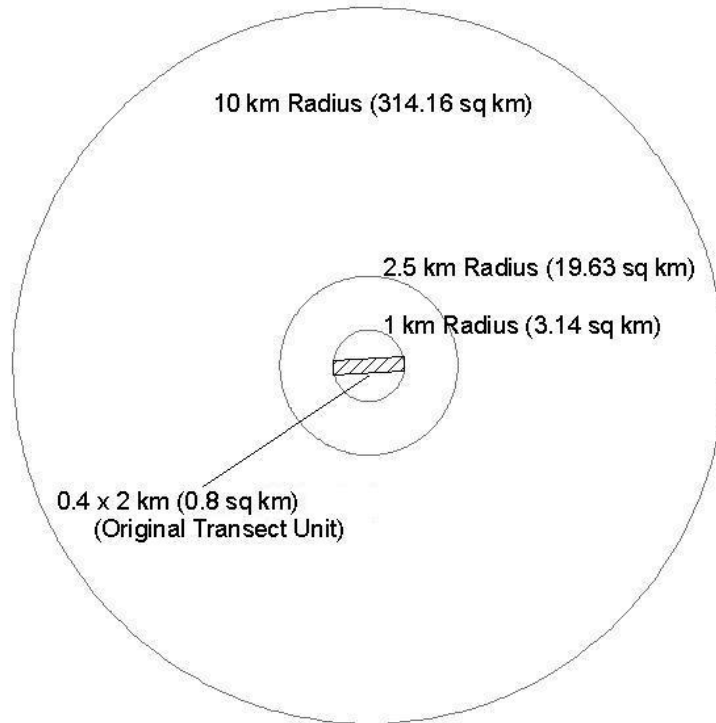


Figure 2.5 Spatial scales used in analyses of National Topographic Database and classified Landsat satellite image covariates in relation to encounters of focal species in the Queen Maud Gulf study area (22-26 June, 2002 and 13-19 June, 2003) and the Rasmussen Lowlands study area (22-24 June, 2006).

CHAPTER 3 ISSUES OF SPATIAL SCALE IN SPECIES-HABITAT RESEARCH

3.1 INTRODUCTION

Landscape ecology acknowledges that habitat selection occurs at a series of hierarchical scales of biological relevance to an organism, including landscape, territory or home range, and patch (Morris 1987, Forman 1995). This multi-scale nature of habitat selection has long been recognized (Owen 1972, Wiens 1973), but may have been articulated best by Johnson (1980). Johnson identified “a natural ordering of selection processes”, originating at the highest spatial scale with a species selecting a geographic range (so-called, *First-order selection*). Within the geographic range, lower-order selection processes operate at the individual [or social group] level. Individuals establish home ranges (*Second-order selection*), differentially use habitat patches within the home range (*Third-order selection*), and use elements (e.g., food items, nest sites, protective cover) disproportionately within patches (*Fourth-order selection*).

In the extensive literature about species-habitat associations and habitat selection, two weaknesses are often apparent: (1) the multi-scale nature of habitat selection is commonly overlooked and habitat variables are often analysed at only one spatial scale (Jorgensen and Demarais 1999); and (2) the selection of spatial scales is frequently made without consideration of the range of scales that have potential relevance to the species under investigation (Rushton et al. 2004).

Detection of ecological patterns often depends on the spatial scale at which such patterns are analysed (Bever and Flather 1999); despite a growing appreciation of this, ecologists have, only recently, begun to consistently incorporate analyses of wildlife-habitat relationships at multiple scales into their research (Lawler and Edwards Jr. 2006). The use of single-scale study designs is common, particularly where data are collected from multiple species. Within such studies, it is likely that different species will respond differently when variation arises in the spatial scales at which habitat features are sampled by both animals and researchers (Holland et al. 2004). Rarely have studies that have incorporated multiple spatial scales into their research examine factors important for determining a species' distribution in connection with other potentially important factors operating at different scales (Collingham et al. 2000); generally, these factors are considered separately in models or in other analyses (e.g., Greenwood et al. 1995, Reynolds et al. 2001). It has been demonstrated, however, that models incorporating

predictor variables at multiple spatial scales may perform better than models where covariates are measured at a single scale (e.g., Stephens et al. 2005).

In species-habitat modeling, habitat covariates are generally summarized within a fixed area or distance (i.e., within a given scale). Rarely, though, is the biological relevance of a single scale under consideration fully evaluated; more often scales are based on anthropogenic boundaries convenient to us, but perhaps less relevant to the organism under study (Rushton et al. 2004). For example, López-López et al. (2006) chose Universal Transverse Mercator square plots to model breeding habitat use in Bonelli's eagles (*Aquila fasciata*) in Spain "so as to be as similar to other habitat preference studies"; while in India, Jeganathan and others (2004) measured vegetation cover within 10 m blocks where prints of an endangered bird, the Jerdon's courser (*Rhinoptilus bitorquatus*), were encountered to model distributions and selected habitats.

Consideration of biologically-relevant scales in habitat selection and modeling research are not absent from the literature. For example, Apps and others (2004) used existing information about grizzly bear (*Ursus arctos horribilis*) ecology to create multi-scale models of grizzly bear distributions in the Canadian Rocky Mountains. Highest scales were based on mean home range sizes of individual bears within their study area, and at the finest scale based on average daily movement distances of bears in another area. Similarly, Bayne et al. (2005) used existing literature and spot-mapping techniques to establish ovenbird territory sizes while studying the effects of boreal forest fragmentation by seismic lines on ovenbird abundance.

The apparent lack of biologically-based scales in research is not to suggest that researchers are necessarily neglecting ecological information when defining scales; in many cases it may reflect that information necessary to define appropriate scales is not available. Unfortunately, information on home range sizes, daily movement distances, or other factors that may be useful when delineating ecologically-based scales, are limited or unavailable for many species. Furthermore, correlative works that examine species' responses at multiple spatial scales to suggest relevant scales are underrepresented. For species considered in my research, information such as home range size, territory sizes, or daily activity budgets is minimal, particularly as it pertains to arctic breeding ground ecology (exceptions include Alison (1976) who tracked pre-fledging long-tailed duck broods, Limpert and Earnst (1994) and Stickney et al. (2002) who estimated territory sizes of breeding tundra swans, and Mehl and Alisauskas (2007) who tracked movement distances of king eider broods in the early brooding phase).

Such knowledge gaps emphasize the need for alternative methods of incorporating biologically-relevant scales into species-habitat research. One of these alternatives is to analyse species-habitat relationships at multiple scales to establish which fits the data best (Holland et al. 2004). Explorative and correlative research such as this may be an effective means toward the identification of biologically-appropriate scales and ultimately permit better inference on specific, causal mechanisms to which individuals respond across landscapes (Stephens et al. 2003).

In this chapter, I identify land cover associations with focal species at various spatial scales to highlight how species-habitat relationships can vary when habitats are analysed at different scales. Multi-scale approaches to species-habitat research are emphasized as a method to further the knowledge about biologically-relevant scales to focal species.

3.2 METHODS

To illustrate variability in species-environment relationships with changes in spatial scale, I tested for differences in land cover attributes at four spatial scales (Figure 2.5) associated with sample units in which individuals of a focal species were encountered or not. Land cover covariates were derived from both the NTDB and classified Landsat satellite imagery (Table 2.2). Note that the waterbody covariate, derived from the NTDB, was partitioned into ‘discrete’ and ‘tapped’ waterbodies. Tapped waterbodies are defined as any NTDB waterbody directly connected to a NTDB river, while discrete waterbodies are those unattached to the river layer.

Transect segments from the QMG study area and the RL study area were considered together in analyses. The following procedure was repeated for each focal species.

3.2.1 Statistical Analysis

Mann-Whitney U-tests were used to gauge differences in land cover variables at each spatial scale for encounters and non-encounters of focal species. The Mann-Whitney U-test is a non-parametric test used to determine if a difference exists between two groups (Zar 2004). Although not testing hypotheses in a traditional sense here, *P*-values and mean differences in encounter and non-encounter segments were used to illustrate species’ associations with land cover variables at each of the different spatial scales. Because the number of independent tests performed for each species was large (22 land cover variables at 4 spatial scales), the Dunn-

Šidák adjustment was applied to ensure that significance levels were appropriate (Sokal and Rohlf 1995). As a result, $\alpha = 0.0005$ was used to conclude significance.

Results of this chapter are summarized in Table 3.1. Complete tables illustrating differences in land cover associations at the four spatial scales where focal species were and were not encountered for each focal species are presented in Appendix B.

3.3 RESULTS

Of 2597 transect segments surveyed in the QMG (2002, 2003) and RL (2006) study areas, white-fronted geese were encountered in 1117 (43%) segments, Canada geese in 1305 (50%) segments, tundra swans 491 (19%) segments, king eiders in 421 (16%) segments, and long-tailed ducks in 598 (23%) segments (Table 2.1).

3.3.1 Scale-independent Associations with NTBD Covariates

Of all focal species, white-fronted geese exhibited the highest number of significant associations with NTDB variables that were consistent across most spatial scales. Encounters were significantly higher where tundra ponds, wetlands, and river area were greater (Tables 3.1, B.1.a). Alternatively, white-fronted geese were less likely to be encountered where the proportion of habitat sample units were composed of tapped waterbodies. White-fronted geese were also negatively associated with sand, although associations were only significant at $P < 0.005$ for most scales.

Of the NTDB variables considered, Canada goose encounters were positively associated at all scales only with wetland area (Tables 3.1, B.1.b). Tundra swans were positively associated with river and discrete waterbody area (Tables 3.1, B.1.c), although the discrete waterbody association was only significant at $P < 0.005$ at the segment scale. King eider encounters were consistently negatively associated with tundra polygon area (Tables 3.1, B.1.d); however this association was significant at $P < 0.0005$ only at highest scale and significant at $P < 0.005$ for remaining scales. Encounters of long-tailed ducks showed no scale-independent association with NTDB variables (Tables 3.1, B.1.e).

3.3.2 Scale-independent Associations with Classified Landsat Covariates

At all spatial scales examined, white-fronted geese were more often encountered where lowland habitats (wet sedge meadow, hummock graminoid tundra, tussock graminoid tundra, low shrub tundra, and shrub thicket) were in higher proportions, and were encountered less often

where clear water, lichen-heath tundra, and exposed peat occurred more extensively (Tables 3.1, B.1.a).

Unlike white-fronted geese, Canada goose presence tended to be positively associated with upland land cover types (moss-lichen tundra, lichen-heath tundra, and bedrock and boulder fields) at most spatial scales (Tables 3.1, B.1.b). Regardless of scale, Canada goose encounters also occurred more often in areas with more moderately turbid water. And, like white-fronted geese, Canada geese showed a negative association with exposed peat at all scales.

Tundra swan presence was associated positively at most scales with increased proportions of turbid water, wet sedge meadow, hummock graminoid tundra, and moss-lichen tundra (Tables 3.1, B.1.c).

Again, both sea duck species demonstrated the fewest scale-independent associations with Landsat covariates. King eider encounters were negatively associated with shrub thicket area; this correlation was significant at $P < 0.0005$ for the three highest scales, but only significant at $P < 0.05$ for the segment scale (Tables 3.1, B.1.d). Eiders were positively associated with moss-lichen tundra at $P < 0.0005$ for two scales, and at $P < 0.005$ for remaining scales. Long-tailed duck encounters were significant at all scales for lichen-heath tundra (positive) and exposed peat (negative, Tables 3.1, B.1.e).

3.3.3 Scale-dependent Associations with NTDB and Landsat Covariates

Encounters of white-fronted geese showed considerable scale-dependence with land cover variables (Tables 3.1, B.1.a). Of NTDB covariates, a negative association with esker area emerged at higher spatial scales, while a positive association became increasingly apparent with discrete waterbody area at these scales. For Landsat variables, a negative association for moderately turbid water was evident at the 1 km scale, but this association became positive and significant at the 2.5 and 10 km scales. Finally, a positive association for bedrock and boulder fields became stronger at higher scales.

Negative associations for Canada geese with esker and tundra polygon area were apparent at higher spatial scales (Tables 3.1, B.1.b). Alternatively, Canada geese were positively correlated with river and tapped waterbody, but most strongly at the finest scales. Similar patterns were evident for Landsat covariates for this species. The only associations with lowland cover types for Canada geese were evident at high spatial scales; here, positive associations with hummock graminoid tundra and tussock graminoid tundra were detected.

Many land cover associations for tundra swan encounters were again only evident at high spatial scales (Tables 3.1, B.1.c). At these scales, greater area of eskers, tundra polygons, tapped waterbodies, and low shrub tundra cover were negatively associated with encounters. Swans were positively correlated at higher scales with sand and marine ice.

Encounters of king eiders were positively correlated with river area at fine scales; however, this variable was negatively associated with encounters ($P < 0.005$) at the highest, 10 km scale (Tables 3.1, B.1.d). A similar pattern was evident with low shrub tundra; in which encounters were positively associated and significant at the 1 km scale, but were negatively associated and significant at the 2.5 and 10 km scales. King eider encounters were positively associated with marine ice, but only at the 10 km scale.

Significant and scale-dependent associations with land cover variables for long-tailed duck encounters were few (Tables 3.1, B.1.e). A pattern of increasing significance with spatial scale for a positive association with wetland area was evident.

3.4 DISCUSSION

Scale can profoundly influence the interpretation of habitat use (Morris 1987). Results of this research support this assertion. Data suggest several land cover types important for, or correlated with, the occurrence of white-fronted geese, Canada geese, tundra swans, king eiders, and long-tailed ducks. However, the identification of species-land cover associations was often dependant on the spatial scale at which land cover data were analysed.

The scale-dependent nature of species-habitat relations revealed in this research was consistent with a number of other studies. When comparing grizzly bear detections from hair-trap sampling with landscape covariates measured at three spatial scales, Apps et al. (2004) found considerable differences in these associations across scales. At the largest scales, bear detections were correlated with higher forest productivity; while at finer scales, detections were more frequent in areas with less overstory cover and low forest productivity. Near Ottawa, Canada, Holland et al. (2004) obtained similar results when examining how abundances of long-horned beetle species differed when forest cover was analysed at multiple scales. The relationship between abundance and the proportion of forest cover varied significantly at different spatial scales for 12 of the 13 species investigated. Results of these investigations, supported by research presented here, imply that the relationship between species-habitat

associations and spatial scale within an area depend on both the environmental metric of interest and the study species.

While species' responses to spatial scale based on correlative associations, such as those used in this research and cited above, may have substantial practical application, we are limited in our ability to infer causal mechanisms behind them. However, some speculation may be made of ultimate factors that influence species presence based on ecological knowledge of the species and habitats under study. At high levels of the habitat selection hierarchy (i.e., second-order selection – the selection of the home range), individuals may choose whether or not to explore an area rather quickly (MacArthur et al. 1966, Cody 1981). At high latitudes, the relatively brief breeding season may expedite this decision (Orians and Wittenberger 1991). During initial scans of potential habitats, it seems reasonable that individuals chose to investigate habitats that offer assets that are spatially extensive (such as food items) before they investigate local features (such as nest sites) that likely require more calculated settlement decisions. In this research, many species-land cover associations that were consistent across all (or most) spatial scales corresponded well with known food preferences of the study species. White-fronted geese and tundra swans exhibited spatially-consistent correlations with several lowland covers from both the NTDB and satellite data. Food items that occur within these habitat types, particularly graminoid plants, are well known as preferred forage for these species (Carriere et al. 1999, Earnst and Rothe 2004). Canada geese demonstrated a positive association with wetland area at all scales, but this species showed most spatially-consistent affinities toward upland land covers. Berries produced by ericaceous plants characteristic of upland cover can provide vital carbohydrates and fats (Bairlein and Gwinner 1994) and may allow these birds to replenish body reserves before migrating south (Ankney and MacInnes 1978).

Habitat features directly related to breeding activities, such as nest sites and brood-rearing habitat, can be weighted heavily in habitat selection choices, often because considerable time is spent there (Orians and Wittenberger 1991). In research about habitat characteristics at multiple spatial scales, one might expect breeding habitat associations only at the finest scales of habitat sampling. In my research, few associations were discernable only at fine scales; examples included Canada goose and king eider correlations with increased river area and a Canada goose association with tapped waterbody area. However, the detection and interpretation of habitat associations only occurring at local scales in this study is limited because of the coarse

resolution of for land cover (30 m²) and species encounter data (400 m X 2 km transect segment). Additionally, because this research was conducted in areas known to be relatively abundant in high quality habitat, the identification of only localized nesting or brooding habitat associations was less likely than it may be in regions where this type of habitat is scarce.

Scalar responses can differ between sites, over time, among individuals, or other factors. Variation among sites (i.e., differences in habitat quality and configuration, species density, etc.) may mean that responses detected in one area may not hold at another site (Levin 1992). Further, substantial research has demonstrated considerable differences in spatial scale responses among individuals of the same species; this has been particularly evident in work pertaining to home range sizes. Home range size differences among individuals have been linked to age (Mannan and Boal 2000), number of nesting attempts (Elchuk and Wiebe 2003), and body size (Dahle et al. 2006). This type of information warrants careful consideration if existing knowledge is to be used to infer species' responses to scale (i.e., in species-habitat modeling or management and conservation applications).

3.4.1 Summary

Data in this research supports the notion that habitat-use patterns for a given species on one spatial scale may not necessarily be predictable from habitat-use patterns based on other scales. While relationships of focal species with land cover covariates were often consistent across scales, numerous cases existed where this was not found. To infer habitat-use responses at one scale may therefore be unfounded unless prior knowledge of relationships among scales can be assumed. Inference of habitat-use patterns from inappropriate scales may lead to inaccurate depictions of how habitat scale influences species and has the potential to lead to poor management decisions for avian conservation (Gutzwiler and Anderson 1987).

How spatial scale is incorporated into ecological studies should depend on whether research interests lie in revealing ultimate or proximate mechanisms behind species' response to habitat (Morris 1987). A mounting number of authors advocate the use of multi-scale study designs to identify scale(s) at which habitat selection processes occur (Johnson et al. 2004). Multi-scale correlative measures, such as those used here, can allow better understanding of proximate factors influencing species-habitat relations. This approach may be useful for development of *a priori* hypotheses to infer causal mechanisms behind species-habitat associations.

Despite considerable evidence that individual species-habitat relationships may vary with spatial scale, the extension of this knowledge into species-habitat models (i.e., including habitat variables at one scale with different covariates at another in a single model) seems to remain the exception. Although multi-scale models may not necessarily perform better than models considering predictors at a single-scale (e.g, Howerter 2003), others (e.g., Stephens et al. 2005, this publication (Chapter 3)) have demonstrated that multi-scale models have the potential to better inform researchers of species' distributions, abundance, or other parameters.

3.5 TABLES

Table 3.1 Sensitivity of focal species' associations with landscape covariates at four spatial scales in the Queen Maud Gulf study area (22-26 June, 2002 and 13-19 June, 2003) and the Rasmussen Lowlands study area (22-24 June, 2006). Variables are derived from the National Topographic Database (NTDB) and classified satellite imagery (Landsat).

