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Cumulative Effects of Human Developments on Arctic Wildlife

by

Chris J. Johnson, Mark S. Boyce, Ray L. Case, H. Dean Cluff, Robert J. Gau, Anne Gunn, and Robert Mulders

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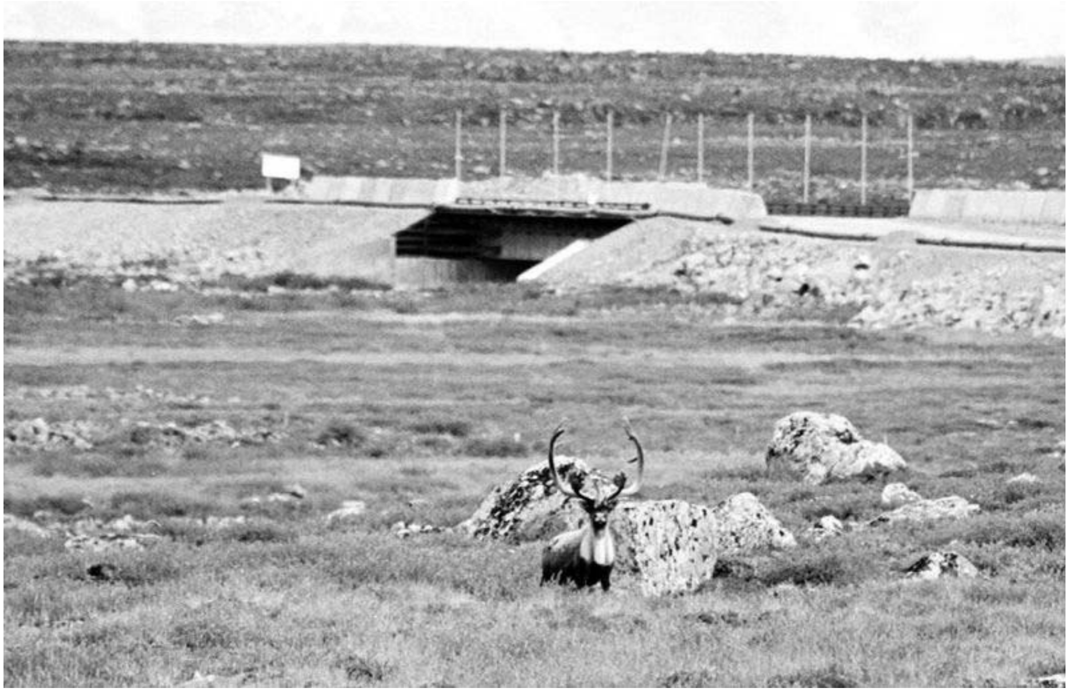

FRONTISPIECE. Barren-ground caribou of the Bathurst herd photographed near a service road for the Ekati diamond mine located in the Canadian central Arctic. Photograph courtesy of BHP Billiton Diamonds Inc.

CUMULATIVE EFFECTS OF HUMAN DEVELOPMENTS ON ARCTIC WILDLIFE

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***Abstract*:** Recent discoveries of diamondiferous kimberlite deposits in the Canadian central Arctic led to unprecedented levels of mineral exploration and development. The cumulative effects of such activities are an issue of concern for government regulatory agencies, regional and international conservation organizations, wildlife managers, and indigenous peoples. We investigated the impacts of human activities and associated infrastructure on the distribution of Arctic wildlife in 190,000 km^2 of the Taiga Shield and Southern Arctic ecozones 400 km northeast of Yellowknife, Northwest Territories, Canada.

We used covariates for vegetation, interspecific interactions, and human disturbance features to develop seasonal resource-selection models for barren-ground caribou (*Rangifer tarandus groenlandicus*), gray wolves (*Canis lupus*), grizzly bears (*Ursus arctos*), and wolverines (*Gulo gulo*). We used an information-theoretic approach to select 11 seasonal models for the 4 species. Nine models were good predictors of species occurrence and vegetation covariates were important components of all models. Mines and other major developments had the largest negative affect on species occurrence, followed by exploration activities, and outfitter camps. We did not, however, record strong avoidance responses by all species during all seasons to each disturbance type (i.e., major developments, mineral exploration sites, outfitter camps) and for some models carnivores selected for disturbance features (i.e., occurred closer to sites than comparison random locations). We used a geographic information system (GIS) to extrapolate each seasonal resource-selection model to the study area and quantified the reduction in habitat effectiveness as a function of modeled and hypothetical disturbance coefficients. Across all models, grizzly bears and wolves demonstrated the strongest negative response to disturbance and corresponding reduction in habitat effectiveness, fol-

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lowed by caribou and wolverines. The largest seasonal effect was recorded for caribou during the post-calving period, where model coefficients suggested a 37% reduction in the area of the highest quality habitats and an 84% increase in the area of the lowest quality habitats.