Source	Variable ^a	white-fronted goose		Canada goose		tundra swan		king eider		long-tailed duck	
		Scale Sensitivity ^b	Association ^c	Scale Dependency	Association	Scale Dependency	Association	Scale Dependency	Association	Scale Dependency	Association
NTDB	ESKER	Sensitive	0 to -	Sensitive	0 to -	Sensitive	0 to -		0		0
NTDB	SAND	Sensitive	0 to -		0	Sensitive	0 to +		0		0
NTDB	POLY		0	Sensitive	0 to -	Sensitive	0 to -	Sensitive	0 to -		0
NTDB	POND		+		0		0		0	Sensitive	0 to -
NTDB	WETLAN D		+		+		0		0	Sensitive	0 to +
NTDB	RIVER	Sensitive	+ to 0	Sensitive	+ to 0		+	Sensitive	+ to 0		0
NTDB	WAT_D	Sensitive	0 to +		0	Sensitive	0 to +		0		0
NTDB	WAT_T		-	Sensitive	+ to 0	Sensitive	0 to -		0		0
Landsat	H ₂ OCLR		-		0		0	Sensitive	+ to 0 to + to 0		0
Landsat	H ₂ OMT	Sensitive	0 to - to +		+		0		0		0
Landsat	H ₂ OTUR		0		0	Sensitive	+ to 0		0		0
Landsat	AD	Sensitive	0 to - to +		0	Sensitive	0 to +		0	Sensitive	0 to -
Landsat	WSM		+		0		+		0		0
Landsat	HGT		+	Sensitive	0 to +	Sensitive	+ to 0 to +		0		0
Landsat	TGT		+	Sensitive	0 to +		0		0		0
Landsat	LST		+		0	Sensitive	0 to -	Sensitive	0 to + to -		0
Landsat	ST		+		0		0	Sensitive	0 to -		0
Landsat	MLT		0	Sensitive	0 to +		+	Sensitive	0 to +		0
Landsat	LHT		-	Sensitive	0 to + to 0		0	Sensitive	0 to + to 0		+
Landsat	BBF	Sensitive	0 to +		+		0		0		0
Landsat	EP		-		-		0		0		-
Landsat	ICE	Sensitive	- to 0 to -	Sensitive	0 to +	Sensitive	0 to +	Sensitive	0 to +		0

^a Abbreviations used: ESKER = esker; SAND = sand; POLY = tundra polygon; POND = tundra pond; WETLAND = wetland; RIVER = river; WAT_D = discrete waterbody; WAT_T = tapped waterbody; H₂OCLR = water, clear; H₂OMT = water, moderately turbid; H₂OTUR = water, turbid; AD = active deposits; WSM = wet sedge meadow; HGT = hummock graminoid tundra; TGT = tussock graminoid tundra; LST = low shrub tundra; ST = shrub thicket; MLT = moss-lichen tundra; LHT = lichen-heath tundra; BBF = bedrock and boulder field; EP = exposed peat.

^b Scale Sensitivity: Sensitive = detection of statistically significant differences between landscape covariates where focal species were and were not encountered varies among spatial scales.

^c Association: 0 = no difference between landscape covariates where focal species were and were not encountered ; + = encounters of focal species increase as a given land cover increase; - = encounters of focal species decrease as a given land cover increase. For sensitive variables, changes in species' associations are presented from finest spatial scale to coarsest spatial scales.

CHAPTER 4 PREDICTIVE MODELING AND MAPPING OF SPECIES OCCURRENCE

4.1 INTRODUCTION

Knowledge of the distribution of organisms across a range of spatial scales is a fundamental matter in both theoretical and applied ecology (Caldow and Racey 2000, Ormerod and Watkinson 2000). Distributional information is valuable to ecological researchers interested in understanding biodiversity, habitat selection, or the co-occurrence of species (MacArthur and MacArthur 1961, Rettie and Messier 2000, Leathwick and Austin 2001), while such data are essential for managers and conservationists wishing to measure rates of decline, locate biodiversity hotspots, or identify areas of endemism (Prendergast et al. 1993, Thomas and Abery 1995, Gaston et al. 1996).

Conventionally, the collection of detailed distributional data over large geographic areas has required extensive surveys that tend to be costly in resources and time. In many areas and for many taxonomic groups, needs for distributional information far exceed resources available to ecologists (Cowley et al. 2000). As such, accurate, extensive, and up-to-date distributional information is often lacking. If resources required for such activities remain limited or unavailable to ecologists, alternative methods for gathering information on species' spatial patterns and distributions may be important for management and increasingly necessary for conservation (Guisan and Zimmermann 2000, Manel et al. 2001).

Recently, modeling approaches to predict spatial distributions of species have been recognized as particularly valuable conservation alternatives or complements to conventional survey methods (Franklin 1995, Guisan and Zimmermann 2000, Scott et al. 2002). Models are generally developed by relating base surveys recording species presence, absence, or abundance to various predictor variables - typically some type of habitat, landscape, or other environmental metric (Pearce and Ferrier 2000). If researchers are able to draw correlations between distribution and abundance patterns with such environmental covariates, models may be useful to predict the likelihood of occurrence for species or communities where environmental covariate data exist but where survey coverage is poor (Guisan and Zimmermann 2000, Jarberg and Guisan 2001).

Practical application seems to be the primary goal of predictive modeling that uses knowledge of species-habitat relationships (Guisan and Zimmermann 2000). However,

modeling techniques go beyond conventional population assessment in their function. Manel and others (2001) have summarized potential uses of distribution modeling, which include:

- (1) Identifying suitable locations for species introduction.
- (2) Guiding site management by manipulating features known to favour target species occurrence or features known to discourage unwanted species.
- (3) Locating distributional gaps and identifying causal factors.
- (4) Locating areas sensitive to extinction of native species or invasion from exotic species.
- (5) Identifying key habitats and areas for species of importance.
- (6) Predicting distribution changes in response to environmental change.

The last two points will be the focus of this chapter.

The occurrence or abundance of a species depends not only on environmental features contained within a particular habitat patch in which individuals are observed, but on characteristics of the surrounding landscape (Fahrig 2001). One method of studying effects of a habitat patch and the surrounding landscape is known as the ‘focal patch’ approach (Holland 2004). In such research, landscape variables are measured within fixed distances centered on the patch or occurrence point; each patch and associated landscape are then treated as a single data point in analyses (Brennen et al. 2002).

In the past, computational limitations and high cost of digital environmental data have impeded research of distributions of organisms over large spatial scales (Osborne et al. 2001). However, recent software developments, and particularly improvements and increased availability of geographic information systems (GIS) and remote sensing resources, have facilitated advances in research about distribution patterns (Buckland and Elston 1993, Cowley et al. 2000, Brotons et al. 2004). Coupled with an improved theoretical framework and refinement of statistical approaches, large-scale distributional research is permitted to progress in a more tractable manner than has been previously possible (Ormerod and Watkinson 2000).

Modeling species-environment relationships to gain insight of species’ distributions seems particularly applicable to remote regions where knowledge of habitat associations and large-scale spatial distribution patterns of wildlife remains limited. Among the least-accessible of terrestrial ecosystems for researchers to gather distributional information are those in the arctic. With a limited transportation infrastructure, in addition to a brief field season with frequent adverse weather conditions, logistical and financial constraints commonly associated

with large-scale ecological research are amplified. As a result, distribution and abundance data for many wildlife species are absent for large areas of the north (Alisauskas 2005). In situations such as this, supplementary approaches to collect distributional data are especially valuable.

The need for improved knowledge of arctic species' distributions and factors guiding their habitat selection are further necessitated by the recent and rapid environmental changes occurring in the north, including intensifying land use and contaminant accumulation (Latour et al. 2008). Such information would greatly aid land managers and policy makers to guide industry and other anthropogenic activity.

The Intergovernmental Panel on Climate Change (2007) suggests that the largest threats to arctic ecosystems are those associated with climate change. High latitude ecosystems are expected to be among the earliest and most affected by global climate change (Barber et al. 2008). Others predicted increases in temperature and precipitation, rising sea levels, thawing of permafrost, yet potential information about impacts to local ecosystems and responses by individual species are less clear (Callaghan and Jonasson 1995). Modeling applications will provide the first insights to how particular species may respond to ecosystem alterations brought on by predicted climate change and may help prioritize management actions. Increasing our knowledge of factors driving wildlife distributions will be vital to management and conservation, specifically as those factors change.

Here, I used the focal patch approach to relate aerial survey data to digital land cover information to model distributions of five waterfowl species breeding in two study areas in Canada's central arctic: the Queen Maud Gulf Migratory Bird Sanctuary (QMGMB) and the Rasmussen Lowlands (RL). Models were used to predict encounters of white-fronted geese (*Anser albifrons frontalis*), Canada geese (*Branta canadensis hutchinsii*), tundra swans (*Cygnus columbianus*), king eiders (*Somateria spectabilis*), and long-tailed ducks (*Clangula hyemalis*) along survey transects and were evaluated against survey data not used in model generation. Model results were extended to produce predicted encounter probability maps for the two areas beyond that covered by aerial survey efforts. Finally, relative land cover types were manipulated to simulate anticipated environmental change in the central arctic so that potential species' responses (i.e., changes in predicted encounter probabilities) could be estimated.

4.2 METHODS

Aerial survey data and land cover and geographic variables (Table 2.2) were incorporated into multi-scale models to predict encounters and describe distributions of focal waterfowl species. National Topographic Database (NTDB) variables were not used in analyses in this chapter. Due to their coarser resolution, the NTDB data demonstrated weak associations with focal species encounters relative to the Landsat dataset. Additionally, NTDB data were highly correlated with Landsat variables and it was decided that they could not be considered independent.

4.2.1 Statistical Analysis

I used binary logistic regression, with species encounters and non-encounters in each transect segment as the dependent variable, to model the spatial distribution of focal species relative to independent land cover and geographic covariates. Steps used to develop and evaluate regression models, and to create predicted encounter probability maps for focal species, are described below. These processes were repeated for each focal species.

4.2.1.1 Model Building

The QMG dataset was used to establish geographic and land cover covariates, x_i , and the scale for land cover variables, x_{ij} , to be used in logistic regression models to predict the encounter probability of focal species, y_i , in transect segments for both study areas.

Because I analysed each land cover variable at four spatial scales of habitat samples, it was first necessary to establish the most appropriate sampling scale of each variable that would be used in the model sets. I incorporated all possible combinations of land cover variables (at all four scales) and geographic variables in regression models in PROC LOGISTIC in SAS (SAS Institute). The SELECTION=SCORE option was used to identify scales of land cover variables that contributed most to models of a given complexity (where complexity refers to the number of predictor variables in a model). The SCORE option uses the ‘branch-and-bound’ algorithm (Furnival and Wilson 1974) to rank models of a given complexity based on their likelihood score. At each complexity level (from one predictor variable to the global model with 17 independent predictors) all possible models, including all possible variable scales, were allowed. The model with the highest likelihood score at each complexity level was carried over to the model selection process such that model selection step included 17 parameterized models and the single null model for each focal species.

As models became more parameterized instances occurred where a model with the highest likelihood score included a predictor variable at more than one scale (e.g., $y_i = \text{MLT}_{2.5} + \text{MLT}_{10}$); however these redundant variables could not be considered independent and such models were not carried over to the model selection process.

4.2.1.2 Model Selection

The top model of each complexity (determined from the SCORE procedure), as well as the null model, were compared using Akaike's Information Criterion (AIC) to determine which model would be used to estimate the spatial distribution of each focal species. AIC is an information-theoretic approach to guide model selection (Burnham and Anderson 2002). The AIC difference (Δ_i) and Akaike weights (w_i) were used to evaluate and choose the most parsimonious model (i.e., the model that uses the fewest variables to explain the greatest amount of variation). Akaike weights provide a normalized comparative score for all specified models and are interpreted as the approximate probability that a given model is the best from the proposed set (Burnham and Anderson 2002).

Examination of AIC differences and model weights indicated that top models were of similar quality (this was the case for model sets for each focal species), suggesting that a model-averaging approach was appropriate for inference (Burnham and Anderson 2002). To determine a confidence set of models that would be used for estimation of model-averaged slopes, I used the evidence ratio, $\mathcal{L}(g_i | x) / \mathcal{L}(g_{min} | x)$, with a cut-off value of 0.0825, where \mathcal{L} is the likelihood of model g_i , given the data x , and where g_{min} is the best-supported model. Burnham and Anderson (2002) favoured this confidence ratio approach over other methods for generating confidence sets because the cut-off remains unchanged with the addition or removal of models.

4.2.1.3 Estimation of Parameters and Model Validation

I calculated model-averaged parameter estimates for a random selection of 80% of transect segments from the QMG study area. These estimates were applied to corresponding habitat layers in the GIS to solve for the dependent species variable in the remaining 20% of QMG segments (hereafter, the 'holdout' group). The inverse logistic transformation, $\exp(y) / (1 + \exp(y))$, was then applied to obtain a probability of encounter of the particular species for those segments.

The AIC provides evidence for selection of the most parsimonious model, but does not permit evaluation of model performance (Pearce and Ferrier 2000). To evaluate model performance in the holdout group I used the Receiver Operating Characteristic (ROC) technique (SPSS 2005). Regularly employed in medical trials (Zweig and Cambell 1993), the ROC method has been increasingly applied in ecological research as a way to validate presence/absence models (e.g., Zaniewski et al. 2002, Greaves et al. 2006, López-López et al. 2006). Traditional methods of assessing discrimination performance of logistic wildlife habitat models typically require the researcher to stipulate a specific threshold probability value that separates sites predicted to be occupied from sites predicted to be unoccupied. However, accuracy of these approaches will depend on the relative prevalence of the species within the study area and interpretation requires prior knowledge of that prevalence (Pearce and Ferrier 2000). Alternatively, the ROC method provides a method of assessing overall model fit to the original data (Gibson et al. 2004) that is independent of both species' frequency and decision threshold effects (Pearce and Ferrier 2000). The ROC curve offers a graphical means of assessing discrimination performance by plotting the number of true positive cases (sensitivity) against corresponding false positive cases (1-specificity) across a range of decision thresholds (Fielding and Bell 1997). Sensitivity and specificity are calculated entirely separately such that the ROC plot is independent of the study species' frequency in the study area.

In the ROC plot, the area under the curve (AUC) provides a single index of overall model accuracy. During the ROC analysis, encounter probabilities are ranked from highest to lowest. The AUC is equal to the probability that two randomly selected samples from different cases (i.e., species encounters and non-encounters) will be ranked in the correct order (Deleo 1993). An AUC value of 0.8, for example, means that a randomly selected segment from the 'encountered' group has a rank larger than a segment chosen from the 'non-encounter' group, 80% of the time. AUC values range from 0.5 (for models with no better discrimination than random chance) to 1.0 (for models with perfect discrimination). Calculation of the AUC and associated standard error were based on the non-parametric assumption (SPSS 2005). Although the ROC technique does not afford a rule for the classification of presences or absences at specific sites (Fielding and Bell 1997), it can be helpful in identifying appropriate decision threshold values for given applications by allowing researchers to weigh the cost of an incorrect classification against the benefit of a correct classification (Hilden 1991).

The process of calculating model-averaged parameter estimates for a random-selection of QMG transect segments, and assessing model fit with a holdout group was repeated (40 iterations) to get an overall assessment of model performance in the QMG study area. Final model-averaged parameter estimates (with corresponding unconditional standard errors) and the final AUC value were attained by averaging across iterations.

Final QMG estimates of slopes between probabilities of waterfowl encounters and Landsat imagery were then applied to land cover and geographic layers for the RL study area to determine the encounter probability of the species for all transect segments in that area. The inverse logistic transformation was again applied to transform results from the logit scale to the probability scale. Application of the ROC method was performed on all RL segments and was conducted once.

4.2.1.4 Encounter Probability Mapping

Using final encounter probabilities for each transect segment (the averaged probabilities for the QMG transect segments, and the single set for the RL segments), I used ordinary kriging in ArcGIS (Environmental Systems Research Institute 2006) to estimate predicted encounter probabilities of focal species for unsampled portions of each study area. Kriging is a geostatistical interpolation technique that uses weighted averages of neighboring samples (in this case, of encounter probabilities in transect segments) and the distance between sample points to estimate an ‘unknown’ value (encounter probability) at an unsampled location. Unlike other interpolation methods, kriging also takes into account the overall spatial arrangement of sample points when calculating values for unsampled areas (Theobald 2003). Estimated predicted encounter probability surfaces were used to highlight important regions within the study areas and to identify the relative proportions of each area judged to be suitable habitat for each focal species.

4.2.1.5 Land Cover Manipulation

I manipulated relative proportions of land cover types in the QMG and RL study areas to simulate anticipated changes (above) to vegetation communities brought on as a result of climate change to forecast potential changes on distributions of focal species. Potential changes were predicted by applying distribution models to adjusted land cover layers and recalculating predicted encounter probability of focal species throughout the study areas. The relative

proportions of each study area deemed to be suitable habitat are presented with original calculations of suitable habitats with unadjusted land cover (see section 4.2.1.4).

Because information on expected land cover change is limited and is summarized in a broad sense, manipulations here are only presented to highlight potential changes in general distributions of focal species (i.e., to illuminate possible directionality in changes to bird distributions, rather than predicting specific extents of such changes). Manipulations were applied to the five lowland land covers, as well as exposed peat and active deposits cover (exposed peat and active deposits can occur as both lowland and upland cover). I limited manipulations to these covers because information of climate-driven impacts to other land cover types is minimal, conflicting, or suggests little change.

Some predict that climate-driven impacts to lowland communities will be more severe than in upland habitats (Komárková and Webber 1980, Hinzman et al. 2005). Modeling and experimental studies suggest the advancement of shrubby vegetation into wet sedge meadow, hummock graminoid tundra, and tussock graminoid tundra habitats (Chapin and Shaver 1985, Chapin et al. 2000, Sturm et al. 2001, Dormann and Woodin 2002). Evidence also suggests that exposed peat cover will increase. Despite increases in precipitation, soils are expected to become drier as evapotranspiration increases with higher temperatures (Dormann and Woodin 2002). Observations of natural drawdown of soil water in wet sedge meadow habitats have transformed these communities to exposed peat in some regions (Didiuk and Ferguson 2005). Increases of exposed peat may be further augmented in some areas where herbivory by arctic geese has already been shown to convert graminoid communities to exposed peat (Alisauskas et al. 2006).

Finally, active deposits are expected to increase primarily as a result of thawing permafrost. The extent of change to active deposit cover is anticipated to be particularly high along watersheds and in coastal areas (ACIA 2005, Walker et al. 2008).

With each manipulation, adjusted land cover values for the seven cover types were calculated in two steps; first, by reducing a proportional extent per transect segment (ranging from 5-20%) from the three land covers that are predicted to be reduced by warming (wet sedge meadow, hummock graminoid tundra, and tussock graminoid tundra) (Table 4.6), and second, by repopulating 'lost' area from the three reduced covers with cover types that are predicted to replace each of the wet sedge and graminoid tundra covers. Because the four 'increasing' covers

are not predicted to increase equally, I weighted the increase of each cover based on predicted contributions in the literature (Table 4.6). Manipulations were applied three times. The first manipulation simulated least proportional change to land cover; subsequent manipulations reflect changes of increasing magnitude.

4.3 RESULTS

For distribution models using logistic regression developed using datasets from the QMG study area, the following were calculated: AIC values, differences between the model with the lowest AIC value and each candidate model (Δ_i), relative Akaike weights (w_i), and the number of predictor variables (K) (Tables 4.1.a – 4.1.e). Akaike weights for best approximating models (white-fronted goose ($w = 0.31$), Canada goose ($w = 0.33$), tundra swan ($w = 0.43$), king eider ($w = 0.18$), and long-tailed duck ($w = 0.20$)) suggested significant model selection uncertainty. Examination of AIC differences and Akaike weights of other top models indicated considerable support for these models; therefore a model-averaging approach was used for inference (Burnham and Anderson 2002). Resulting confidence sets for each focal species included the following number of models: white-fronted goose, 5 models; Canada goose, 6 models; tundra swans, 7 models; king eider, 11 models; long-tailed duck, 10 models.

During the model validation procedure, model-averaged parameter estimates and unconditional standard errors were calculated for each of the 40 iterations. Final estimates and unconditional standard errors, presented in Figures 4.1.a – 4.1.e, were averaged across iterations.

Geographic covariates (latitude, longitude, coast distance, and elevation) considered during the model building process varied with respect to their inclusion in final models and effect among focal species (Figures 4.1.a – 4.1.e). Final predictive models using model-averaged parameter estimates included elevation for four species, with the lone exception being the long-tailed duck model. In all four cases, species encounters were negatively associated with increases in elevation. Latitude showed considerable influence for white-fronted goose, Canada goose, and tundra swan. Canada geese and tundra swans were more often encountered at higher latitudes in the QMG study area, while white-fronted goose encounters occurred more frequently at lower latitudes.