This is the first study to demonstrate the cumulative effects of multiple sources of human disturbance for caribou, wolves, bears, and wolverines found across the Canadian central Arctic. Resource selection models and corresponding maps of important habitats can be used to guide and evaluate future development proposals and can serve as a component of a regional environmental assessment. However, inferences from large-scale modeling efforts should be carefully evaluated when making detailed prescriptive recommendations. Study design, sample size, reliability of GIS data, and accuracy of model predictions are important considerations when evaluating the strength and scale of inference of correlative resource selection studies such as this. We recommend that regional cumulative effects analyses serve as the coarsest framework for understanding the impacts of human developments on wide-ranging animals. Monitoring and research should be conducted at various behavioral scales leading to a body of knowledge that fully describes the range and strength of impacts resulting from cumulative effects.

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***Key words*:** Arctic, barren-ground caribou, *Canis lupus*, cumulative effects, gray wolf, grizzly bear, *Gulo gulo*, human disturbance, *Rangifer tarandus groenlandicus*, resource selection function, *Ursus arctos*, wolverine

EL EFECTO CUMULATIVO DEL DESARROLLO HUMANO SOBRE FAUNA DE LAS ZONAS ÁRTICAS

Resumen: Los descubrimientos recientes de depósitos de kimberlite diamondiferous en el Ártico Central Canadiense, han llevado a niveles de exploración mineral y desarrollo sin precedentes. El efecto acumulativo de tales actividades son un motivo de preocupación para las agencias regulatorias del gobierno, las organizaciones de conservación regional e internacional, los administradores de la vida salvaje y los indígenas. Nosotros investigamos los impactos de las actividades humanas y de la infraestructura asociada en la distribución de la vida salvaje en el Ártico en 190.000 km2 del escudo de la Taiga y el Ártico del Sur eco-zonas a 400 km. al Noreste de Yellowknife, Territorios al Noroccidente de Canadá.

Nosotros usamos covariantes para vegetación, interacciones interespecificas y características de la alteración humana para desarrollar modelos de estación en la selección de recursos para el caribú de las tierras áridas (*Rangifer tarandus groenlandicus*), lobos grises (*Canis lupus*), osos grizzli (*Ursus arctos*) y carcayús (*Gulo gulo*). Nosotros usamos un acercamiento informático-teórico para seleccionar 11 modelos de temporada para las cuatro especies. Nueve modelos fueron buenos predictores de la presencia de las especies y las covariantes de vegetación fueron componentes importantes de todos los modelos. Minas y otros desarrollos importantes tuvieron el mayor efecto negativo en las ocurrencias de las especies, seguido por actividades de exploración y campamentos de Guia de excursionistas. Nosotros no registramos, sin embargo la fuerte respuesta esquiva de todas las especias durante todas las estaciones hacia todo tipo de disturbios. Por ejemplo, construcciones mayores, sitios de exploraciones minerales y campamentos guia de excursionistas, ni tampoco por algunos modelos carnívoros seleccionados por las características de disturbios (Lo que ocurre mas cerca a los sitios comprado con las ubicaciones o locaciones al azar). Nosotros usamos un sistema de información geográfica (SEG) para extrapolar cada modelo de recurso-selección para el estudio del área y cuantificamos la reducción en la efectividad del hábitat como una función de coeficiente de disturbio modelado e hipotético. A través de todos los modelos los osos grizzli y los lobos demostraron la respuesta negativa más fuerte hacia el disturbio y la correspondiente reducción en la efectividad del hábitat, seguido por el caribú y los carcayús. El caribú registró el efecto estacional mayor después del periodo de posternero donde los coeficientes modelos sugieran un 37% de reducción en el área del hábitat de mayor calidad y 84% de incremento en el área del hábitat de mas baja calidad.

Este es el primer estudio para demostrar el efecto cumulativo de las múltiples fuentes de disturbio humano para el caribú, el lobo, el oso y los carcayús encontrado a través del ártico-central canadiense. Modelos de la selección de recursos y los mapas correspondientes de los hábitats pueden ser usados para guiar y evaluar propuestas para futuro desarrollo y pueden servir como un componente de evaluación del medio ambiente regional. Sin embargo, inferencias de esfuerzos de modelos de larga escala deben ser cuidadosamente evaluadas cuando esta haciendo una recomendación prescriptiva detallada. El diseño del estudio, el tamaño de la muestra, la confiabilidad de los datos de SEG. y la exactitud de los modelos de preedición son consideraciones importantes cuando se evalúa la fuerza y el grado de inferencia de estudio de selección de recursos correlativos tal como este. Nosotros recomendamos que los análisis de los efectos acumulativos regionales sirvan como un andamio básico para el entendimiento del impacto del desarrollo humano en un amplio rango de animales. El monitoreo y las investigaciones deben ser conducidas en varios escalas de comportamiento llevando a un cuerpo de conocimiento que describa completamente el rango y la importancia del impacto resultante de los efectos cumulativos.

EFFETS CUMULATIFS DU DÉVELOPPEMENT ANTHROPIQUE SUR LA FAUNE ARCTIQUE

***Résumé*:** Les découvertes récentes de dépôts de kimberlite diamantifère au centre de l'Arctique canadien ont engendré l'essor sans précédent de l'exploitation et de la prospection minières. Or, les effets cumulatifs de telles activités préoccupent les agences de réglementation gouvernementales, les organismes de conservation tant au niveau régional qu'international, les aménagistes fauniques et les populations autochtones. Nous avons étudié l'impact de l'activité humaine et des infrastructures qui y sont reliées sur la répartition de la faune arctique sur un territoire de 190,000 km^2 situé dans les écozones de la taïga et du sud de l'Arctique, à 400 km au nord-est de Yellowknife (Territoires du Nord-Ouest, Canada).

Pour cela, nous avons utilisé des covariables caractérisant la végétation, les interactions interspécifiques et les perturbations humaines afin de développer des modèles saisonniers de la sélection des ressources pour le caribou (*Rangifer tarandus groenlandicus*), le loup (*Canis lupus*), le grizzli (*Ursus arctos*), le carcajou (*Gulo gulo*). Nous avons sélectionné 11 modèles saisonniers pour ces 4 espèces en s'appuyant sur une approche basée sur la théorie de l'information. Neuf modèles étaient de bons prédicteurs de la présence de l'espèce et les covariables de végétation étaient importantes pour tous les modèles. Les mines et les autres développements majeurs affectaient davantage la présence de ces espèces que les activités de prospection et celles des pourvoiries.

Cependant, pour chacune des espèces, nous n'avons pas détecté de fortes réponses d'évitement durant toutes les saisons pour chaque type de perturbation (i.e., les développements majeurs, l'exploitation minière, les pourvoiries). Selon quelques modèles, les carnivores ont sélectionné les sites perturbés (i.e., présence plus importante près des sites comparativement à des localisations aléatoires). Nous avons utilisé un système d'information géographique (SIG) pour extrapoler les prédictions de chaque modèle saisonnier de sélection des ressources à l'ensemble de l'aire d'étude et nous avons quantifié la réduction de la qualité de l'habitat en fonction de coefficients de perturbations modélisés et hypothétiques. Parmi tous les modèles, les grizzlis et les loups étaient ceux qui répondaient le plus négativement aux perturbations et à la réduction de l'habitat résultante, venaient ensuite les caribous et les carcajous. L'effet saisonnier le plus important a été détecté pour le caribou après la mise bas. Les modèles suggèrent alors une réduction de 37% de la superficie des meilleurs habitats et une augmentation de 84% de la surface couverte par les habitats de plus mauvaise qualité.