Of land cover covariates derived from Landsat satellite imagery, lowland habitat types were most highly associated with encounters of focal species (Figures 4.1.a – 4.1.e). Lowland

covers include wet sedge meadow, hummock graminoid tundra, tussock graminoid tundra, low shrub tundra, and shrub thicket. Selection of lowland habitats is consistent with the bias toward lower elevations observed in models for most of the focal species.

Wet sedge meadow cover proved to be the principle determinant of encounters of the white-fronted geese, tundra swans, king eiders, and long-tailed ducks. For all of these species, wet sedge meadow contributed most to their respective models at the landscape scale (10 km). Canada goose encounters exhibited a modest positive association with wet sedge meadow, but its contribution was strongest at the finest (segment) scale.

Beyond wet sedge meadow cover, estimates of white-fronted goose encounters indicate further associations with other lowland cover types; these include hummock graminoid tundra, tussock graminoid tundra, and shrub thicket. Canada goose encounters were also associated with hummock graminoid tundra and shrub thicket, but were negatively correlated with tussock graminoid tundra and low shrub tundra. Encounters of both goose species were reduced in segments where marine ice cover was present.

Tundra swan encounters were more frequent in landscapes where active deposits and lichen-heath tundra habitats were relatively high (both of these variables were included in the tundra swan model at the landscape scale).

The seaducks, king eider and long-tailed duck, were the only focal species to demonstrate an affinity toward marine ice. These species also displayed common associations with hummock graminoid tundra and lichen-heath tundra, both at finer scales. Interestingly, king eiders and long-tailed ducks shared positive associations toward landscapes where turbid waterbodies were more common, but showed considerable aversion to landscapes proportionally higher in moderately turbid waterbodies.

Exposed peat was among the most influential land cover variable on species' absence for all species; this variable was generally included in models at higher spatial scales.

4.3.1 Implementation of Models in the GIS

The logistic regression equations of the final models for each focal species were implemented into the GIS by combining appropriate geographic and land cover raster layers as defined by equations 1 – 5 (Table 4.2) to solve for the dependent species variable, y_i , in each transect segment using the map calculator function in ArcGIS Spatial Analyst (Environmental Systems Research Institute 2006). Recall that QMG study area transect segments were validated

with multiple iterations; for those segments, parameter estimates presented in equations 1 – 5 represent averaged estimates across iterations. Because segments for the RL study area were not used in the development of the logistic regression models, parameter estimates shown in equations 1 – 5 are those used in the validation step for those segments. The inverse logistic transformation, $\exp(y) / (1 + \exp(y))$, was then applied to obtain a probability of encounter of the particular species for those segments.

4.3.2 Model Validation

ROC plots for focal species models in the QMG study area and the RL study area are presented in figures 4.2.a – 4.2.e. In the QMG study area, models for all focal species were highly significant at $P < 0.001$ (i.e., given a null model having an AUC value ≤ 0.50). AUC values and associated confidence intervals from the ROC analyses provide an indication of model fit. Averaged AUC values for white-fronted goose, Canada goose, and tundra swan models in the QMG study area were calculated as 0.765 ± 0.010 , 0.709 ± 0.011 , and 0.708 ± 0.014 , respectively (Table 4.3). AUC values between 0.7 and 0.9 indicate reasonable model discrimination between segments in which the species were and were not encountered (Swets 1988). Performance of these models in the RL study area fell short of 0.7 (AUC white-fronted goose = 0.680 ± 0.029 , Canada goose = 0.651 ± 0.032 , tundra swan = 0.655 ± 0.035), although all remained significant at $P < 0.001$ (Table 4.4). While significant at $P < 0.001$ in the QMG study area (Table 4.3), performance of distribution models for the sea duck species, king eider and long-tailed duck, indicated poor discrimination (AUC = 0.656 ± 0.015 and 0.580 ± 0.014 , respectively). In the RL study area, king eider and long-tailed duck models showed no difference from null models (Table 4.4).

4.3.3 Encounter Probability Mapping

Predicted encounter probability maps for each focal species within the QMG and RL study areas generated using ordinary kriging are presented in figures 4.3 and 4.4, respectively. Below, encounter probabilities are described in relation to prominent topographic features (Figures 1.2, 1.4).

Predicted encounter probabilities in the QMG study area were highest for white-fronted and Canada geese (in some areas, probabilities exceeded 0.9). Predicted white-fronted goose encounters showed a tendency toward lowland regions associated with watersheds of major rivers, with the highest predicted encounter probabilities occurring along the Perry River

drainage and in the extensive watersheds of two unnamed rivers that converge near Atkinson Point on the shore of QMG. Significantly high predicted encounter probabilities for white-fronted geese also occur further west in lowlands surrounding the Ellice, Tingmeak, and Kuugaariuk Rivers, and a more isolated pocket in the east of the study area near the McNaughton River.

In the RL study area, highest predicted probabilities (0.5 – 0.8) of white-fronted goose encounters occurred in the Inglis River drainage, particularly where it empties into the Rae Strait. Only slightly lower probabilities were predicted in lowland habitats surrounding the Castor and Pollux River and the Kitingujaalik River in the south of the study area.

Predicted encounter probabilities for Canada geese were high along the coastline for the entire extent of the QMG study area. The highest and most extensive probabilities for Canada goose encounters occurred in the McNaughton River watershed and extend onto the Klutschak Peninsula. Smaller areas of high predicted encounters were found in the west of the QMG study area near Atkinson Point, and in the Ellice, Tingmeak, and Kuugaariuk River drainages. The probability of Canada goose encounters was predicted to be high in all areas of the RL study area.

The highest predicted encounter probabilities for tundra swans in the QMG study area also occur in the outflow of McNaughton River and onto the Klutschak Peninsula. However, predicted probabilities for this species were low throughout the study area (probabilities never exceeded 0.40). Despite low predicted encounter probabilities, an affinity for coastal regions relative to other portions was evident.

Encounter probabilities of tundra swans were predicted to be significantly higher in the RL study area than in the QMG area, ranging from 0.1 – 0.9. The watershed of the Inglis River again was forecasted to be important for swan encounters, as were some upland areas including the Ross Hills.

Like the tundra swan, encounters of king eiders in the QMG study area were predicted to be highest along the coast, particularly in the eastern portion of the study area. Here, predicted encounters of king eiders did not exceed probabilities 0.6. Areas surrounding the Inglis and Murchison Rivers were calculated to have highest probabilities of king eider encounters in the RL study area, although encounter probabilities again remained rather low (not exceeding 0.5).

Predicted encounters of long-tailed ducks exhibited the highest spatial variation in both the QMG and RL study areas, with highest probabilities occurring in both upland and lowland habitats. Overall probability of long-tailed duck encounters were relatively low, not surpassing 0.5 in either of the study areas.

Based on predicted encounter probability maps for each species, proportions of each study area judged to be suitable habitat for each species are summarized in table 4.5. In the QMG study, percentages of habitats calculated as moderately or highly suitable (i.e., having a predicted encounter probability greater than 0.5) were 39.3% for white-fronted goose and 53.2% for Canada goose. Modeling results suggested no areas in the QMG study area are moderately or highly suitable for the tundra swan, king eider, and long-tailed duck. Percentages of moderately or highly suitable habitats in the RL study area were estimated at 4.1% for white-fronted goose, 100% for Canada goose, and 39.9% for tundra swans. Again, no habitat was estimated to be moderately or highly suitable for king eider or long-tailed duck in the RL. However, it must be noted that model fit, indicated through the ROC analysis, was relatively modest for white-fronted goose, Canada goose, and tundra swan distribution models in the RL, and was especially poor for king eider and long-tailed duck models in both the QMG and RL study areas. Interpretation of estimated suitable habitats must take this model fit into account.

4.3.4 Land Cover Manipulation

Proportions and direction of land cover adjustments for each of the three manipulations are given in table 4.6. Based on Friedman's tests, predicted encounter probabilities differed among the non-manipulated land covers and the three manipulated land covers within the QMG study area (white-fronted goose $\chi_r^2 = 6628.2$; Canada goose $\chi_r^2 = 3121.3$; tundra swan $\chi_r^2 = 6589.9$; king-eider $\chi_r^2 = 6702.0$; long-tailed duck $\chi_r^2 = 6702.0$, where d.f. = 3, $P < 0.05$). The same result was obtained with using data from the RL study area (white-fronted goose $\chi_r^2 = 1080.7$; Canada goose $\chi_r^2 = 949.6$; tundra swan $\chi_r^2 = 1089.0$; king-eider $\chi_r^2 = 1089.0$; long-tailed duck $\chi_r^2 = 1089.0$, where d.f. = 3, $P < 0.001$). For all focal species, proportional manipulations of land covers resulted in lower predicted area judged to be suitable habitat (Table 4.7 and Table 4.8).

4.4 DISCUSSION

Conservationists are increasingly placing emphasis on landscape scale efforts (Cowley et al. 2000). Applications of species-habitat modeling have potential to provide effective means of assessing and managing wildlife and habitats at such scales. GIS-based databases of land cover and geographic variables allow for efficient quantification of landscapes; such digital inventories are becoming more and more advanced and are increasingly available. However, when associating occurrence of wildlife with such variables, particularly at extensive spatial scales, geographic and land cover covariates serve only as surrogates of functional elements of habitats linked to feeding, mating, rearing, or avoidance activities (Johnson et al. 2005). Interpretation of these covariates, and subsequent management decisions based on them, must be done with this in mind; this is particularly true when variables are modeled for predictive purposes and not selected in an *a priori* fashion.

Although distribution models applied here were developed for predictive purposes, species-land cover associations evident in models may still provide certain evidence of food habits and breeding and habitat ecology of focal species in the QMG and RL study areas.

4.4.1 Species Ecology Related to Associated Land Covers

Feeding geese are known to select plants according to nutrient content, particularly those high in nitrogen (Owen 1972, Gauthier and Bédard 1990, Kristiansen et al. 1998, Therkildsen and Madsen 1999, Cadieux et al. 2005). Smaller herbivores such as geese tend to have limited abilities to digest fibre (Demment and Van Soest 1985) and tend to select foods low in fibre and high in protein (Owen et al. 1977). Graminoid species characteristic of lowland habitats are known to have among the highest content of nitrogen among arctic plants (Cadieux et al. 2005) and constitute large proportions of both white-fronted and Canada goose diets. Observations of white-fronted geese and Canada geese by Carriere and others (1999) on the Kent Peninsula, Nunavut, found that *Carex* spp. and *Dupontia fisheri* constituted over 50% of adult bird diets once all habitats are snow-free. Even higher dependence on graminoid plants were found in Canada geese on the northeast coast of Hudson Bay (Cadieux et al. 2005). Here, over 65% of food items ingested by adult Canada geese consisted of *Carex aquatilis*, *Eriophorum* spp., and other graminoids during the first four weeks of brood-rearing.

For white-fronted geese, selection of hummock graminoid tundra or tussock graminoid tundra may also relate to nesting habits. In the treeless tundra habitat, this species nests

cryptically (Carriere et al. 1999), typically building nests in tall grass or in hollows between hummock or tussock mounds in lowland graminoid habitats (Bellrose 1980).

Reliance of white-fronted geese and Canada geese on lowland habitats is evident; however, studies suggest that upland land covers are also important for these species (e.g., Cadieux et al. 2005, this publication (Chapter 2)). For white-fronted geese, model results somewhat support this (a modest affinity for landscapes with lichen-heath tundra was evident). Relevance of uplands may again be related to dietary requirements. As the growing season progresses, adult white-fronted geese and Canada geese exhibit a dietary shift from protein-rich graminoids toward other forbs and berries (Cadieux et al. 2005). The fibre content of a typical graminoid leaf increases over time (Dale 1982) making this food less profitable for geese. Berries are rich in soluble carbohydrates and fats (Bairlein and Gwinner 1994) which are necessary to rebuild body reserves prior to the fall migration (Ankney and MacInnes 1978). Berry-producing ericaceous plants characteristic of upland lichen-heath tundra, including *Vaccinium vitis-idaea*, *Arctostaphylos alpina*, and *Empetrum nigrum*, likely permit this adjustment.

The Canada goose distribution model showed only modest evidence for reliance on upland land covers for this species. However, timing of aerial surveys coincided with late nesting and early brooding stages for Canada geese (Hines and Wiebe 2004) when lowland foods remained the most important (Cadieux et al. 2005). The dietary shift and associated move toward areas with more extensive uplands may occur later in the season than when our aerial surveys were completed (Cadieux and others (2005) observed this shift in the late brooding phase) such that models may not reflect the importance of upland habitats for this species.

Encounters of tundra swans most frequently occurred in low-lying areas. Locations of tundra swan encounters in this study are consistent with previous surveys in the central arctic (Stewart and Bernier 1989, Johnston et al. 2000, Hines et al. 2003). Highest densities of tundra swans during these surveys correspond to zones of postglacial marine transgression, especially where significant deposits of marine sand and silt exist (Bird 1967). Model predictions of tundra swan encounters in the QMG and RL study areas match these observations reasonably well.

As was the case with the focal goose species, tundra swan reliance on lowland areas is best attributed to dietary requirements. Adult swans spend considerable time on the breeding grounds (Petrie and Wilcox 2003) and require substantial amounts of food (Wilmore 1979).

Emergent and submerged aquatic plants contribute substantially to tundra swan diets (Wilmore 1979, Bellrose 1980). Again, protein-rich sedges and other graminoids are among preferred foods in terrestrial habitats, sedges being especially important for developing cygnets (Earnst 2002, Earnst and Rothe 2004). As would be expected, wet sedge meadow cover proved to be an important determinant of tundra swan encounters.

Lichen-heath tundra, an upland habitat, was also strongly associated with swan encounters in this study. Tundra swans usually use drier microhabitats for nest sites (Monda et al. 1994, Stickney et al. 2002), which may partially explain the affinity for lichen-heath tundra detected here. These elevated microhabitats typically thaw faster than other tundra surfaces allowing earlier nest initiation and likely provide better views of potential predators (Monda 1991).

Breeding tundra swans are territorial (Dau 1981). Territories can be over 2 km² and consist of at least one large lake (Stickney et al. 2002). Almost always, nests are placed within 100 m of a lake or pond (Monda et al. 1994, Stickney et al. 2002) or commonly on a small islet within a lake (Wilmore 1979). While aquatic vegetation occurring in this ‘primary lake’ may provide sustenance for both adults and developing cygnets, it serves primarily as protection from terrestrial predators. Here, an attraction to both clear and turbid waterbodies was noticeable. The draw for clear waterbodies was included in the model at the segment scale and may signify the primary lake location. Clear waterbodies tend to be associated with upland habitats such as lichen-heath tundra; a land cover strongly associated with swan encounters. An association with turbid waterbodies, also evident, may further reflect dietary requirements of adults and cygnets later in their development; these waterbodies tend to occur in lowland areas where turbidity is a result of muddy substrates and shallow water depths (vegetation associated with these ponds and surrounding lowlands is known as preferred forage). These small turbid waterbodies may further benefit adult swans as they contain high concentrations of calcium necessary for egg production (Stewart and Bernier 1989).

Several authors (e.g., Lensink 1973, McLaren and McLaren 1984, Monda et al. 1994) suggest that coastal regions are especially important for breeding tundra swans. These studies have observed parents with broods on open-ocean waters at times when inland waters are frozen in late August or September. While predicted swan encounter probabilities were often calculated to be highest nearest the coast (particularly for the QMG study area), the distance to the coast

variable included in the tundra swan distribution model displayed a negative, although slight, association with encounters. However, lack of support for the coastal influence may reflect survey timing.

Relatively poor performance of king eider and long-tailed duck predictive distribution models limits the ability to interpret land cover and geographic associations for these species. Several factors might have contributed to relatively weak model performance for these species. Habitat features important for king eiders and long-tailed ducks may operate at finer scales than those discernible here. Given the resolution of satellite imagery (30 m²) and that observations of species were summarized within the 2 km x 400 m segment, specific land cover associations for king eiders and long-tailed ducks may have been limited to mechanisms that operate on finer scales.

Timing of aerial surveys may further diminish predictive performance of models for king eiders and long-tailed ducks. At the time of all surveys, breeding individuals of other focal species are in the mid-late nesting phase (McLaren and McLaren 1984, Carriere et al. 1999); however, in the central arctic, king eiders and long-tailed ducks tend to be at the early stages of nest initiation (Kellett and Alisauskas 1997, Mehl 2004, Kellett et al. 2005). Surveys conducted in the Queen Maud Gulf study area in 2003 were particularly early (13-19 June) for these species. Habitat associations as they relate to nesting ecology are likely not evident at this time.

Where habitat selection is complicated by social interaction, the identification of a species' 'preferred' habitat may become more difficult. Although king eiders and long-tailed ducks are typically considered solitary nesters, reports exist of these species nesting in loose groups; often the two species nesting near each other or with species such as arctic tern (*Sterna paradisaea*) (Kellett and Alisauskas 1997, Kear 2005). The 'semicolonial' nature of king eiders and long-tailed ducks on the breeding grounds may then have contributed to poor model fit for these species.

An implicit assumption of species-habitat modeling is that species are in equilibrium with their environment (Franklin 1995). However, if a species is not at carrying capacity within the landscape under investigation, model fit may be poor. Factors operating beyond the temporal and spatial scope of the data used to develop the models (e.g., low recruitment in previous breeding seasons or factors limiting populations on the wintering grounds) likely influence the detection of habitat associations and may have diminished model precision in this research.

4.4.2 Identification of Key Areas for Focal Species

Despite varying performance of predictive models, key regions for focal species were evident in both study areas. In the QMG study area, lowland areas in close proximity to the coast display the highest value for most species examined. As suggested by the models, these areas tend to correspond with extensive watersheds of major rivers where lowland habitats are most abundant. Models identify the McNaughton River area to the base of the Klutschak Peninsula to be particularly important for Canada geese, tundra swans, king eiders, and long-tailed ducks. The drainage south and east of Atkinson Point was calculated to be significant for white-fronted geese, Canada geese, king eiders, and long-tailed ducks; while in the northwest of the study area, the Kuugaarriuk River and Tingmeak River region also was estimated to be valuable for these species. Further, the Perry River drainage exhibited additional importance for white-fronted geese.

Previous surveys of white-fronted geese and tundra swans in the RL study area (McLaren and McLaren 1984, Hines et al. 2003) provide support for model predictions of these species here. In the RL study area, the foremost region for white-fronted geese and tundra swans was the lowlands surrounding the Murchison River and Inglis River (the Inglis River area was estimated to be especially valuable). The Ross Hills in the north of the RL study area, an area characterized by large lakes, was also forecast to be significant for tundra swan encounters. White-fronted geese were further predicted to have relatively high encounter probabilities in southern regions of the study area, especially in the watersheds of the Castor and Pollux River and Kitingujaalik River.

Specific regions significant for Canada geese were not identifiable in the RL study area as encounters were predicted to be high throughout. Although the high predicted encounter probabilities estimated for this species are clearly exaggerated, the uniform distribution calculated throughout the study area is consistent with observations by Hines and others (2003).

Relative to other areas, model results suggest that the Inglis River and Murchison River region is important for king eiders, although during the validation procedure this model was found to be not significantly different than the null 'random classifier' model in RL study area. Similarly, ROC results for the long-tailed duck model in the RL study area indicated that identification of important regions for this species was not reliable with the environment variates that I considered.

4.4.3 Summary

Although predictive precision varied among focal waterfowl species in this research, important land covers and key regions were identifiable for most species considered. Landscapes with abundant wet sedge meadow cover were demonstrated to be the most notable for encounters of focal species. The land cover manipulation exercise predicted significant reductions in high quality landscapes for all focal species and suggests that probabilities of encountering focal species will be diminished throughout the QMG and RL study areas. While specific effect sizes of such landscape-level change are debatable, overall directions of predicted trends are less contentious. The importance of lowland land covers was apparent for most focal species, and it is these habitats that are projected to be most affect by climate-driven changes (Komárková and Webber 1980, Hinzman et al. 2005). Loss or degradation of these lowland land cover types may have considerable consequence for species considered.

This study provides evidence that broad-scale species-habitat models are able to increase our understanding of species ecology and offer data for management planning. Detailed and fine-grained ecological data collected through intensive surveys to assess populations, distributions, or habitat selections factors are inevitably restricted to a few species and are limited in their spatial scope and temporal replication. Major environmental issues facing natural lands and species however, are increasingly occurring on broad spatial scales; namely those associated with habitat and climate change. The application of modeling approaches to estimate large-scale species' distributions based on habitat covariates is therefore both advantageous and ever more realistic. "The feasibility of species/habitat models should be explored as a matter of urgency" (Cowley et al. 2000).

The use of species-habitat methodology is particularly attractive for those species inhabiting remote lands such as those in the arctic. Given the sensitivity and vastness of arctic areas (Walker and Walker 1991), proactive planning tools will be necessary to minimize cumulative environmental impacts to species and habitats (Walker et al. 1987). I believe habitat-based model predictions provide guidance as to the potential effects of environmental change on the distribution of arctic wildlife and draw attention to habitats and regions that require special emphasis in conservation and management plans.

4.5 TABLES

Table 4.1 Candidate multi-scale models to estimate encounters of focal species in the Queen Maud Gulf study area (22-26 June, 2002 and 13-19 June, 2003) in relation to geographic and land cover covariates. Models are ranked by Akaike's information criterion (AIC). Also included are the difference in AIC units between the respective model and the best model (Δ_i), Akaike weight (w), and number of estimable parameters (K). Results for the null model and those models included in model-averaging confidence sets are displayed. Spatial scale of land cover variables are given in subscript following the variable code.

Table 4.1.a White-fronted goose

MODEL ^a	AIC	Δ_i	w	K
LON + LAT + ELEV + H ₂ OCLR ₁₀ + H ₂ OTUR ₁ + AD _{2.5} + WSM ₁₀ + HGT ₁ + TGT _{2.5} + ST _{seg} + MOSS _{2.5} + BBF ₁₀ + EP ₁₀ + ICE _{seg}	2577.99	0.00	0.31	15
LON + ELEV + H ₂ OCLR ₁₀ + H ₂ OTUR ₁ + AD _{2.5} + WSM ₁₀ + HGT ₁ + TGT _{2.5} + ST _{seg} + MOSS _{2.5} + BBF ₁₀ + EP ₁₀ + ICE _{seg}	2578.71	0.71	0.22	14
LON + LAT + ELEV + H ₂ OCLR ₁₀ + H ₂ OTUR ₁ + AD _{2.5} + WSM ₁₀ + HGT ₁ + TGT _{2.5} + ST _{seg} + MOSS _{2.5} + LHT ₁₀ + BBF ₁₀ + EP ₁₀ + ICE _{seg}	2578.82	0.83	0.21	16
ELEV + H ₂ OCLR ₁₀ + H ₂ OTUR ₁ + AD _{2.5} + WSM ₁₀ + HGT ₁ + TGT _{2.5} + ST _{seg} + MOSS _{2.5} + BBF ₁₀ + EP ₁₀ + ICE _{seg}	2579.30	1.31	0.16	13
LON + LAT + ELEV + H ₂ OCLR ₁₀ + H ₂ OMT ₁₀ + H ₂ OTUR ₁ + AD _{2.5} + WSM ₁₀ + HGT ₁ + TGT _{2.5} + ST _{seg} + MOSS _{2.5} + LHT ₁₀ + BBF ₁₀ + EP ₁₀ + ICE _{seg}	2580.60	2.60	0.09	17
null	3073.15	495.15	0.00	2

^a Abbreviations used: ELEV = elevation; LON = longitude; LAT = latitude; CSTDIST = distance to the coast; H₂OCLR = water, clear; H₂OMT = water, moderately turbid; H₂OTUR = water, turbid; AD = active deposits; WSM = wet sedge meadow; HGT = hummock graminoid tundra; TGT = tussock graminoid tundra; LST = low shrub tundra; ST = shrub thicket; MLT = moss-lichen tundra; LHT = lichen-heath tundra; BBF = bedrock and boulder field; EP = exposed peat.

Table 4.1.b Canada goose

MODEL ^a	AIC	Δ_i	w	K
LON + LAT + ELEV + H ₂ OCLR _{seg} + H ₂ OMT _{seg} + WSM _{seg} + HGT _{2.5} + TGT _{seg} + LST ₁₀ + ST ₁₀ + LHT _{seg} + BBF ₁ + EP ₁₀ + ICE _{seg}	2806.02	0.00	0.33	15
LON + LAT + ELEV + H ₂ OCLR _{seg} + H ₂ OMT _{seg} + AD ₁₀ + WSM _{seg} + HGT _{2.5} + TGT _{seg} + LST ₁₀ + ST ₁₀ + LHT _{seg} + BBF ₁ + EP ₁₀ + ICE _{seg}	2806.88	0.86	0.22	16
LON + LAT + ELEV + H ₂ OCLR _{seg} + H ₂ OMT _{seg} + H ₂ OTUR ₁₀ + AD ₁₀ + WSM _{seg} + HGT _{2.5} + TGT _{seg} + LST ₁₀ + ST ₁₀ + LHT _{seg} + BBF ₁ + EP ₁₀ + ICE _{seg}	2807.59	1.57	0.15	17
LON + LAT + ELEV + H ₂ OCLR _{seg} + H ₂ OMT _{seg} + WSM _{seg} + TGT _{seg} + LST ₁₀ + ST ₁₀ + LHT _{seg} + BBF ₁ + EP ₁₀ + ICE _{seg}	2808.22	2.20	0.11	14
LON + LAT + ELEV + H ₂ OCLR _{seg} + H ₂ OMT _{seg} + H ₂ OTUR ₁₀ + AD ₁₀ + WSM _{seg} + HGT _{2.5} + TGT _{seg} + LST ₁₀ + ST ₁₀ + MOSS ₁ + LHT _{seg} + BBF ₁ + EP ₁₀ + ICE _{seg}	2809.22	3.20	0.07	18
LON + LAT + ELEV + H ₂ OCLR _{seg} + H ₂ OMT _{seg} + WSM _{seg} + LST ₁₀ + ST ₁₀ + LHT _{seg} + BBF ₁ + EP ₁₀ + ICE _{seg}	2809.28	3.26	0.07	13
null	3082.80	276.78	0.00	2

^a Abbreviations used: ELEV = elevation; LON = longitude; LAT = latitude; CSTDIST = distance to the coast; H₂OCLR = water, clear; H₂OMT = water, moderately turbid; H₂OTUR = water, turbid; AD = active deposits; WSM = wet sedge meadow; HGT = hummock graminoid tundra; TGT = tussock graminoid tundra; LST = low shrub tundra; ST = shrub thicket; MLT = moss-lichen tundra; LHT = lichen-heath tundra; BBF = bedrock and boulder field; EP = exposed peat.

Table 4.1.c Tundra swan

MODEL ^a	AIC	Δ_i	w	K
LON + LAT + ELEV + H ₂ OCLR _{seg} + H ₂ OTUR _{2.5} + AD ₁₀ + WSM ₁₀ + HGT _{seg} + LHT ₁₀ + EP ₁	1953.32	0.00	0.43	11
LON + LAT + ELEV + H ₂ OCLR _{seg} + H ₂ OTUR _{2.5} + AD ₁₀ + WSM ₁₀ + HGT _{seg} + MOSS _{seg} + LHT ₁₀ + EP ₁	1955.01	1.69	0.18	12
LON + LAT + ELEV + H ₂ OCLR _{seg} + H ₂ OMT ₁₀ + H ₂ OTUR _{2.5} + AD ₁₀ + WSM ₁₀ + HGT _{seg} + MOSS _{seg} + LHT ₁₀ + EP ₁	1956.30	2.99	0.10	13
LON + LAT + ELEV + H ₂ OCLR _{seg} + H ₂ OMT ₁₀ + H ₂ OTUR _{2.5} + AD ₁₀ + WSM ₁₀ + HGT _{seg} + TGT ₁ + MOSS _{seg} + LHT ₁₀ + EP ₁	1956.80	3.48	0.08	14
LON + LAT + ELEV + CSTDIST + H ₂ OCLR _{seg} + H ₂ OTUR _{2.5} + AD ₁₀ + WSM ₁₀ + HGT _{seg} + TGT ₁ + MOSS _{seg} + LHT ₁₀ + EP ₁ + ICE _{seg}	1957.50	4.18	0.05	15
LAT + ELEV + H ₂ OCLR _{seg} + H ₂ OTUR _{2.5} + AD ₁₀ + WSM ₁₀ + HGT _{seg} + LHT ₁₀	1958.02	4.70	0.04	9
LAT + ELEV + H ₂ OCLR _{seg} + H ₂ OTUR _{2.5} + AD ₁₀ + WSM ₁₀ + HGT _{seg} + LHT ₁₀ + EP ₁	1958.28	4.96	0.04	10
null	2113.88	160.56	0.00	2

^a Abbreviations used: ELEV = elevation; LON = longitude; LAT = latitude; CSTDIST = distance to the coast; H₂OCLR = water, clear; H₂OMT = water, moderately turbid; H₂OTUR = water, turbid; AD = active deposits; WSM = wet sedge meadow; HGT = hummock graminoid tundra; TGT = tussock graminoid tundra; LST = low shrub tundra; ST = shrub thicket; MLT = moss-lichen tundra; LHT = lichen-heath tundra; BBF = bedrock and boulder field; EP = exposed peat.

Table 4.1.d King eider

MODEL ^a	AIC	Δ_i	w	K
ELEV + H ₂ OCLR _{seg} + AD _{seg} + WSM ₁₀ + HGT _{seg} + LST ₁₀ + LHT _{2.5} + ICE ₁₀	1955.03	0.00	0.18	9
ELEV + H ₂ OCLR _{seg} + AD _{seg} + WSM ₁₀ + HGT _{seg} + LST ₁₀ + LHT _{2.5} + EP _{2.5} + ICE ₁₀	1955.32	0.29	0.15	10
ELEV + H ₂ OCLR _{seg} + AD _{seg} + WSM ₁₀ + LST ₁₀ + LHT _{2.5} + ICE ₁₀	1955.43	0.41	0.15	8
LAT + H ₂ OCLR _{seg} + H ₂ OMT ₁₀ + H ₂ OTUR ₁₀ + AD _{seg} + WSM ₁₀ + HGT _{seg} + LST ₁₀ + LHT _{2.5} + EP _{2.5} + ICE ₁₀	1955.95	0.93	0.11	12
ELEV + H ₂ OCLR _{seg} + WSM ₁₀ + LST ₁₀ + LHT _{2.5} + ICE ₁₀	1956.48	1.46	0.09	7
H ₂ OCLR _{seg} + H ₂ OMT ₁₀ + H ₂ OTUR ₁₀ + AD _{seg} + WSM ₁₀ + HGT _{seg} + LST ₁₀ + LHT _{2.5} + EP _{2.5} + ICE ₁₀	1956.55	1.53	0.08	11
ELEV + H ₂ OCLR _{seg} + H ₂ OMT ₁₀ + H ₂ OTUR ₁₀ + AD _{seg} + WSM ₁₀ + HGT _{seg} + LST ₁₀ + MOSS _{2.5} + LHT _{2.5} + BBF _{2.5} + EP _{2.5} + ICE ₁₀	1956.78	1.76	0.07	14
ELEV + H ₂ OCLR _{seg} + H ₂ OMT ₁₀ + H ₂ OTUR ₁₀ + AD _{seg} + WSM ₁₀ + HGT _{seg} + LST ₁₀ + MOSS _{2.5} + LHT _{2.5} + EP _{2.5} + ICE ₁₀	1957.81	2.79	0.04	13
ELEV + H ₂ OCLR _{seg} + H ₂ OMT ₁₀ + H ₂ OTUR ₁₀ + AD _{seg} + WSM ₁₀ + HGT _{seg} + LST ₁₀ + ST _{seg} + MOSS _{2.5} + LHT _{2.5} + BBF _{2.5} + EP _{2.5} + ICE ₁₀	1957.82	2.79	0.04	15
ELEV + H ₂ OCLR _{seg} + MOSS _{2.5} + LHT _{2.5} + BBF _{2.5}	1957.86	2.83	0.04	6
ELEV + H ₂ OCLR _{seg} + H ₂ OMT ₁₀ + H ₂ OTUR ₁₀ + AD _{seg} + WSM ₁₀ + HGT _{seg} + TGT _{2.5} + LST ₁₀ + ST _{seg} + MOSS _{2.5} + LHT _{2.5} + BBF _{2.5} + EP _{2.5} + ICE ₁₀	1959.41	4.39	0.02	16
null	2033.25	78.22	0.00	2

^a Abbreviations used: ELEV = elevation; LON = longitude; LAT = latitude; CSTDIST = distance to the coast; H₂OCLR = water, clear; H₂OMT = water, moderately turbid; H₂OTUR = water, turbid; AD = active deposits; WSM = wet sedge meadow; HGT = hummock graminoid tundra; TGT = tussock graminoid tundra; LST = low shrub tundra; ST = shrub thicket; MLT = moss-lichen tundra; LHT = lichen-heath tundra; BBF = bedrock and boulder field; EP = exposed peat.

Table 4.1.e Long-tailed duck

MODEL ^a	AIC	Δ_i	w	K
H ₂ OMT ₁₀ + H ₂ OTUR _{seg} + WSM ₁₀ + HGT ₁ + LHT ₁ + EP ₁₀	2529.26	0.00	0.20	7
H ₂ OMT ₁₀ + H ₂ OTUR _{seg} + WSM ₁₀ + HGT ₁ + MOSS ₁₀ + LHT ₁ + EP ₁₀	2529.45	0.19	0.18	8
H ₂ OMT ₁₀ + WSM ₁₀ + HGT ₁ + LHT ₁ + EP ₁₀	2530.22	0.96	0.12	6
H ₂ OCLR ₁₀ + H ₂ OTUR _{seg} + WSM ₁₀ + HGT ₁ + ST _{2.5} + MOSS ₁₀ + LHT ₁ + BBF _{2.5} + ICE _{2.5}	2530.46	1.20	0.11	10
H ₂ OMT ₁₀ + H ₂ OTUR _{seg} + WSM ₁₀ + HGT ₁ + MOSS ₁₀ + LHT ₁ + BBF _{2.5} + EP ₁₀	2530.60	1.34	0.10	9
H ₂ OCLR ₁₀ + H ₂ OMT ₁₀ + H ₂ OTUR _{seg} + WSM ₁₀ + HGT ₁ + ST _{2.5} + MOSS ₁₀ + LHT ₁ + BBF _{2.5} + ICE _{2.5}	2531.05	1.79	0.08	11
H ₂ OMT ₁₀ + H ₂ OTUR _{seg} + WSM ₁₀ + LHT ₁	2531.30	2.04	0.07	5
CSTDIST + H ₂ OCLR ₁₀ + H ₂ OMT ₁₀ + H ₂ OTUR _{seg} + WSM ₁₀ + HGT ₁ + ST _{2.5} + MOSS ₁₀ + LHT ₁ + BBF _{2.5} + ICE _{2.5}	2532.86	3.60	0.03	12
H ₂ OMT ₁₀ + WSM ₁₀ + LHT ₁	2533.27	4.01	0.03	4
H ₂ OCLR ₁₀ + H ₂ OMT ₁₀ + H ₂ OTUR _{seg} + WSM ₁₀ + HGT ₁ + TGT _{2.5} + ST _{2.5} + MOSS ₁₀ + LHT ₁ + BBF _{2.5} + EP ₁₀ + ICE _{2.5}	2533.64	4.38	0.02	13
null	2545.87	16.61	0.00	2

^a Abbreviations used: ELEV = elevation; LON = longitude; LAT = latitude; CSTDIST = distance to the coast; H₂OCLR = water, clear; H₂OMT = water, moderately turbid; H₂OTUR = water, turbid; AD = active deposits; WSM = wet sedge meadow; HGT = hummock graminoid tundra; TGT = tussock graminoid tundra; LST = low shrub tundra; ST = shrub thicket; MLT = moss-lichen tundra; LHT = lichen-heath tundra; BBF = bedrock and boulder field; EP = exposed peat.

Table 4.2 Logistic regression equations of final (model-averaged) models used to estimate encounters, $y_i = 0$ or 1, of focal species in the Queen Maud Gulf study area, 2002-2003, and the Rasmussen Lowlands study area, 2006. For the Queen Maud Gulf study area, parameter estimates represent averaged estimates over multiple (40) iterations. Spatial scale of each land cover variable is given as subscript following the variable code.

Focal Species ^a	Equation ^b
WFGO (eqn 1)	$y_i = 19.627 + 0.082(\text{LON}) - 0.401(\text{LAT}) - 0.985(\text{ELEV}) - 0.462(\text{H2OCLR}_{10}) + 0.005(\text{H2OMT}_{10}) - 0.217(\text{H2OTUR}_1) - 0.150(\text{AD}_{2.5}) + 0.784(\text{WSM}_{10}) + 0.306(\text{HGT}_1) + 0.287(\text{TGT}_{2.5}) + 0.269(\text{ST}_{\text{seg}}) - 0.230(\text{MLT}_{2.5}) + 0.083(\text{LHT}_{10}) + 0.452(\text{BBF}_{10}) - 0.771(\text{EP}_{10}) - 0.436(\text{ICE}_{\text{seg}})$
CAGO (eqn. 2)	$y_i = -70.270 - 0.123(\text{LON}) + 1.252(\text{LAT}) - 0.477(\text{ELEV}) + 0.152(\text{H2OCLR}_{\text{seg}}) + 0.086(\text{H2OMT}_{\text{seg}}) - 0.029(\text{H2OTUR}_{10}) + 0.053(\text{AD}_{10}) + 0.191(\text{WSM}_{\text{seg}}) + 0.092(\text{HGT}_{2.5}) - 0.094(\text{TGT}_{\text{seg}}) - 0.310(\text{LST}_{10}) + 0.511(\text{ST}_{10}) - 0.003(\text{MLT}_1) - 0.163(\text{LHT}_{\text{seg}}) + 0.135(\text{BBF}_1) - 0.591(\text{EP}_{10}) - 0.427(\text{ICE}_{\text{seg}})$
TUSW (eqn. 3)	$y_i = -109.955 - 0.103(\text{LON}) + 1.698(\text{LAT}) - 0.259(\text{ELEV}) - 0.006(\text{CSTDIST}) + 0.183(\text{H2OCLR}_{\text{seg}}) - 0.017(\text{H2OMT}_{10}) + 0.148(\text{H2OTUR}_{2.5}) + 0.289(\text{AD}_{10}) + 0.711(\text{WSM}_{10}) + 0.128(\text{HGT}_{\text{seg}}) + 0.011(\text{TGT}_1) + 0.017(\text{MLT}_{\text{seg}}) + 0.461(\text{LHT}_{10}) - 0.356(\text{EP}_1) - 0.007(\text{ICE}_{\text{seg}})$
KIEI (eqn. 4)	$y_i = -7.500 + 0.053(\text{LAT}) - 0.201(\text{ELEV}) + 0.188(\text{H2OCLR}_{\text{seg}}) - 0.084(\text{H2OMT}_{10}) + 0.088(\text{H2OTUR}_{10}) + 0.104(\text{AD}_{\text{seg}}) + 0.752(\text{WSM}_{10}) + 0.063(\text{HGT}_{\text{seg}}) + 0.001(\text{TGT}_{2.5}) - 0.343(\text{LST}_{10}) + 0.005(\text{ST}_{\text{seg}}) + 0.033(\text{MLT}_{2.5}) + 0.464(\text{LHT}_{2.5}) + 0.031(\text{BBF}_{2.5}) - 0.199(\text{EP}_{2.5}) + 0.112(\text{ICE}_{10})$
LTDU (eqn. 5)	$y_i = -2.961 - 0.001(\text{CSTDIST}) + 0.054(\text{H2OCLR}_{10}) - 0.215(\text{H2OMT}_{10}) + 0.085(\text{H2OTUR}_{\text{seg}}) + 0.537(\text{WSM}_{10}) + 0.092(\text{HGT}_1) + 0.001(\text{TGT}_{2.5}) + 0.036(\text{ST}_{2.5}) + 0.076(\text{MLT}_{10}) + 0.197(\text{LHT}_1) + 0.041(\text{BBF}_{2.5}) - 0.217(\text{EP}_{10}) + 0.051(\text{ICE}_{2.5})$

^a Abbreviations used: WFGO = white-fronted goose; CAGO = Canada goose; TUSW = tundra swan; KIEI = king eider; LTDU = long-tailed duck.