Notre étude est la première qui montre les effets cumulatifs de plusieurs sources de perturbations humaines pour les caribous, les loups, les ours et les carcajous établis à travers la région centrale de l'Arctique canadien. Les modèles de sélection des ressources et les cartes des habitats importants qui en découlent peuvent être utilisés pour guider et évaluer des propositions de développement et servir dans le cadre d'une évaluation environnementale régionale. Cependant, l'inférence à partir des efforts de modélisation à grande échelle devrait être considérée avec prudence lors de la formulation de recommandations détaillées. Le plan expérimental, l'effort d'échantillonnage, la fiabilité des données SIG et l'exactitude des prédictions des modèles sont importants à considérer pour évaluer la puissance et l'échelle d'inférence lors d'études de sélection des ressources basées sur des corrélations, comme celles présentées ici. Nous recommandons que les analyses sur les effets cumulatifs servent de cadre général pour comprendre l'impact du développement anthropique sur les groupes d'animaux dont la répartition est associée à de grandes échelles spatiales. Le suivi des espèces et les recherches devraient s'appuyer sur diverses échelles comportementales afin d'acquérir des connaissances permettant de décrire toute l'étendue et l'intensité des impacts résultants d'effets cumulatifs.

CONTENTS

INTRODUCTION

Human impacts pervade most North American ecosystems. Exploration and development of oil and gas, minerals, and forest products; the expansion of rural and suburban housing; and increases in leisure, travel, and recreation activities have resulted in a greater presence of people across areas that were once exclusive habitat for flora and fauna (Ceballos and Ehrlich 2002). The impacts of such developments on wildlife populations are a major focus of conservation research (Gill et al. 1996, Abbitt et al. 2000, Underhill and Angold 2000). The range of potential and documented effects are extensive and often vary across species, populations, and time, including seasons or following a period of exposure (Blumstein et al. 2003, Beale and Monaghan 2004). The construction of facilities, such as roads, trails, or buildings, and increased presence of humans, beyond some threshold, will result in a direct loss of habitats, or indirectly following avoidance behavior of affected wildlife (McLellan and Shackelton 1988, Cameron et al. 1992, Mace and Waller 1996, Stevens and Boness 2003). Human facilities, especially roads, trails, pipelines and other linear developments, also can fragment and isolate habitats (Baldwin et al. 2004, Deng and Zheng 2004, Jedrzejewski et al. 2004, McDonald and St. Clair 2004, Vistnes et al. 2004). In addition to a loss or reduction in the effectiveness of habitats, disturbance may result in response behaviors with negative social or physiological consequences (Van Dyke et al. 1986, Skogland and Grøvan 1988, Bradshaw et al. 1997). Disruption of breeding or rearing activities, for example, can reduce fecundity and recruitment (White and Thurow 1985, Goodrich and Berger 1994, Linnell et al. 2000, Mullner et al. 2004). The nutritional or hormonal costs of avoiding or responding to a disturbance may have cumulative and important implications for individual fitness and population productivity (MacArthur et al. 1979, Fowler 1999, Kerley et al. 2002, Constantine et al. 2004). More directly, human access can increase mortality through nonmonitored and controlled hunting, vehicle collisions, or the removal or destruction of problem animals (Johnson and Todd 1977, Johnson 1985, Del Frate and Spraker 1991, Wilkie et al. 2000, Johnson et al. 2004*a*). Human presence and activities also can alter interspecific interactions, namely rates of predation (Bergerud et al. 1984, Rich et al. 1994, James and Stuart-Smith 2000, Marchand and Litvaitis 2004).

The literature is rich with studies quantifying the responses of wildlife to disturbance. However, the majority of those studies focused on relatively well researched threatened or declining populations. Impacts have been evaluated through retrospective analyses with the aim of mitigating or understanding existing widespread, long-term or high-impact disturbances (Merrill et al. 1999, Carroll et al. 2001, Mahoney and Schaefer 2002). Rapid expansion of humans during the twentieth century has left few opportunities to implement comprehensive conservation plans for the mitigation of cumulative effects of existing, proposed, and future developments across broad geographic areas that encompass ecosystems.