^b Abbreviations used: ELEV = elevation; LON = longitude; LAT = latitude; CSTDIST = distance to the coast; H₂OCLR = water, clear; H₂OMT = water, moderately turbid; H₂OTUR = water, turbid; AD = active deposits; WSM = wet sedge meadow; HGT = hummock graminoid tundra; TGT = tussock graminoid tundra; LST = low shrub tundra; ST = shrub thicket; MLT = moss-lichen tundra; LHT = lichen-heath tundra; BBF = bedrock and boulder field; EP = exposed peat.

Table 4.3 Area under the curve (AUC) results from receiver operating characteristic analyses for logistic regression models used to predict encounters of focal species in the Queen Maud Gulf (QMG) study area, 2002-2003. AUC estimates have been averaged across 40 iterations of sub-samples of the QMG data. The AUC is equal to the probability that two randomly selected segments from the encounters and non-encounters groups will be correctly discriminated by a given model. *P* refers to the probability that the AUC of a given model is significantly different than the null model (where $AUC \leq 0.5$).

Species	Area Under the Curve	Standard Error	Asymptotic 95% Confidence Interval		<i>P</i>
			Lower Bound	Upper Bound	
white-fronted goose	0.765	0.010	0.746	0.785	0.000
Canada goose	0.709	0.011	0.688	0.730	0.000
tundra swan	0.708	0.014	0.682	0.735	0.000
king eider	0.656	0.015	0.627	0.686	0.000
long-tailed duck	0.580	0.014	0.553	0.607	0.000

Table 4.4 Area under the curve (AUC) results from receiver operating characteristic analyses for logistic regression models used to predict encounters of focal species in the Rasmussen Lowlands study area, 2006. The AUC is equal to the probability that two randomly selected segments from the encounters and non-encounters groups will be correctly discriminated by a given model. *P* refers to the probability that the AUC of a given model is significantly different than the null model (where $AUC \leq 0.5$).

Species	Area Under the Curve	Standard Error	Asymptotic 95% Confidence Interval		<i>P</i>
			Lower Bound	Upper Bound	
white-fronted goose	0.680	0.029	0.622	0.738	0.000
Canada goose	0.651	0.032	0.588	0.714	0.000
tundra swan	0.655	0.035	0.587	0.723	0.000
king eider	0.591	0.048	0.498	0.685	0.051
long-tailed duck	0.462	0.061	0.343	0.581	0.527

Table 4.5 Proportions of the Queen Maud Gulf study area and the Rasmussen Lowlands study area predicted as suitable habitat for each focal species, as guided by the probability of species encounter. Predictions are based on encounter probability models calculated using classified satellite image variables.

Species ^a	Suitability	Probability of Encounter	QMG		RL	
			% Area	Area (km ²)	% Area	Area (km ²)
WFGO	Very Low Suitability	0 - 0.25	25.2	7783.0	61.9	6492.7
	Low Suitability	0.25 - 0.50	35.4	10923.3	34.0	3564.7
	Moderately Suitable	0.50 - 0.75	33.5	10347.1	4.1	425.4
	Highly Suitable	0.75 - 1	5.8	1803.8	0.0	5.2
CAGO	Very Low Suitability	0 - 0.25	3.6	1118.7	0.0	0.0
	Low Suitability	0.25 - 0.50	43.2	13331.4	0.0	0.0
	Moderately Suitable	0.50 - 0.75	42.6	13141.7	2.1	222.3
	Highly Suitable	0.75 - 1	10.6	3265.4	97.9	10265.7
TUSW	Very Low Suitability	0 - 0.25	99.0	30554.9	9.1	957.3
	Low Suitability	0.25 - 0.50	1.0	302.2	50.9	5342.0
	Moderately Suitable	0.50 - 0.75	0.0	0.0	39.7	4167.4
	Highly Suitable	0.75 - 1	0.0	0.0	0.2	21.3
KIEI	Very Low Suitability	0 - 0.25	81.8	25255.3	59.9	6280.3
	Low Suitability	0.25 - 0.50	18.1	5599.0	40.1	4207.7
	Moderately Suitable	0.50 - 0.75	0.0	2.8	0.0	0.0
	Highly Suitable	0.75 - 1	0.0	0.0	0.0	0.0
LTDU	Very Low Suitability	0 - 0.25	36.0	11106.0	19.2	2014.2
	Low Suitability	0.25 - 0.50	64.0	19751.1	80.8	8473.6
	Moderately Suitable	0.50 - 0.75	0.0	0.0	0.0	0.2
	Highly Suitable	0.75 - 1	0.0	0.0	0.0	0.0

^a Abbreviations used: WFGO = white-fronted goose; CAGO = Canada goose; TUSW = tundra swan; KIEI = king eider; LTDU = long-tailed duck.

Table 4.6 Proportion of land cover types adjusted in the land cover manipulation exercise used to simulate climate-driven vegetation responses with predicted climate change.

Land Cover ^a	Direction of Change	Proportional Change (%)		
		Manipulation 1	Manipulation 2	Manipulation 3
WSM	-	10.0	15.0	20.0
HGT	-	0.0	5.0	10.0
TGT	-	0.0	10.0	15.0
LST	+	2.0	6.6	10.4
ST	+	4.0	10.2	14.0
AD	+	2.0	6.6	10.4
EP	+	2.0	6.6	10.4

^a Abbreviations used: WSM = wet sedge meadow; HGT = hummock graminoid tundra; TGT = tussock graminoid tundra; LST = low shrub tundra; ST = shrub thicket; AD = active deposits; EP = exposed peat.

Table 4.7 Proportions of the Queen Maud Gulf study area predicted as suitable habitat for each focal species before and after climate-driven land cover manipulations. Suitability is guided by the probability of species encounter. Predictions are based on encounter probability models calculated using classified satellite image variables. In manipulations 1-3, land covers were adjusted to simulate future climate-driven changes to arctic vegetation; % areas of predicted encounter probabilities were obtained by applying the species' distribution model to all manipulations.

Species ^a	Suitability	Probability of Encounter	% Area			
			No Manipulation	Manipulation 1	Manipulation 2	Manipulation 3
WFGO	Very Low Suitability	0 - 0.25	25.2	28.9	36.5	41.8
	Low Suitability	0.25 - 0.50	35.4	39.1	41.9	42.9
	Moderately Suitable	0.50 - 0.75	33.5	28.1	19.7	14.2
	Highly Suitable	0.75 - 1	5.8	3.9	1.9	1.1
CAGO	Very Low Suitability	0 - 0.25	3.6	3.6	3.5	4.6
	Low Suitability	0.25 - 0.50	43.2	44.3	47.0	48.7
	Moderately Suitable	0.50 - 0.75	42.6	42.1	41.1	39.8
	Highly Suitable	0.75 - 1	10.6	10.0	8.4	6.9
TUSW	Very Low Suitability	0 - 0.25	99.0	99.3	99.5	99.8
	Low Suitability	0.25 - 0.50	1.0	0.7	0.5	0.2
	Moderately Suitable	0.50 - 0.75	0.0	0.0	0.0	0.0
	Highly Suitable	0.75 - 1	0.0	0.0	0.0	0.0
KIEI	Very Low Suitability	0 - 0.25	81.8	86.6	91.7	94.4
	Low Suitability	0.25 - 0.50	18.1	13.4	8.3	5.6
	Moderately Suitable	0.50 - 0.75	0.0	0.0	0.0	0.0
	Highly Suitable	0.75 - 1	0.0	0.0	0.0	0.0
LTDU	Very Low Suitability	0 - 0.25	36.0	53.7	69.8	81.6
	Low Suitability	0.25 - 0.50	64.0	46.3	30.2	18.4
	Moderately Suitable	0.50 - 0.75	0.0	0.0	0.0	0.0
	Highly Suitable	0.75 - 1	0.0	0.0	0.0	0.0

^a Abbreviations used: WFGO = white-fronted goose; CAGO = Canada goose; TUSW = tundra swan; KIEI = king eider; LTDU = long-tailed duck.

Table 4.8 Proportions of the Rasmussen Lowlands study area predicted as suitable habitat for each focal species before and after climate-driven land cover manipulations. Suitability is guided by the probability of species encounter. Predictions are based on encounter probability models calculated using classified satellite image variables. In manipulations 1-3, land covers were adjusted to simulate future climate-driven changes to arctic vegetation; % areas of predicted encounter probabilities were obtained by applying the species' distribution model to all manipulations.

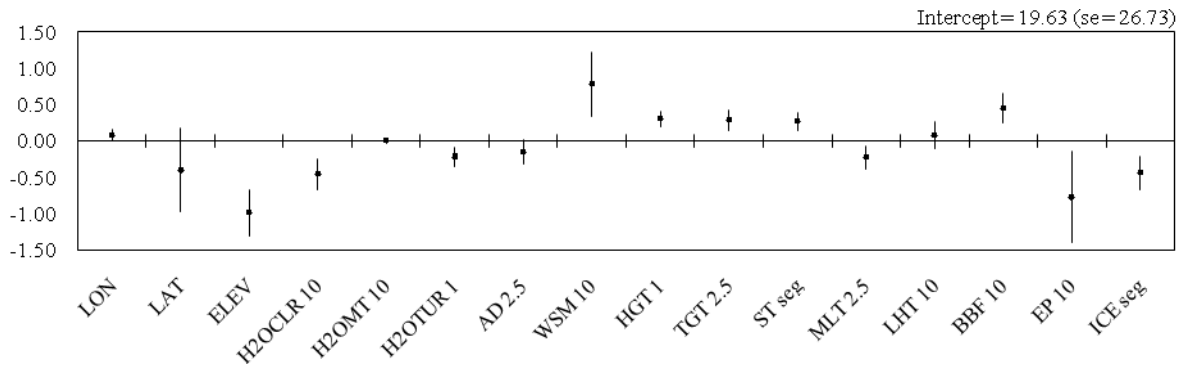
Species ^a	Suitability	Probability of Encounter	% Area			
			No Manipulation	Manipulation 1	Manipulation 2	Manipulation 3
WFGO	Very Low Suitability	0 - 0.25	61.9	69.4	78.7	86.1
	Low Suitability	0.25 - 0.50	34.0	27.5	19.2	12.7
	Moderately Suitable	0.50 - 0.75	4.1	3.1	2.1	1.2
	Highly Suitable	0.75 - 1	0.0	0.0	0.0	0.0
CAGO	Very Low Suitability	0 - 0.25	0.0	0.0	0.0	0.0
	Low Suitability	0.25 - 0.50	0.0	0.0	0.0	0.0
	Moderately Suitable	0.50 - 0.75	2.1	2.1	2.1	2.2
	Highly Suitable	0.75 - 1	97.9	97.9	97.9	97.8
TUSW	Very Low Suitability	0 - 0.25	9.1	18.5	22.4	27.3
	Low Suitability	0.25 - 0.50	50.9	49.3	50.0	48.0
	Moderately Suitable	0.50 - 0.75	39.7	32.2	27.6	24.6
	Highly Suitable	0.75 - 1	0.2	0.0	0.0	0.0
KIEI	Very Low Suitability	0 - 0.25	59.9	81.3	92.5	97.0
	Low Suitability	0.25 - 0.50	40.1	18.7	7.5	3.0
	Moderately Suitable	0.50 - 0.75	0.0	0.0	0.0	0.0
	Highly Suitable	0.75 - 1	0.0	0.0	0.0	0.0
LTDU	Very Low Suitability	0 - 0.25	19.2	20.2	20.7	21.3
	Low Suitability	0.25 - 0.50	80.8	79.8	79.3	78.7
	Moderately Suitable	0.50 - 0.75	0.0	0.0	0.0	0.0
	Highly Suitable	0.75 - 1	0.0	0.0	0.0	0.0

^a Abbreviations used: WFGO = white-fronted goose; CAGO = Canada goose; TUSW = tundra swan; KIEI = king eider; LTDU = long-tailed duck.

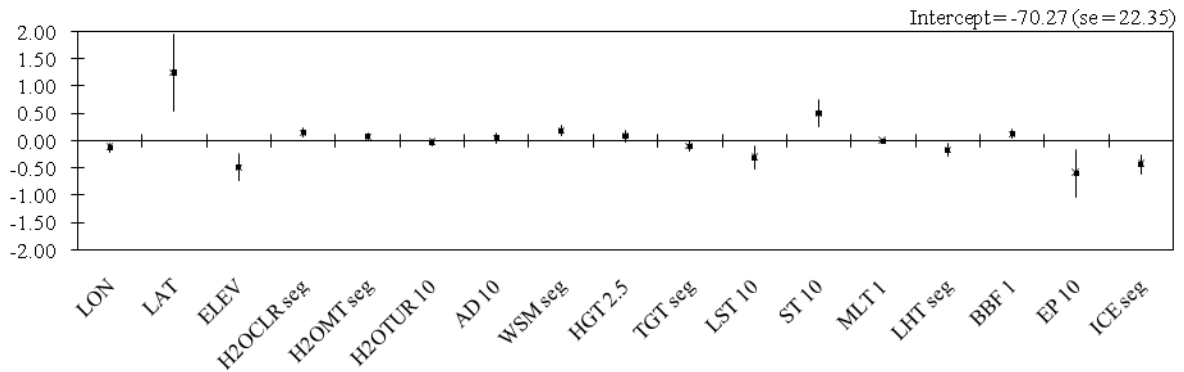
4.6 FIGURES

Figure 4.1 Parameter estimates and 95% confidence intervals for geographic and land cover predictor variables used to estimate encounters of focal species in the Queen Maud Gulf study area (22-26 June, 2002 and 13-19 June, 2003). Spatial scale of land cover variables are given following the variable code.

4.1.a White-fronted goose



4.1.b Canada goose



4.1.c Tundra swan

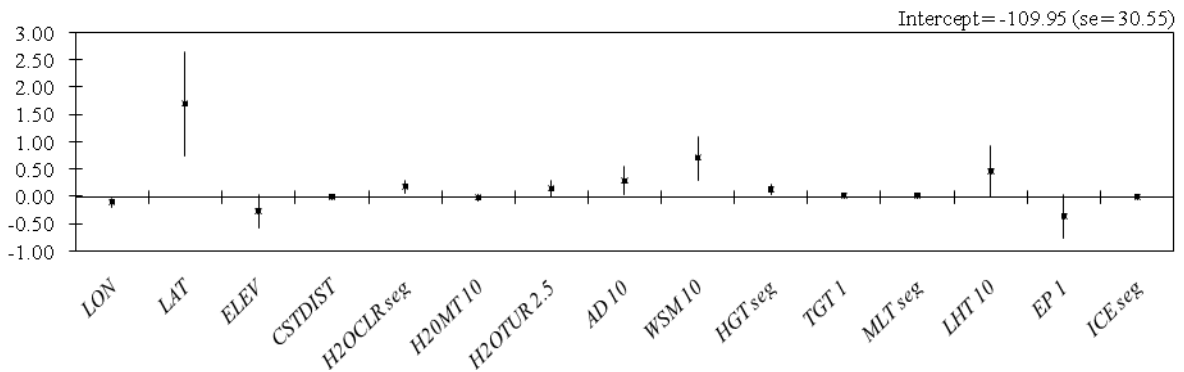
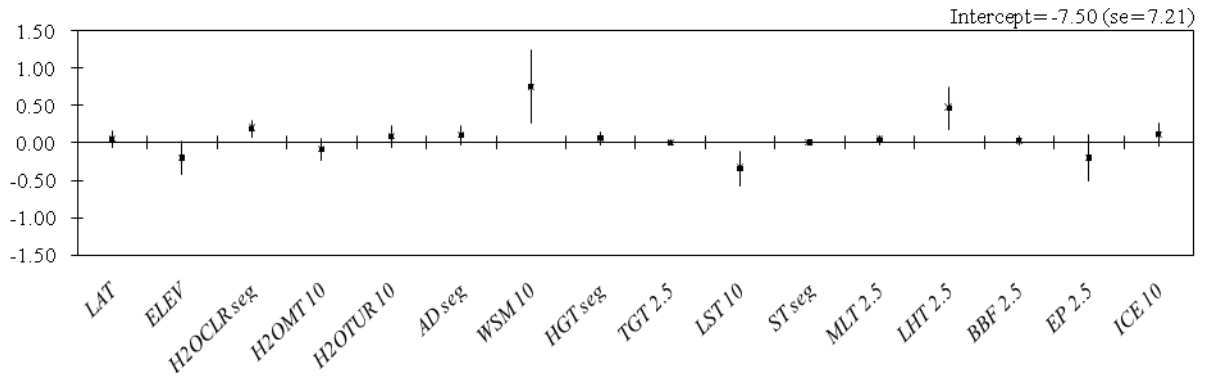


Figure 4.1 (continued) Parameter estimates and 95% confidence intervals for geographic and land cover predictor variables used to estimate encounters of focal species in the Queen Maud Gulf study area (22-26 June, 2002 and 1 3-19 June, 2003). Spatial scale of land cover variables are given following the variable code.

4.1.d King eider



4.1.e Long-tailed duck

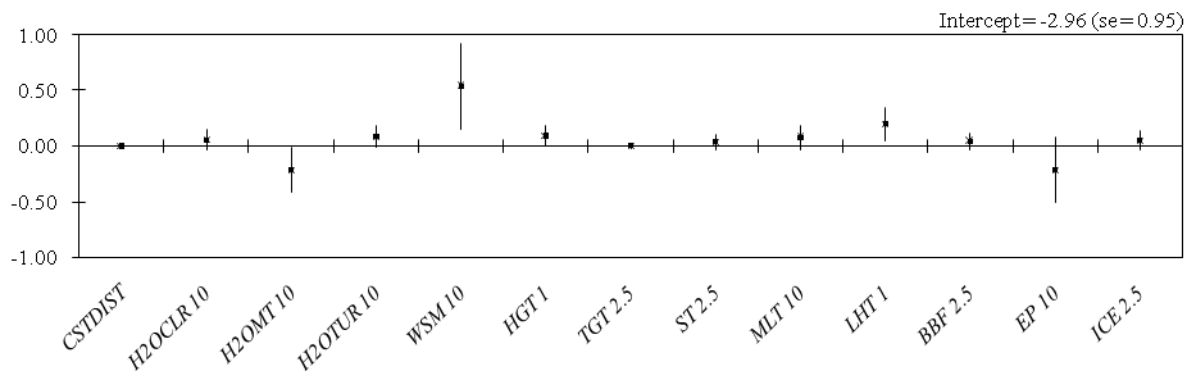


Figure 4.2 Receiver operating characteristic plots for logistic regression models used to predict encounters of focal species in the Queen Maud Gulf study area, 2002-2003, and Rasmussen Lowlands study area 2006.

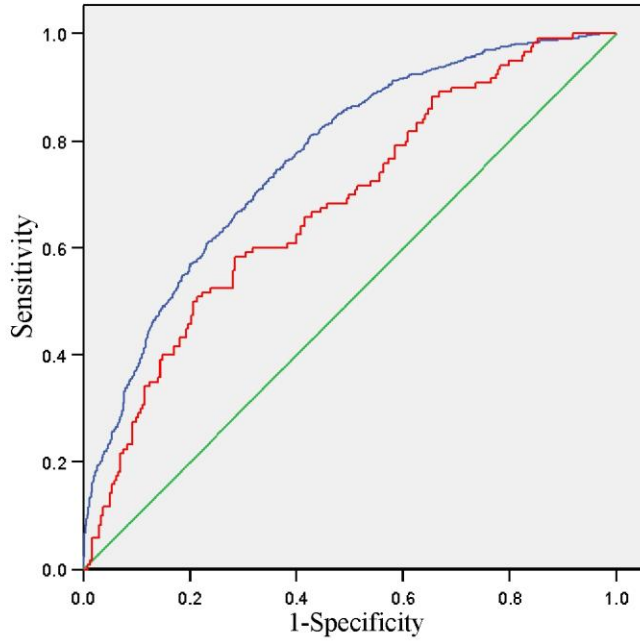


Figure 4.2.a White-fronted goose

- Queen Maud Gulf Model
- Rasmussen Lowlands Model
- Random Classifier

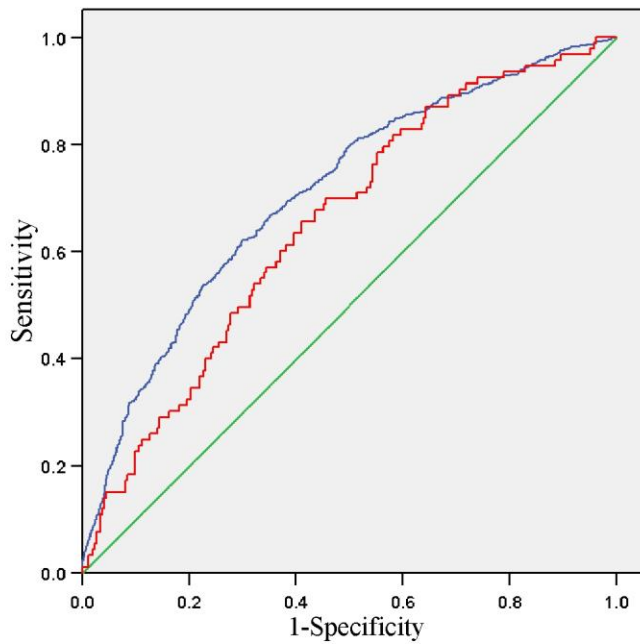


Figure 4.2.b Canada goose

- Queen Maud Gulf Model
- Rasmussen Lowlands Model
- Random Classifier

Figure 4.2 (continued) Receiver operating characteristic plots for logistic regression models used to predict encounters of focal species in the Queen Maud Gulf study area, 2002-2003, and Rasmussen Lowlands study area 2006.

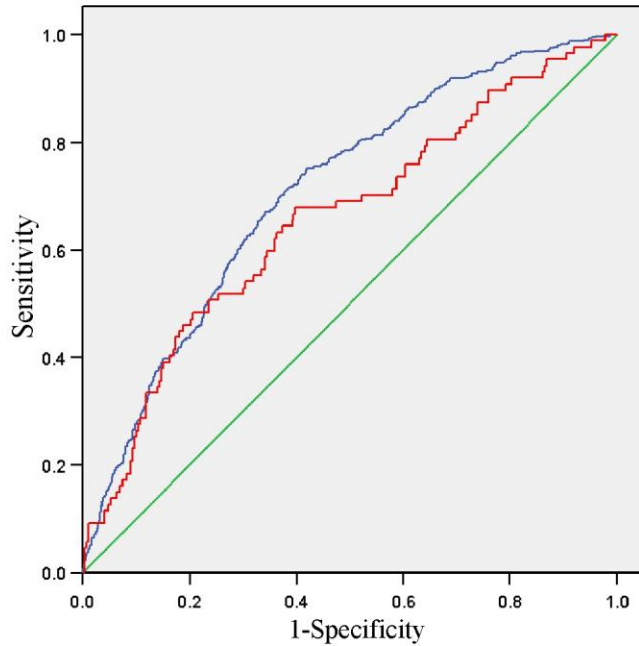


Figure 4.2.c Tundra swan

- Queen Maud Gulf Model
- Rasmussen Lowlands Model
- Random Classifier

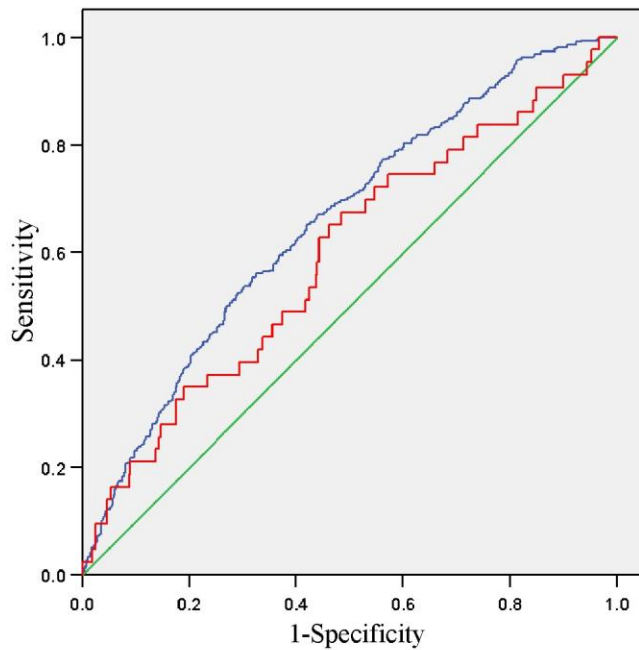


Figure 4.2.d King eider

- Queen Maud Gulf Model
- Rasmussen Lowlands Model
- Random Classifier

Figure 4.2 (continued) Receiver operating characteristic plots for logistic regression models used to predict encounters of focal species in the Queen Maud Gulf study area, 2002-2003, and Rasmussen Lowlands study area 2006.

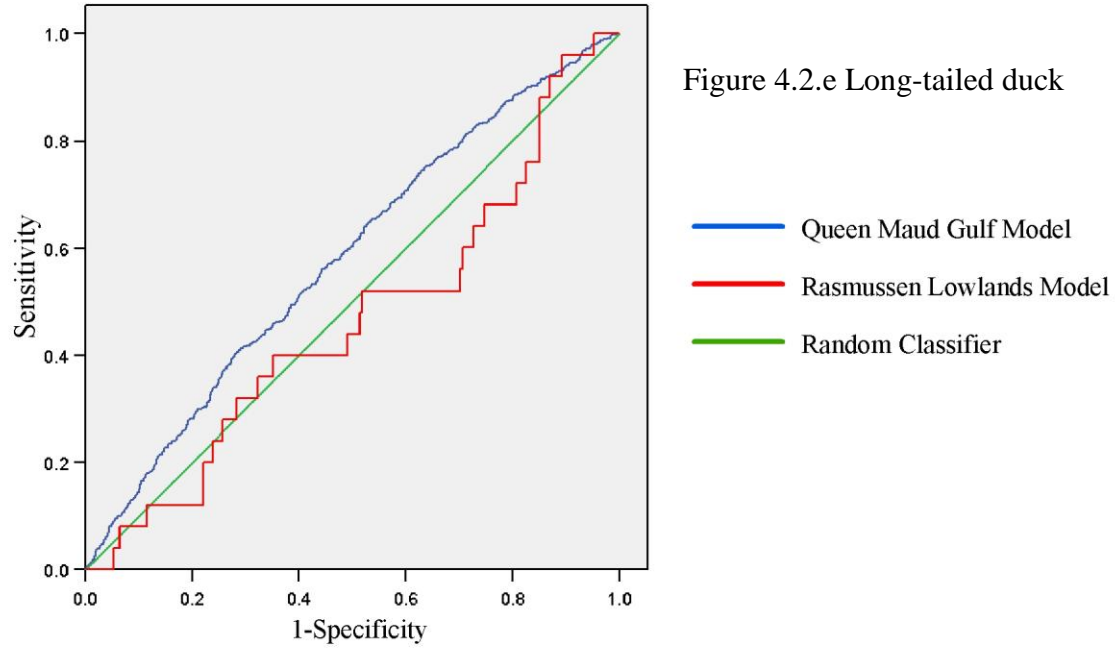


Figure 4.3 Predicted encounter probabilities of focal species within the Queen Maud Gulf study area. Probabilities are generated from logistic models of species encounters relative to classified satellite imagery land cover variables. Abbreviations used: WFGO = white-fronted goose; CAGO = Canada goose; TUSW = tundra swan; KIEI = king eider; LTDU = long-tailed duck.

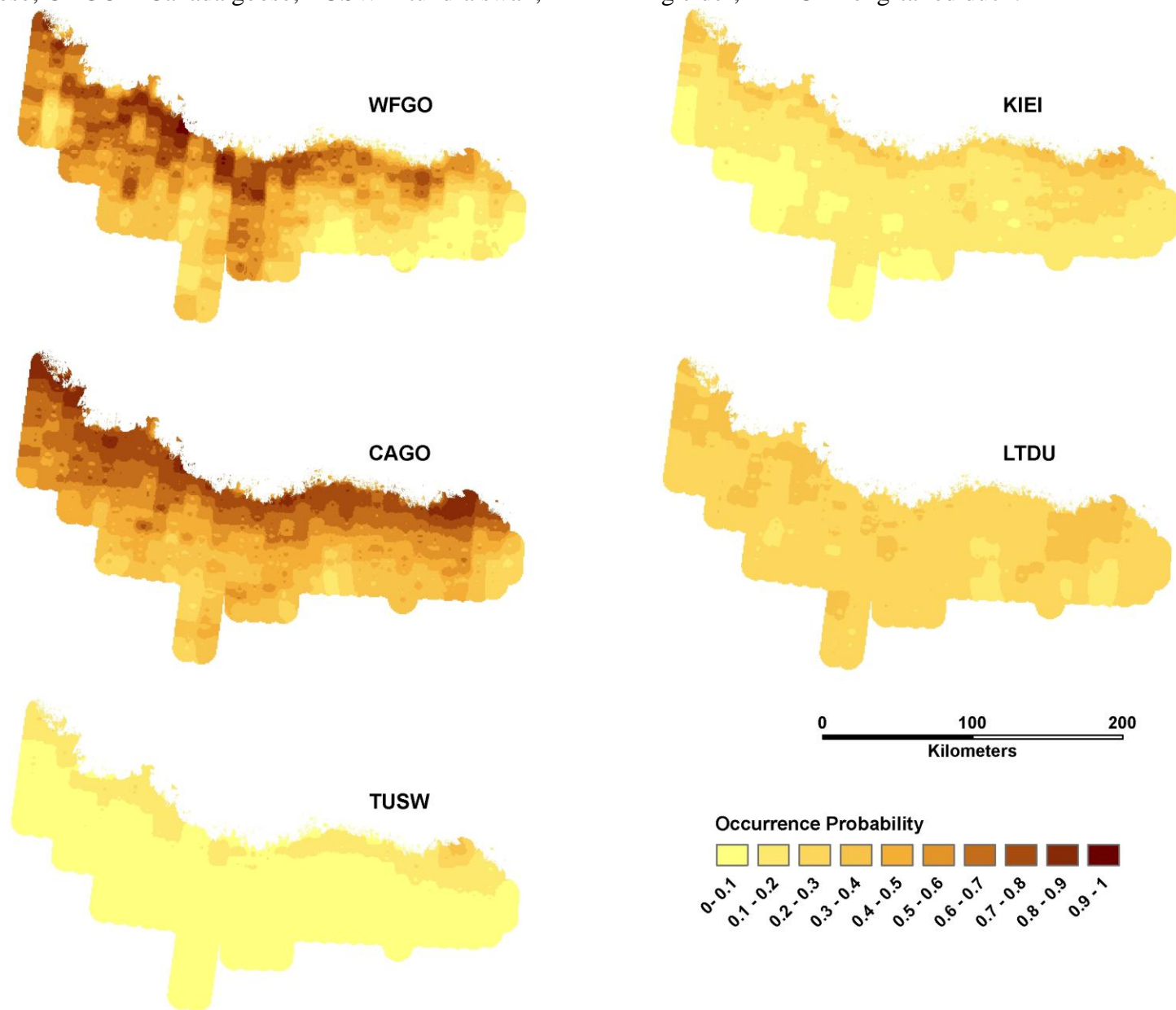
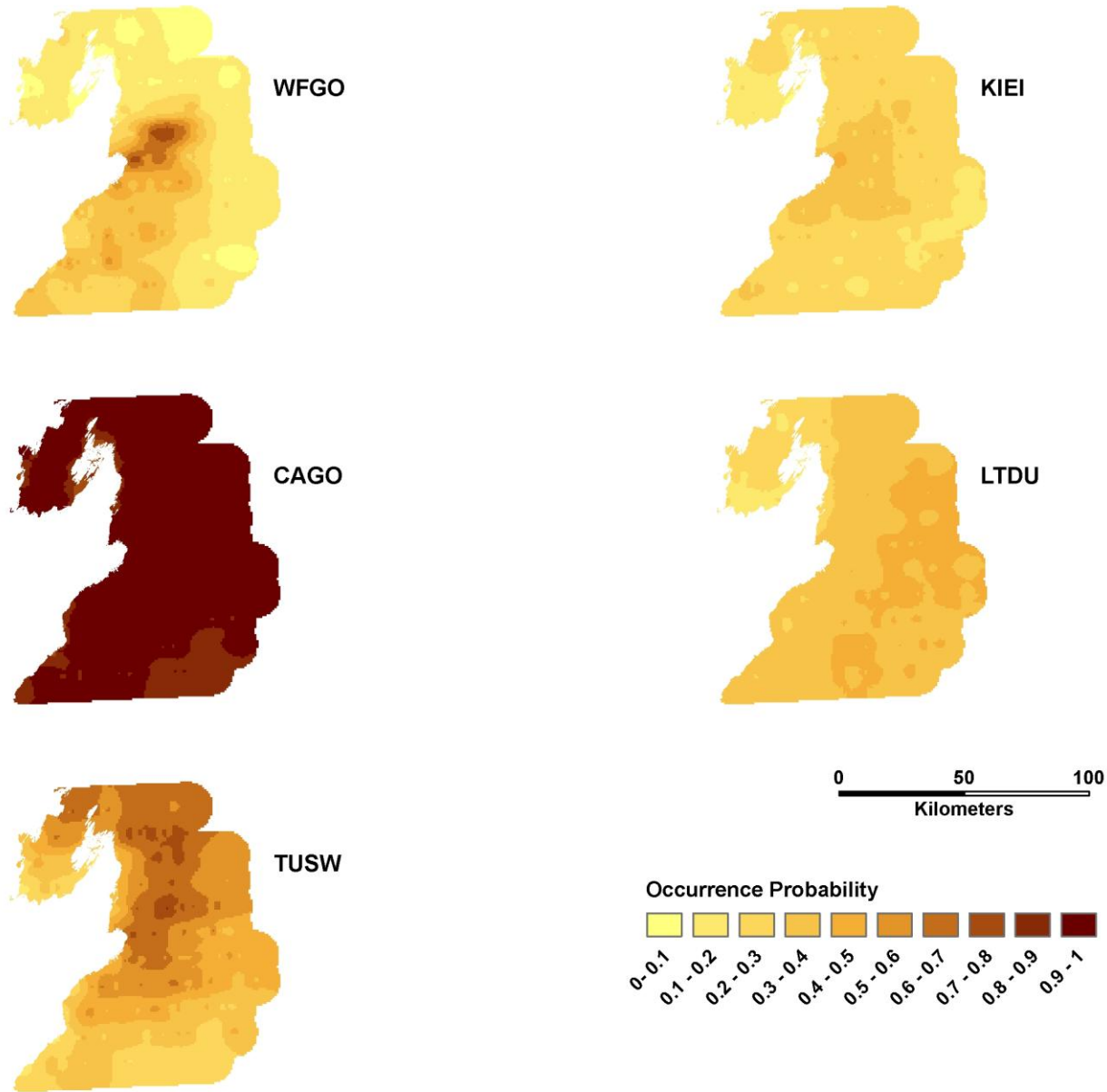


Figure 4.4 Predicted encounter probabilities of focal species within the Rasmussen Lowlands study area. Probabilities are generated from logistic models of species encounters relative to classified satellite imagery land cover variables. Abbreviations used: WFGO = white-fronted goose; CAGO = Canada goose; TUSW = tundra swan; KIEI = king eider; LTDU = long-tailed duck.



CHAPTER 5 SYNTHESIS

Attempts to quantify ecological relationships have generally focused on small groups of organisms and over relatively small geographic areas (May 1994). Recently however, the need to direct ecological research at broader spatial scales covering more of a species' range has been recognized. Among environmental issues thought to be most pressing, including climate change, habitat alteration, and species decline, are those driven by processes operating at larger scales (Gaston and Blackburn 1999). Consequently, management and conservation of species and ecosystems should appropriately proceed on equivalent scales. For such management, fundamental knowledge of species' ranges and spatial distribution is a prerequisite. However, for many species and for many regions, distributional data do not exist.

Digital habitat inventories are increasing our ability to quantify landscape features at large spatial scales (Wheatley et al. 2005). Species-habitat modeling using such digital information can assist in identifying habitat needs and delineate distributions through extrapolative methods. If distributions can be sufficiently modeled, distributions can be monitored and future changes can be predicted (Buckland and Elston 1993).

When using correlative measures to identify habitat needs or to estimate spatial distributions, a number of things must be considered. Species-habitat models normally make the assumption that animals select high-quality habitat (Fretwell and Lucas 1970, Morris 2003). It is expected that high-quality habitat results in higher survival and productivity. In studies that test this assumption it is typically verified (Sergio and Newton 2003, Zimmermann et al. 2003), although this is not always the case (Kristan III 2007). Potentially important determinants of fitness, particularly biotic factors, may mean that individuals occupy areas where abiotic components of habitat are not optimal. Competition, territoriality, predation, and other factors contribute to defining a species' distribution to varying degrees and the incorporation of such factors into species distribution assessments may be necessary in some cases.

For migratory wildlife, understanding habitat use and spatial distribution is complicated by spatial and temporal changes in habitat associations (Brower and Malcolm 1991). Waterfowl species considered in this research exhibit acute changes in habitat use, even within the breeding season. For this reason, timing of species observations must be strongly factored into interpretations of species-habitat associations.

Although my data suggest that (1) spatial scale considerably influenced the identification of species-habitat relationships for species investigated, and (2) remotely-sensed land cover data can be used to model and predict distributions of most focal species, a number of methodological problems could have influenced results. First, coarse resolution of both land cover and species encounter data likely limited recognition of species-land cover associations. Landsat satellite imagery used in the study, at spatial resolution of 30 m², and NTDB at a scale of 1:50 000, may not illuminate finer scale habitat attributes that may be important for these species. Unfortunately, availability and cost of high-resolution land cover data still restricts habitat research on large spatial scales; however, advancements and increasing availability of other digital land cover data (e.g., SPOT satellite imagery) hold promise.

The method of summarizing observations of focal species also limited my ability to distinguish land cover associations. Encounters of focal species were summarized within each transect segment such that a specific land cover that a given individual occupied was not retained. The survey method was not designed to relate species observations to habitat features. Future efforts would be well served to record observations in a method that permits more specific habitat linkage.

Further, during aerial surveys and in data analyses, I did not discriminate encounters of focal species among active breeders, failed breeders, and juveniles; all observations of a given species were treated the same. It is likely that these groups have unique habitat associations, and interpretation of some associations may have been obscured by grouping them together.

In this research, it was assumed that the probability of detection of individuals of the same species did not vary among habitats. Aerial surveys can displace birds from one habitat to another (Laursen et al. 2008), and it is known that detection for these species is not perfect (Alisauskas 2005). However, the absence of vertical vegetative cover in all habitats encountered suggests that the assumption that detection probability of focal animals should have been similar in all habitats, conditional on their presence, is justified.

5.1 MANAGEMENT APPLICATIONS AND FUTURE RESEARCH

Implicit in many recent initiatives for comprehensive management and conservation of North American birds, including the “*North American Waterbird Conservation Plan*” (Kushlan et al. 2002), Canada’s “*Wings Over Water*” (Milko et al. 2003), and “*Opportunities for*

Improving Avian Monitoring” (U.S. NABCI Monitoring Subcommittee 2007), is a recognition that habitat-based information be incorporated into management plans. For large spatial extents and for remote regions, digital habitat inventories provide a significant step towards improved knowledge of species-habitat relations and increases the ability to properly manage and conserve wildlife.