Arctic ecosystems are rich in economic goods, but have a relatively short history and limited area of industrial development. Petroleum extraction is concentrated across small areas in the western Arctic and exploitation of mineral reserves is widespread but limited by the high costs of operations located far from roads and other infrastructure (Cronin et al. 1998). Across the Canadian central Arctic, recent discoveries of diamondiferous kimberlite have increased the presence and impacts of humans. As diamond exploration and extraction increases, improved infrastructure and access likely will result in the development of other mineral reserves (e.g., gold, base metals). Increased human activities could have an impact on the regions wildlife populations. Potentially sensitive carnivores include grizzly bear, wolf, and wolverine, all of which have a history of negative behavioral and population responses to human presence and developments (Weaver et al. 1996). The dominant herbivore in the central Arctic, barren-ground caribou, is a major prey for the 3 carnivore species, is of significant cultural and subsistence value for aboriginal people, and has been the focus of management attention across areas where oil and gas facilities have encroached upon migration routes and calving grounds (Cronin et al. 1998). While these 4 species do not fully represent the complex ecological relationships in the Arctic, caribou and the large carnivores might act as keystone species having impacts on many other plant and animal species, far beyond what might be expected from a consideration of their biomass or abundance alone (Simberloff 1998).

To date, development of diamond deposits across the central Arctic has required federal and territorial regulatory approval facilitated through project-specific environmental assessments. The cumulative impact of mines on wildlife populations was a major concern voiced by the public and resource managers (MacLachlan, L, 1996, Northwest Territories diamonds project—report of the environmental assessment panel. Canadian Environmental Assessment Agency, Ottawa, Ontario, Canada). Although companies monitor wildlife movements and behavior across their mine-sites, there is little effort to quantify disturbance effects across the geographic range of affected species. Failure to assess all impacts of human presence will prevent informed decision-making for future development proposals and preclude effective remediation efforts, if necessary. Considering the expanse and sensitivity of relatively pristine Arctic ecosystems (Walker and Walker 1991), and the opportunity for a proactive planning process, a regional environmental assessment is important (Walker et al. 1987).

A regional environmental assessment is a decision support tool that allows for the systematic evaluation of the environmental consequences of a series of developments. Advantages of this approach include long-term regional plans; identification of environmental effects early in the planning process; provision of a framework for considering cumulative environmental effects of different cross-sectoral projects located throughout large areas; and collection and organization of environmental data, identification of data gaps, and assessment of baseline conditions (Davey et al. 2000). We recognize that a comprehensive regional environmental assessment would include a range of social, economic, and ecological values. As the first step toward a more comprehensive approach, we developed a set of predictive models that could be applied to large geographic areas while quantifying the impacts of a number of sources of disturbance on the distribution of terrestrial wildlife.

As the framework for quantifying disturbance effects, we used telemetry data, classified satellite imagery, and locations of recreation and industrial developments to generate resource-selection models for barren-ground caribou, grizzly bear, wolf, and wolverine. Our primary objective was to develop predictive models describing the response of the 4 species to variables representing vegetation, interactions among species, and avoidance or use of outfitter camps, mineral exploration areas, active mines, and settlements. Coefficients from these models allowed us to generate maps that depicted the distribution of habitats with a relatively high probability of use that we assumed were important for each species during biologically derived seasons. Where animals demonstrated avoidance of human developments, we performed a set of spatial analyses to calculate the reduction in habitat effectiveness across the study area. Thus, cumulative effects represented the reduction in availability and quality of habitats resulting from the avoidance by monitored animals of major industrial developments, areas of resource exploration, recreation outfitters, and roads. We recognized that developments may act as attractants to carnivores. Although, we could not measure the demographic and distribution implications of the destruction and relocation of problem animals we report and discuss models that suggest such behaviors.

Given the expanse of the study area, the diffuse and low density of disturbances, and relatively small sample sizes for some species our results are preliminary and require corroboration from further study at a range of behavioral scales. However, we believe that model predictions provide guidance as to the potential effects of development on the distribution of important wildlife species across the central Arctic and highlight habitats that require emphasis in conservation plans.

Acknowledgments.—We thank P. D. McLoughlin and L. R. Walton for originally collecting and screening the grizzly bear and wolf data. S. B. Matthews' insight on Canadian environmental assessment and regulatory processes was essential for making the link between science and policy. C. C. Hanks answered numerous questions about the development of the Ekati mine and provided GIS data of roads and infrastructure. C. Carroll and D. H. Heard provided insightful comments on an earlier version of this manuscript. We appreciate the guidance and perceptive suggestions of the Editor, P. R. Krausman, Consulting Editors, W. P. Smith and L. H. Suring, and Technical Editor H. Johnson.