In chapter three, I confirmed that some land cover associations of focal waterfowl species were independent of the scale that habitat was sampled, but other associations were greatly affected by the spatial scale at which the habitat data were analysed. This emphasizes the need to incorporate scale in an appropriate manner in species-habitat research. By selecting biologically-relevant scales and by analyzing habitat features at multiple spatial scales more meaningful interpretation and application of such research will be facilitated.

In chapter four, a multi-scale approach to predictive modeling of waterfowl presence was used to estimate distributions of these species in the QMG and RL study areas. Land cover associations and distribution models indicated considerable dependence on low-lying habitats, particularly regions with extensive wet sedge meadow cover. These low-lying habitats can be especially susceptible to development (oil and gas reserves correspond strongly with these areas), and are expected to be most sensitive to any change in climate (Forbes et al. 2000, Hinzman et al. 2005). Within the study areas, highest proportions of lowland habitats occur in marine-transgression zones adjacent to the coast or along major drainages (Didiuk and Ferguson 2005, Latour et al. 2008). Due to potential sea-level rise and thawing of permafrost, lowland habitats may be severely degraded or completely lost in some areas (Shaw et al. 1998, Reynolds et al. 2008). My manipulation of land cover suggested that changes in the spatial distribution of species strongly associated with such habitats may be substantial.

Pressure to develop oil, gas, and mineral resources has increased significantly in recent years in arctic Canada (Natural Resources Canada 1996). Sizeable diamond and mineral resources have been identified in and around the QMGMS and the RL (Latour et al. 2008). The QMGMS is protected as a Migratory Bird Sanctuary under the Migratory Bird Convention Act of 1917 though it has been suggested that its size be reduced to allow mineral exploration (Conservation Advisory Committee 1990), although new sanctuary boundaries have not yet been proposed (Didiuk and Ferguson 2005). In the late 1970s, a pipeline was proposed to run through the centre of the RL to service natural gas deposits to the east, though the project was later

deemed 'not viable' (Hines et al. 2003, Environment Canada 2008). Despite frequent calls for designation as a National Wildlife Area (Johnston et al. 2000), the RL remain the only Ramsar site in northern Canada without formal protection (Latour et al. 2008). By identifying key habitats, modeling applications such as the one demonstrated here may help managers better balance conservation and development interests.

Future work is necessary to refine species-habitat modeling techniques and to enhance its validity in both practical and theoretical applications. Detailed habitat inventories, more comprehensive in their spatial and temporal coverage, remain among the most pertinent information needs. Such inventories will be essential for the development of models and the application of them in management and conservation efforts.

Where (and when) suitable inventories are available, further validation of models such as those presented here will help to refine modeling techniques. Specific to this research, it would be beneficial to first test the accuracy of the land cover classification method used to assign land cover types in the RL study area with on-site ground-truthing procedures. In this way, one may be able to differentiate model-performance errors with potential error due to inaccuracies in the land cover classification.

Surveys recording presence and absence have been recommended or used for a variety of monitoring programs; particularly those conducted at large scales (MacKenzie et al. 2006). There are several reasons that the use of presence/absence data is advantageous to estimations of absolute abundance in these studies; these primarily relate to labour, logistic, and financial concerns (Pollock et al. 2002). However, problems may arise when using presence/absence to infer species-habitat relationships or to monitor (or predict) occurrence changes in space or time. Presence/absence data alone assume that the probability of detecting an animal does not differ spatially or temporally. When this detection probability does vary, especially over time, estimates of distributional changes may be significantly biased (MacKenzie et al. 2006). Temporally, aerial surveys can displace birds from one habitat to another (Laursen et al. 2008), and detection for species included in this work is not perfect (Alisauskas 2005). Here, I assumed that the detection probability for focal species did not differ among different habitats; however, future surveys would be well served to quantify detection probabilities in all habitats to validate this assumption. Such a step may be particularly necessary of other surveys conducted in regions where vegetation structure is more complex than it is in the tundra. When abundance or

densities are of interest, occurrence data are often used as proxies for these metrics. Although it has been widely demonstrated that distribution and abundance of a species are often positively related (in a predictable way), contrary examples exist (Gaston et al. 2000). If the relationship between occurrence-abundance is not interpreted appropriately, biased estimates of abundance may arise.

Perhaps the most critical assumption that needs to be addressed is the notion species are in equilibrium with their environment. Where species are not at the carrying capacity in the landscape under study, the detection and interpretation of species-habitat relationships may be significantly skewed. Fit of models developed using species-habitat relationships where species are not in equilibrium with their environment may be poor, and applications of such models have potential to lead to inappropriate management decisions. As anthropogenic factors impact species and the environment to increasing degrees, it seems likely that this assumption will be violated more often. Future research may be needed to reveal methods to incorporate temporally-dynamic species-habitat relationships into distribution modeling to account for this.

Research presented here demonstrates the potential to model species' distributions over large spatial scales using coarse habitat data. Ultimately, the incorporation of landscape level correlates with knowledge of species-habitat associations operating at local scales will lead to a stronger ability to predict species' occurrence (and other parameters) and increase our understanding of mechanisms determining habitat use. Future research should attempt to clarify causal mechanisms behind such response of species with habitat and landscapes metrics, something that correlative approaches are limited in their ability to do. However, exploratory approaches such as those demonstrated here may provide useful background to develop *a priori* hypotheses to better understand ultimate mechanisms driving species' distributions and species-habitat relationships.

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APPENDIX A LAND COVER TYPES DESIGNATED FROM CLASSIFIED SATELLITE IMAGERY (adapted from Didiuk and Ferguson 2005)

Clear Water (H₂OCLR) – Extremely clear water bodies, commonly with substrates visible to the deepest portions. Shorelines generally dominated by bedrock.

Moderately Turbid Water (H₂OMT) – Partially turbid water bodies, substrates visible only at depths of 1 meter or less. Shorelines not characterized by bedrock, but commonly occur in bedrock areas. Water bodies are often coloured aqua-marine.

Turbid Water (H₂OTUR) – Extremely murky water bodies, occurring in alluvial plains and major drainages. Water body substrates are not visible.

Active Deposits (AD) – Exposed sediment, light in colour. Commonly occur along river banks, coastlines, or on eroding slopes. Significant vegetation cover is lacking. Substrates include silt, sand, gravel, or clay.

Wet Sedge Meadow (WSM) – Level areas consisting of saturated sedge or *Sphagnum* peat, occurring along drainages, lakes and ponds, or down slope of snow beds. Drainage is limited, often with areas remaining sodden throughout the growing-season, some with standing water. Vegetation is dominated by semi-aquatic graminoids, particularly of the *Carex*, *Eriophorum*, and *Dupontia* genera. Common forbs include members of the *Potentilla*, *Pedicularis*, and *Ranunculus* genera.

Hummock Graminoid Tundra (HGT) – Level lowland areas characterized by a somewhat irregular pattern of rounded hummocks, created by soil accretion around the roots of bunchgrasses. Substrate consists of sedge peat. Soil in the troughs is often saturated, while hummock tufts range from moist to dry. Bunchgrass species tend to be *Carex aquatilis*, *Festuca brachyphylla*, and *Arctagrostis latifolia*. Prostrate shrub species (generally *Salix* or ericaceous species) may occur on hummock tufts, as do an assortment of forbs such as *Dryas*, *Potentilla*, *Cerastium*, *Stellaria*, *Saxifraga*, *Castilleja*, and *Pyrola*. Troughs are dominated by mosses.

Tussock Graminoid Tundra (TGT) – Level or gently sloping areas of regularly patterned tussocks, occurring in lowlands or in depressions of upland areas. Substrate is chiefly sedge and *Sphagnum* peat. Tussocks of *Eriophorum vaginatum* dominate cover. Trough soil is generally moist, with tussock tufts moist or dry. Prostrate shrubs are similar to that of the hummock graminoid tundra, but *Betula glandulosa* may also be supported. Shrub cover can range up to 25%. Herbaceous genera occurring on tussock tufts again include *Cerastium*, *Dryas*, *Saxifraga*, and *Pyrola*, as well as *Pedicularis* and *Polygonum*. Troughs consist of moss carpets, with occasional graminoids or forbs.

Low Shrub Tundra (LST) – Lowland areas of hummock or tussock habitats, including a low shrub cover ranging from 25 to 75%. Shrub heights average 30 cm, but vary between 15 and 85 cm. Typically occurs in areas of high-centred polygons, somewhat sheltered from wind. Dominant shrub species are *Salix planifolia* and *Betula glandulosa*. Graminoid and herbaceous species are those typical of hummock and tussock graminoid tundra habitats.

Shrub Thicket (ST) – Lowland areas, often associated with sheltered depressions or alluvial sediments along lakes, rivers, and drainages. Low shrub cover comprises greater than 75% total cover and shrub heights range from 15 to 100 cm (with an average of 50 cm). Understory habitat is generally that of the tussock graminoid tundra.

Moss-lichen Tundra (MLT) – Occurs on upland terraces, moderate slopes, and lower edges of eskers, or on lowland deposits of sand or gravel adjacent to major drainages. Exposed boulders and frost-heaved polygons are common. Relatively dry substrate of sand and gravel, saturated only in early spring. Moss and lichen species dominate, with cover up to 90%. Ericaceous species and other prostrate shrubs are common but contribute little to the overall cover. Scattered graminoids and forbs include *Hierochloe alpina*, *Luzula*, *Juncus*, *Oxytropis*, and *Dryas* species. Bare sand or gravel patches are common.

Lichen-heath Tundra (LHT) – Upland areas such upper slopes, ridges, eskers where substrates of coarse sands or gravel are rapidly drained. Exposed boulders, stones, and rock outcrops are frequent, although vegetated areas make up greater than 75% of the overall cover. Vegetated

areas are principally dominated by lichen and, to a lesser degree, mosses; together comprising up to 75% of plant cover. Vascular plants are dominated by ericaceous species, the remaining graminoid/forb community similar to that of the moss-lichen tundra.

Bedrock and Boulder Field (BBF) – Upland areas of exposed granite and boulder fields where slope or exposure prevents significant soil establishment. Bedrock and boulders comprise greater than 75% cover. Crustose and foliose lichens are the most common forms of vegetation. Sheltered ledges or crevices may support prostrate shrubs, graminoids such as *Hierochloe alpina*, forbs including *Saxifraga tricuspidata* and *Arnica louiseana*, or the fern *Dryopteris fragrans*. Localized depressions may sustain lichen-heath or tussock graminoid tundra vegetation, or may be filled with standing water.

Exposed Peat (EP) – Lowland areas formerly existing as wet sedge meadow, hummock graminoid tundra, or tussock graminoid tundra. Exposed peat cover may occur where diminishing surface and soil water levels of wet sedge meadow communities no longer support vascular plant species, leaving bare carpets of peat; this type of exposed peat commonly occurs in patches or along the edges of sedge meadows. Exposed peat may also occur when hummock or tussock graminoid tundra habitats are denuded by grazing and nest-building activities of arctic-nesting birds, particularly Ross' and snow geese.

APPENDIX B SUPPLEMENTAL TABLES FROM CHAPTER 3

Table B.1 Differences between landscape covariates at four spatial scales where focal species were and were not encountered in the Queen Maud Gulf study area (22-26 June, 2002 and 13-19 June, 2003) and the Rasmussen Lowlands study area (22-24 June, 2006). Variables are derived from the National Topographic Database (NTDB) and classified satellite imagery (Landsat).

Table B.1.a White-fronted goose

Scale	Segment						1 km					2.5 km					10 km						
	Present n = 1117		Absent n = 1480		Diff ^b	Present n = 1117		Absent n = 1480		Diff	Present n = 1117		Absent n = 1480		Diff	Present n = 1117		Absent n = 1480		Diff			
Source	Variable ^a	Mean	SE	Mean		SE	Mean	SE	Mean		SE	Mean	SE	Mean		SE	Mean	SE	Mean		SE	Mean	SE
NTDB	ESKER	0.02	0.01	0.03	0.01	-	0.02	0.00	0.04	0.01	--	0.01	0.00	0.02	0.00	---	0.01	0.00	0.02	0.00	---	---	---
NTDB	SAND	0.49	0.11	1.24	0.18	--	0.59	0.11	1.22	0.15	--	0.62	0.08	1.08	0.11	--	0.70	0.06	0.73	0.05	---	---	---
NTDB	POLY	2.58	0.29	2.18	0.24	+	2.68	0.24	2.22	0.20	+	2.56	0.18	2.03	0.14	o	1.94	0.09	1.83	0.08	o	o	o
NTDB	POND	3.97	0.40	1.55	0.22	+++	3.87	0.35	1.51	0.18	+++	3.39	0.24	1.60	0.13	+++	3.17	0.14	1.87	0.09	+++	+++	+++
NTDB	WETLAND	5.26	0.37	2.87	0.22	+++	4.75	0.27	2.98	0.18	+++	4.15	0.19	2.91	0.14	+++	3.71	0.12	2.93	0.09	+++	+++	+++
NTDB	RIVER	3.05	0.09	2.40	0.07	+++	3.02	0.06	2.49	0.05	+++	1.21	0.02	1.12	0.02	+++	1.13	0.02	1.13	0.02	o	o	o
NTDB	WAT_D	0.94	0.07	0.87	0.08	+	0.91	0.06	0.85	0.06	+	0.85	0.04	0.85	0.04	++	0.80	0.03	0.80	0.03	+++	+++	+++
NTDB	WAT_T	12.34	0.42	16.50	0.48	---	12.66	0.33	16.20	0.38	---	13.14	0.23	15.90	0.30	---	13.40	0.16	15.50	0.22	---	---	---
Landsat	H ₂ OCLR	6.77	0.30	10.93	0.37	---	6.98	0.25	10.92	0.32	---	7.19	0.20	10.74	0.26	---	7.64	0.17	10.34	0.18	---	---	---
Landsat	H ₂ OMT	6.01	0.33	6.38	0.35	-	6.12	0.26	6.15	0.27	---	6.21	0.19	5.96	0.20	+++	6.10	0.13	5.91	0.16	+++	+++	+++
Landsat	H ₂ OTUR	1.65	0.16	1.93	0.17	o	1.62	0.13	1.80	0.13	o	1.71	0.08	1.72	0.07	o	1.59	0.04	1.63	0.03	o	o	o
Landsat	AD	3.09	0.19	3.02	0.18	o	2.96	0.15	3.12	0.17	--	3.11	0.12	3.19	0.14	---	3.38	0.08	2.93	0.08	+++	+++	+++
Landsat	WSM	17.25	0.56	15.56	0.51	+++	16.80	0.51	15.58	0.48	+++	16.38	0.47	15.68	0.46	+++	15.61	0.45	15.58	0.45	+++	+++	+++
Landsat	HGT	8.17	0.34	4.90	0.23	+++	8.10	0.30	4.89	0.19	+++	7.81	0.24	5.26	0.16	+++	7.17	0.17	5.48	0.12	+++	+++	+++
Landsat	TGT	9.53	0.32	6.76	0.23	+++	9.56	0.29	6.94	0.21	+++	9.06	0.24	7.09	0.19	+++	8.29	0.18	7.25	0.15	+++	+++	+++
Landsat	LST	9.76	0.36	7.24	0.26	+++	9.69	0.33	7.48	0.25	+++	9.49	0.29	7.67	0.23	+++	8.75	0.22	7.89	0.19	+++	+++	+++
Landsat	ST	3.08	0.19	1.94	0.14	+++	2.97	0.17	2.01	0.12	+++	2.84	0.13	1.99	0.10	+++	2.35	0.08	1.94	0.07	+++	+++	+++
Landsat	MLT	3.73	0.19	3.55	0.16	o	3.70	0.17	3.46	0.13	o	3.60	0.14	3.52	0.12	o	3.63	0.10	3.46	0.08	o	o	o
Landsat	LHT	19.47	0.43	22.42	0.45	---	19.49	0.37	22.14	0.39	---	19.72	0.31	21.58	0.33	---	19.62	0.26	21.26	0.30	---	---	---
Landsat	BBF	10.54	0.37	10.71	0.35	o	10.85	0.33	10.58	0.30	+	11.19	0.28	10.50	0.26	++	11.35	0.19	9.98	0.18	+++	+++	+++
Landsat	EP	0.41	0.04	0.76	0.05	---	0.39	0.04	0.75	0.05	---	0.37	0.03	0.72	0.04	---	0.34	0.03	0.70	0.03	---	---	---
Landsat	ICE	0.41	0.11	3.70	0.43	---	0.50	0.12	3.86	0.43	---	1.04	0.16	4.06	0.41	-	4.00	0.30	5.37	0.38	---	---	---

^a Abbreviations used: ESKER = esker; SAND = sand; POLY = tundra polygon; POND = tundra pond; WETLAND = wetland; RIVER = river; WAT_D = discrete waterbody; WAT_T = tapped waterbody; H₂OCLR = water, clear; H₂OMT = water, moderately turbid; H₂OTUR = water, turbid; AD = active deposits; WSM = wet sedge meadow; HGT = hummock
graminoid tundra; TGT = tussock graminoid tundra; LST = low shrub tundra; ST = shrub thicket; MLT = moss-lichen tundra; LHT = lichen-
heath tundra; BBF = bedrock and boulder field; EP = exposed peat.

^b Differences (Mann-Whitney U-tests) are indicated by +++/-- (P<0.0005), ++/-- (P<0.005), +/- (P<0.05), or "o" (P>0.05).