STUDY AREA

The study was centered at Contwoyto Lake (65° 30′ N, 110° 30′ W), approximately 400 km northeast of Yellowknife, Northwest Territories, Canada; boundaries were dictated by a vegetation mapping project conducted in conjunction with animal monitoring (Matthews et al. 2001). The study area included 190,000 km^2 of the Taiga Shield and Southern Arctic ecozones (Ecological Stratification Working Group. 1996. A national ecological framework for Canada. Environment Canada, State of the Environment Directorate, Ecozone Analysis Branch, Ottawa, Ontario, Canada). The northern extent of the Taiga Shield is marked by treeline, beyond which the open stunted forests of black (*Picea mariana*) and white spruce (*P. glauca*) are unable to grow (Fig. 1). Permafrost, forest fires, and soil productivity dictate the mosaic of plant communities found across the area. Forested sites are characterized by white and black spruce, pine (*Pinus banksiana*), and in the south, larch (*Larix laricina*). Understory composition varies with site productivity, but typically consists of a combination of lichen and shrubs. Wet, riparian, and recently disturbed sites are devoid of coniferous trees and accommodate plant communities dominated by sedge (*Carex* spp.), birch (*Betula* spp.), willow (*Salix* spp.), and alder (*Alnus* spp.). Fens and bogs occur across poorly drained areas of discontinuous permafrost.

Approximately 95% of the study area was contained within the Southern Arctic ecozone (Ecological Stratification Working Group 1996). Landform geomorphology was shaped by past glacial actions and includes esker complexes, boulder moraines, outwash aprons of sand and gravel, glacial erratics, raised ridges of ancient beaches, and numerous lakes. Permafrost is continuous through the zone. Creeks, rivers, and seepage areas are the most productive growing sites, accommodating birch and willow 2–5 m high. Vast shrub communities of willow, shrub birch, and Labrador tea (*Ledum decumbens*) dominate areas with adequate soil development. Mats of lichens, mosses, and low shrubs are found across exposed rocky sites. Climate is variable across the study area, but in general is characterized as semi-arid with annual precipitation of approximately 300 mm. Summers are short and cool with average temperatures of 10°C whereas winter temperatures are commonly <–30°C (BHP Diamonds Inc, 1995, Ecological mapping: 1995 baseline study update, Yellowknife, Northwest Territories, Canada, unpublished report).

Historical and Current Land Use

Aboriginal peoples occurred across the study area long before the settlement of Europeans and continue to occupy, trap, and hunt their traditional lands. Industrial mining operations were first established in the 1930s, focusing primarily on the discovery and extraction of gold, silver, and associated base metals. In 1991, diamondiferous kimberlites were discovered near Lac De Gras. Currently, several deposits are being exploited at the Ekati and Diavik diamond mines, and regulatory approval is being sought for a mine at Snap Lake by. The Lupin gold mine, in operation since 1982, is the only other active mine found in the study area. The 495 km Tibbitt to Contwoyto winter road and 3 associated camps service the Ekati, Diavik, and Lupin operations. The road is normally open from late January to early April and lies primarily (87%) across frozen lakes (Tibbitt to Contwoyto Winter Road Joint Venture, 2001, Tibbitt to Contwoyto winter road project description report, Department of Indian Affairs and Northern Development, Yellowknife, Northwest Territories, Canada, unpublished report). A 29 km all-season road connects pits at the Ekati diamond mine with the win-