Table B.1.b Canada goose

Scale		Segment					1 km					2.5 km					10 km				
Source	Variable ^a	Present n = 1305		Absent n = 1292			Present n = 1305		Absent n = 1292			Present n = 1305		Absent n = 1292			Present n = 1305		Absent n = 1292		
		Mean	SE	Mean	SE	Diff ^b	Mean	SE	Mean	SE	Diff	Mean	SE	Mean	SE	Diff	Mean	SE	Mean	SE	Diff
NTDB	ESKER	0.03	0.01	0.03	0.01	o	0.03	0.01	0.03	0.01	o	0.01	0.00	0.01	0.00	o	0.01	0.00	0.02	0.00	---
NTDB	SAND	0.71	0.13	1.12	0.19	o	0.76	0.11	1.14	0.17	o	0.81	0.09	0.96	0.11	o	0.74	0.05	0.70	0.05	+
NTDB	POLY	1.79	0.22	2.92	0.30	-	1.99	0.19	2.86	0.25	-	1.89	0.14	2.63	0.16	---	1.54	0.07	2.21	0.10	---
NTDB	POND	2.37	0.28	2.82	0.33	o	2.35	0.25	2.70	0.27	o	2.26	0.18	2.47	0.19	o	2.43	0.12	2.42	0.12	++
NTDB	WETLAND	4.39	0.29	3.40	0.28	+++	4.12	0.21	3.35	0.23	+++	3.73	0.15	3.16	0.18	+++	3.39	0.09	3.13	0.11	+++
NTDB	RIVER	2.93	0.07	2.43	0.07	+++	2.92	0.05	2.51	0.05	+++	1.11	0.02	1.21	0.03	o	1.05	0.01	1.21	0.02	o
NTDB	WAT_D	0.77	0.06	1.03	0.10	o	0.77	0.05	0.98	0.07	-	0.75	0.03	0.95	0.05	o	0.70	0.02	0.90	0.03	o
NTDB	WAT_T	15.23	0.44	14.19	0.50	+++	14.71	0.33	14.64	0.40	+	14.70	0.24	14.73	0.31	o	14.42	0.18	14.77	0.22	o
Landsat	H ₂ OCLR	9.29	0.33	8.99	0.38	++	9.34	0.28	9.11	0.32	+	9.19	0.23	9.24	0.27	o	9.06	0.18	9.29	0.19	o
Landsat	H ₂ OMT	6.82	0.34	5.62	0.34	+++	6.31	0.25	5.96	0.29	+++	6.22	0.18	5.91	0.22	+++	6.07	0.13	5.91	0.17	+++
Landsat	H ₂ OTUR	1.85	0.17	1.77	0.17	+	1.73	0.12	1.71	0.13	o	1.78	0.08	1.65	0.07	o	1.58	0.03	1.64	0.04	o
Landsat	AD	3.09	0.19	3.00	0.18	+	3.02	0.17	3.09	0.16	-	3.12	0.13	3.20	0.13	o	3.10	0.08	3.15	0.08	o
Landsat	WSM	14.18	0.41	18.41	0.63	o	13.74	0.36	18.50	0.60	o	13.22	0.32	18.77	0.58	-	12.58	0.27	18.64	0.57	o
Landsat	HGT	6.88	0.29	5.73	0.26	o	6.82	0.26	5.72	0.23	+	6.97	0.21	5.73	0.18	+++	6.79	0.15	5.61	0.13	+++
Landsat	TGT	8.19	0.27	7.71	0.26	o	8.42	0.25	7.71	0.24	o	8.47	0.22	7.40	0.20	++	8.23	0.16	7.15	0.16	+++
Landsat	LST	8.09	0.28	8.56	0.33	o	8.23	0.27	8.63	0.30	o	8.30	0.25	8.61	0.27	o	8.12	0.20	8.40	0.21	o
Landsat	ST	2.37	0.15	2.50	0.17	o	2.36	0.14	2.48	0.14	o	2.36	0.12	2.35	0.12	o	2.10	0.08	2.13	0.08	-
Landsat	MLT	4.12	0.19	3.12	0.15	++	4.04	0.17	3.09	0.13	+++	4.09	0.14	3.02	0.11	+++	4.03	0.10	3.03	0.08	+++
Landsat	LHT	21.72	0.41	20.58	0.49	++	21.98	0.36	20.02	0.41	+++	21.82	0.29	19.73	0.36	+++	21.36	0.25	19.75	0.33	+
Landsat	BBF	11.69	0.38	9.57	0.35	+++	11.98	0.33	9.39	0.30	+++	11.90	0.27	9.68	0.25	+++	11.37	0.18	9.75	0.19	+++
Landsat	EP	0.45	0.05	0.77	0.05	---	0.44	0.04	0.75	0.05	---	0.41	0.03	0.74	0.04	---	0.38	0.03	0.71	0.04	---
Landsat	ICE	1.16	0.23	3.42	0.45	-	1.35	0.24	3.49	0.44	o	1.93	0.24	3.60	0.42	o	5.07	0.33	4.48	0.38	+++

^a Abbreviations used: ESKER = esker; SAND = sand; POLY = tundra polygon; POND = tundra pond; WETLAND = wetland; RIVER = river; WAT_D = discrete waterbody; WAT_T = tapped waterbody; H₂OCLR = water, clear; H₂OMT = water, moderately turbid; H₂OTUR = water, turbid; AD = active deposits; WSM = wet sedge meadow; HGT = hummock
graminoid tundra; TGT = tussock graminoid tundra; LST = low shrub tundra; ST = shrub thicket; MLT = moss-lichen tundra; LHT = lichen-heath tundra; BBF = bedrock and boulder field; EP = exposed peat.

^b Differences (Mann-Whitney U-tests) are indicated by +++/- - - (P<0.0005), ++/- - - (P<0.005), +/- (P<0.05), or "o" (P>0.05).

Table B.1.c Tundra swan

Scale		Segment					1 km					2.5 km					10 km				
Source	Variable ^a	Present n = 491		Absent n = 2106			Present n = 491		Absent n = 2106			Present n = 491		Absent n = 2106			Present n = 491		Absent n = 2106		
		Mean	SE	Mean	SE	Diff ^b	Mean	SE	Mean	SE	Diff	Mean	SE	Mean	SE	Diff	Mean	SE	Mean	SE	Diff
NTDB	ESKER	0.03	0.01	0.03	0.01	o	0.03	0.01	0.03	0.00	o	0.01	0.00	0.01	0.00	o	0.01	0.00	0.02	0.00	---
NTDB	SAND	0.78	0.21	0.95	0.13	o	0.94	0.20	0.95	0.11	-	1.07	0.17	0.84	0.08	+	1.03	0.10	0.65	0.04	+++
NTDB	POLY	1.75	0.35	2.50	0.21	o	2.11	0.33	2.49	0.17	-	1.91	0.25	2.34	0.12	---	1.67	0.14	1.92	0.06	---
NTDB	POND	4.06	0.64	2.25	0.22	++	3.91	0.55	2.20	0.18	++	3.21	0.37	2.17	0.14	+	3.11	0.21	2.27	0.09	+
NTDB	WETLAND	5.12	0.61	3.61	0.21	o	4.87	0.50	3.48	0.15	o	4.51	0.39	3.19	0.11	++	4.05	0.27	3.08	0.07	+
NTDB	RIVER	3.15	0.12	2.57	0.06	+++	3.18	0.09	2.61	0.04	+++	1.34	0.04	1.12	0.02	+++	1.26	0.03	1.10	0.01	+++
NTDB	WAT_D	1.05	0.12	0.87	0.06	++	1.15	0.11	0.81	0.05	+++	1.08	0.08	0.80	0.03	+++	1.02	0.06	0.75	0.02	+++
NTDB	WAT_T	13.32	0.62	15.03	0.38	o	13.31	0.49	14.99	0.30	o	13.76	0.35	14.94	0.23	o	13.35	0.27	14.88	0.16	---
Landsat	H ₂ OCLR	9.01	0.49	9.17	0.29	o	9.15	0.43	9.25	0.24	o	8.94	0.34	9.28	0.20	o	8.68	0.27	9.29	0.14	o
Landsat	H ₂ OMT	4.96	0.45	6.52	0.28	o	4.88	0.34	6.43	0.22	o	5.33	0.24	6.24	0.17	o	5.22	0.18	6.17	0.12	--
Landsat	H ₂ OTUR	2.09	0.25	1.74	0.13	+++	2.10	0.19	1.63	0.10	+++	2.06	0.12	1.64	0.06	+++	1.73	0.06	1.58	0.03	++
Landsat	AD	3.62	0.30	2.91	0.15	+	3.49	0.25	2.95	0.13	+	3.56	0.21	3.07	0.10	+	3.70	0.14	2.99	0.06	+++
Landsat	WSM	18.94	0.93	15.67	0.41	+++	18.74	0.88	15.49	0.38	+++	18.46	0.85	15.40	0.36	+++	17.50	0.80	15.15	0.35	+++
Landsat	HGT	7.49	0.49	6.03	0.21	+++	7.53	0.45	5.98	0.18	+++	7.19	0.35	6.16	0.15	++	6.73	0.23	6.08	0.11	+++
Landsat	TGT	8.57	0.47	7.81	0.21	o	8.85	0.44	7.89	0.19	o	8.37	0.36	7.84	0.16	o	7.94	0.27	7.64	0.13	o
Landsat	LST	6.87	0.41	8.66	0.25	o	6.62	0.35	8.85	0.23	--	6.53	0.32	8.90	0.21	---	6.45	0.27	8.68	0.17	---
Landsat	ST	1.81	0.16	2.58	0.13	o	1.74	0.15	2.58	0.12	o	1.73	0.12	2.50	0.10	o	1.71	0.10	2.21	0.06	-
Landsat	MLT	4.57	0.33	3.41	0.13	+++	4.39	0.28	3.37	0.11	+++	4.19	0.23	3.41	0.10	+++	4.04	0.15	3.42	0.07	+++
Landsat	LHT	19.60	0.67	21.51	0.36	o	19.81	0.60	21.28	0.31	o	20.14	0.53	20.93	0.26	o	19.44	0.47	20.82	0.23	o
Landsat	BBF	10.19	0.57	10.74	0.29	o	10.09	0.49	10.84	0.25	o	10.33	0.41	10.91	0.21	o	10.14	0.28	10.67	0.15	o
Landsat	EP	0.66	0.09	0.60	0.04	o	0.63	0.08	0.59	0.03	o	0.60	0.06	0.57	0.03	o	0.59	0.06	0.53	0.02	o
Landsat	ICE	1.28	0.39	2.52	0.30	o	1.55	0.41	2.62	0.30	o	2.16	0.40	2.90	0.29	o	5.82	0.56	4.53	0.28	+++

^a Abbreviations used: ESKER = esker; SAND = sand; POLY = tundra polygon; POND = tundra pond; WETLAND = wetland; RIVER = river; WAT_D = discrete waterbody; WAT_T = tapped waterbody; H₂OCLR = water, clear; H₂OMT = water, moderately turbid; H₂OTUR = water, turbid; AD = active deposits; WSM = wet sedge meadow; HGT = hummock
graminoid tundra; TGT = tussock graminoid tundra; LST = low shrub tundra; ST = shrub thicket; MLT = moss-lichen tundra; LHT = lichen-heath tundra; BBF = bedrock and boulder field; EP = exposed peat.

^b Differences (Mann-Whitney U-tests) are indicated by +++/- - - (P<0.0005), ++/- - - (P<0.005), +/- (P<0.05), or "o" (P>0.05).

Table B.1.d King eider

Scale		Segment					1 km					2.5 km					10 km				
Source	Variable ^a	Present n = 421		Absent n = 2176			Present n = 421		Absent n = 2176			Present n = 421		Absent n = 2176			Present n = 421		Absent n = 2176		
		Mean	SE	Mean	SE	Diff ^b	Mean	SE	Mean	SE	Diff	Mean	SE	Mean	SE	Diff	Mean	SE	Mean	SE	Diff
NTDB	ESKER	0.04	0.02	0.03	0.01	o	0.05	0.01	0.03	0.00	+	0.01	0.00	0.01	0.00	o	0.01	0.00	0.02	0.00	o
NTDB	SAND	1.16	0.34	0.87	0.12	o	1.31	0.33	0.88	0.10	o	1.18	0.23	0.83	0.07	o	0.93	0.11	0.68	0.04	+
NTDB	POLY	1.05	0.29	2.61	0.21	--	1.37	0.26	2.62	0.18	--	1.51	0.21	2.40	0.12	--	1.53	0.13	1.94	0.07	---
NTDB	POND	3.10	0.61	2.50	0.23	o	2.77	0.51	2.48	0.19	o	2.32	0.34	2.37	0.14	o	2.43	0.21	2.43	0.09	o
NTDB	WETLAND	4.58	0.58	3.76	0.21	o	4.19	0.45	3.65	0.17	o	3.84	0.30	3.37	0.12	o	3.37	0.18	3.24	0.08	o
NTDB	RIVER	3.09	0.14	2.60	0.06	+++	3.04	0.10	2.65	0.04	+++	1.16	0.03	1.16	0.02	+	1.11	0.03	1.14	0.02	--
NTDB	WAT_D	1.13	0.20	0.86	0.05	o	0.97	0.12	0.85	0.05	+	0.90	0.08	0.84	0.03	o	0.82	0.06	0.79	0.02	o
NTDB	WAT_T	15.22	0.73	14.61	0.37	+	15.19	0.60	14.57	0.29	+	15.26	0.42	14.61	0.22	+	14.61	0.32	14.59	0.16	o
Landsat	H ₂ OCLR	10.64	0.62	8.85	0.27	+++	10.43	0.53	9.00	0.23	++	10.25	0.41	9.01	0.19	+++	9.69	0.32	9.08	0.14	o
Landsat	H ₂ OMT	5.94	0.59	6.28	0.27	o	5.99	0.49	6.17	0.21	o	5.87	0.32	6.10	0.16	o	5.70	0.24	6.05	0.12	o
Landsat	H ₂ OTUR	1.98	0.31	1.78	0.13	o	1.77	0.21	1.71	0.10	o	1.84	0.14	1.69	0.06	o	1.63	0.06	1.60	0.03	o
Landsat	AD	3.43	0.38	2.97	0.14	o	3.40	0.35	2.98	0.12	o	3.39	0.28	3.11	0.10	o	3.24	0.16	3.10	0.06	o
Landsat	WSM	14.65	0.79	16.60	0.42	o	14.35	0.73	16.44	0.40	o	14.09	0.67	16.34	0.38	o	13.55	0.61	15.99	0.36	o
Landsat	HGT	6.72	0.49	6.23	0.21	o	6.65	0.44	6.20	0.19	o	6.51	0.35	6.32	0.15	o	6.24	0.24	6.20	0.11	o
Landsat	TGT	7.86	0.46	7.97	0.21	o	8.32	0.44	8.02	0.19	o	8.28	0.38	7.87	0.16	o	7.98	0.29	7.64	0.12	o
Landsat	LST	6.69	0.44	8.64	0.25	o	6.18	0.37	8.86	0.23	+++	6.29	0.33	8.87	0.21	---	6.61	0.29	8.58	0.17	---
Landsat	ST	1.55	0.17	2.60	0.13	-	1.43	0.14	2.61	0.12	---	1.49	0.13	2.52	0.09	---	1.59	0.10	2.22	0.06	---
Landsat	MLT	4.53	0.37	3.45	0.13	++	4.49	0.33	3.39	0.11	++	4.48	0.28	3.38	0.09	+++	4.13	0.18	3.42	0.07	+++
Landsat	LHT	22.29	0.73	20.93	0.35	+	22.77	0.63	20.66	0.30	++	22.71	0.52	20.40	0.26	+++	21.74	0.47	20.32	0.23	+
Landsat	BBF	11.04	0.63	10.56	0.28	+	11.21	0.52	10.60	0.25	+	11.39	0.42	10.68	0.21	++	11.00	0.30	10.48	0.15	+
Landsat	EP	0.48	0.08	0.64	0.04	o	0.48	0.07	0.62	0.04	o	0.46	0.06	0.59	0.03	o	0.48	0.05	0.56	0.03	o
Landsat	ICE	2.07	0.55	2.32	0.28	o	2.27	0.55	2.44	0.28	o	2.68	0.53	2.78	0.27	-	6.19	0.64	4.50	0.27	+++

^a Abbreviations used: ESKER = esker; SAND = sand; POLY = tundra polygon; POND = tundra pond; WETLAND = wetland; RIVER = river; WAT_D = discrete waterbody; WAT_T = tapped waterbody; H₂OCLR = water, clear; H₂OMT = water, moderately turbid; H₂OTUR = water, turbid; AD = active deposits; WSM = wet sedge meadow; HGT = hummock graminoid tundra; TGT = tussock graminoid tundra; LST = low shrub tundra; ST = shrub thicket; MLT = moss-lichen tundra; LHT = lichen-heath tundra; BBF = bedrock and boulder field; EP = exposed peat.

^b Differences (Mann-Whitney U-tests) are indicated by +++/- - - (P<0.0005), ++/- - - (P<0.005), +/- (P<0.05), or "o" (P>0.05).

Table B.1.e Long-tailed duck

Scale		Segment					1 km					2.5 km					10 km				
Source	Variable ^a	Present n = 598		Absent n = 1999		Diff ^b	Present n = 598		Absent n = 1999		Diff	Present n = 598		Absent n = 1999		Diff	Present n = 598		Absent n = 1999		Diff
		Mean	SE	Mean	SE		Mean	SE	Mean	SE		Mean	SE	Mean	SE		Mean	SE	Mean	SE	
NTDB	ESKER	0.04	0.01	0.03	0.01	o	0.05	0.01	0.03	0.00	+	0.02	0.00	0.01	0.00	o	0.02	0.00	0.02	0.00	o
NTDB	SAND	0.61	0.20	1.00	0.13	o	0.70	0.15	1.02	0.12	o	0.67	0.11	0.95	0.08	-	0.59	0.06	0.76	0.04	o
NTDB	POLY	1.91	0.32	2.49	0.22	o	2.01	0.25	2.54	0.19	o	2.09	0.19	2.31	0.13	o	1.78	0.10	1.90	0.07	o
NTDB	POND	1.57	0.32	2.90	0.26	--	1.76	0.30	2.76	0.22	-	1.64	0.22	2.58	0.16	---	1.86	0.15	2.60	0.10	---
NTDB	WETLAND	4.15	0.41	3.82	0.23	o	3.93	0.29	3.68	0.18	++	3.60	0.17	3.40	0.14	+++	3.34	0.10	3.24	0.09	+++
NTDB	RIVER	2.87	0.12	2.62	0.06	o	2.85	0.08	2.68	0.04	+	1.03	0.02	1.20	0.02	o	1.00	0.02	1.17	0.02	o
NTDB	WAT_D	0.79	0.11	0.93	0.06	o	0.71	0.07	0.92	0.05	o	0.67	0.04	0.90	0.04	o	0.60	0.03	0.86	0.03	-
NTDB	WAT_T	15.24	0.63	14.55	0.38	+	14.81	0.47	14.63	0.31	+	15.04	0.34	14.62	0.24	+	15.13	0.27	14.43	0.17	++
Landsat	H ₂ OCLR	9.15	0.47	9.13	0.30	o	9.17	0.38	9.25	0.25	o	9.35	0.31	9.17	0.21	+	9.63	0.26	9.04	0.15	+
Landsat	H ₂ OMT	6.82	0.51	6.04	0.28	o	6.60	0.39	6.00	0.22	+	6.59	0.29	5.91	0.16	++	6.27	0.21	5.91	0.12	+
Landsat	H ₂ OTUR	2.15	0.30	1.71	0.13	+	1.79	0.21	1.70	0.10	++	1.62	0.12	1.75	0.06	--	1.53	0.05	1.63	0.03	-
Landsat	AD	2.38	0.25	3.24	0.15	--	2.43	0.21	3.24	0.14	--	2.43	0.16	3.38	0.11	---	2.58	0.10	3.28	0.07	---
Landsat	WSM	12.42	0.52	17.44	0.46	-	12.42	0.45	17.21	0.43	-	12.14	0.38	17.13	0.41	-	11.82	0.34	16.72	0.40	o
Landsat	HGT	6.44	0.40	6.27	0.22	o	6.48	0.36	6.21	0.20	o	6.36	0.28	6.35	0.16	o	6.25	0.21	6.19	0.12	o
Landsat	TGT	8.70	0.41	7.73	0.21	+	8.88	0.37	7.83	0.20	+	8.77	0.32	7.69	0.17	++	8.35	0.24	7.50	0.13	++
Landsat	LST	9.02	0.46	8.12	0.25	+	8.93	0.42	8.28	0.23	+	8.86	0.37	8.33	0.21	++	8.71	0.29	8.13	0.17	++
Landsat	ST	2.68	0.27	2.36	0.12	o	2.56	0.23	2.38	0.11	o	2.44	0.19	2.33	0.09	o	2.16	0.12	2.11	0.06	o
Landsat	MLT	3.97	0.28	3.52	0.13	o	3.90	0.24	3.46	0.12	o	3.83	0.20	3.47	0.10	o	3.87	0.14	3.43	0.07	++
Landsat	LHT	23.42	0.60	20.47	0.37	+++	23.48	0.50	20.26	0.32	+++	23.26	0.41	20.04	0.27	+++	22.77	0.35	19.89	0.24	+++
Landsat	BBF	11.21	0.56	10.46	0.29	o	11.41	0.47	10.48	0.26	+	11.79	0.40	10.50	0.21	++	11.37	0.28	10.33	0.15	++
Landsat	EP	0.31	0.05	0.70	0.04	---	0.32	0.04	0.68	0.04	---	0.32	0.04	0.65	0.03	---	0.30	0.03	0.62	0.03	---
Landsat	ICE	1.30	0.34	2.58	0.31	o	1.48	0.35	2.69	0.31	o	2.06	0.38	2.97	0.30	o	4.28	0.47	4.93	0.29	o

^a Abbreviations used: ESKER = esker; SAND = sand; POLY = tundra polygon; POND = tundra pond; WETLAND = wetland; RIVER = river; WAT_D = discrete waterbody; WAT_T = tapped waterbody; H₂OCLR = water, clear; H₂OMT = water, moderately turbid; H₂OTUR = water, turbid; AD = active deposits; WSM = wet sedge meadow; HGT = hummock graminoid tundra; TGT = tussock graminoid tundra; LST = low shrub tundra; ST = shrub thicket; MLT = moss-lichen tundra; LHT = lichen-heath tundra; BBF = bedrock and boulder field; EP = exposed peat.

^b Differences (Mann-Whitney U-tests) are indicated by +++/- - - (P<0.0005), ++/- - (P<0.005), +/- (P<0.05), or "o" (P>0.05).