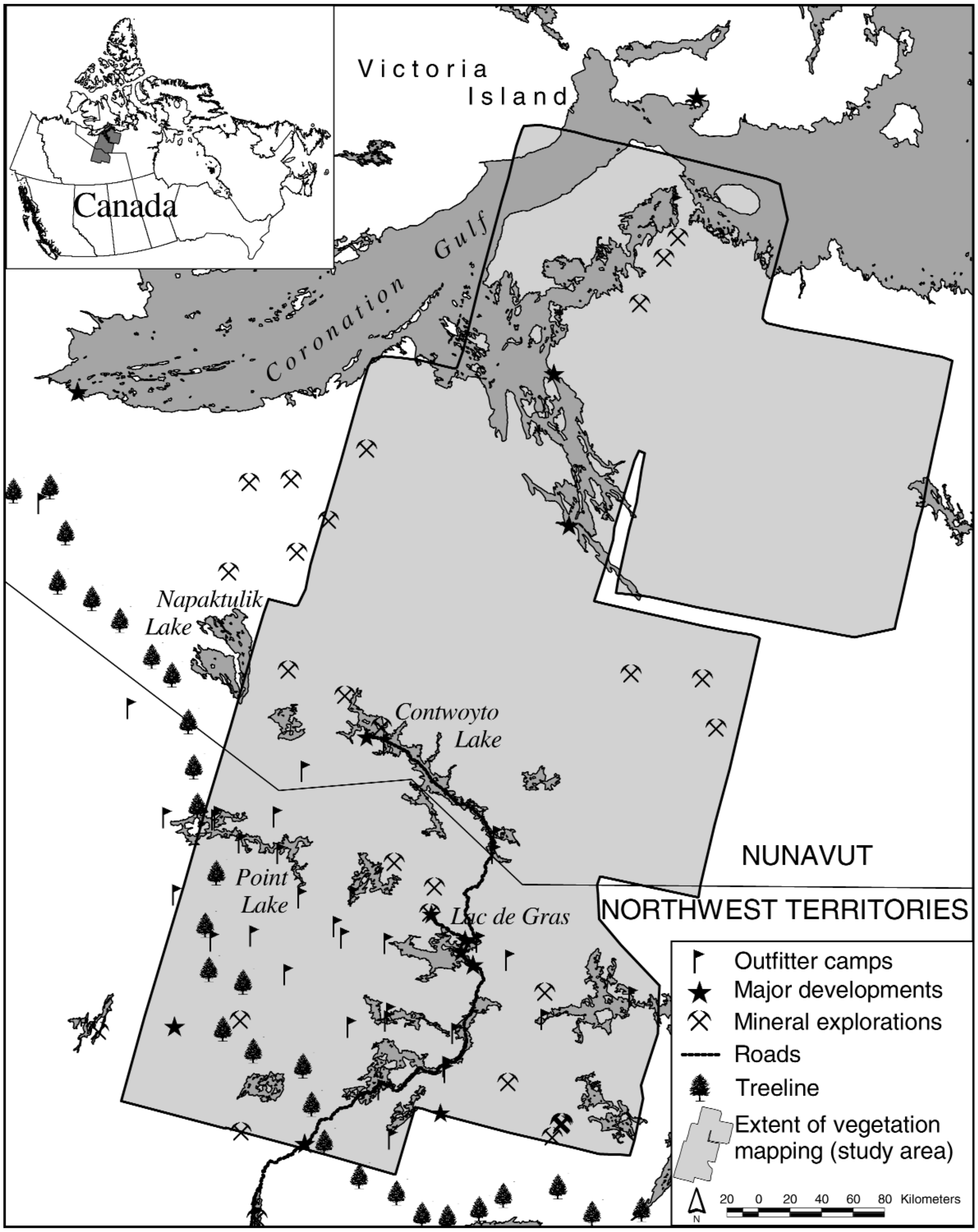

Figure. 1. Location of study area and distribution of disturbance features across the Canadian central Arctic, 2000. Treeline represents the northern extent of coniferous forest.

ter road. In 2001, $86.6 million was spent on mineral exploration across the Northwest Territories (Government of Northwest Territories 2001). Exploration activities included airborne magnetic and electromagnetic surveys, till and rock sampling, and drilling programs. Helicopter flights and temporary camps for housing work crews and field-testing samples are typically associated with such activities. Fish and hunting guides operate across the study area. Hunting occurs during late summer and autumn, with most outfitters guiding for caribou. Fishing camps are in operation from early June through autumn.

METHODS

Animal Capture and Monitoring

Our analyses were based on animal locations collected during previous studies of barren-ground caribou, gray wolf, grizzly bear, and wolverine (McLoughlin 2000, Mulders 2000, Walton et al. 2001, Gunn et al. 2002). The geographic extent of capture efforts, relocation frequency, and the distribution of monitored animals varied among studies. For all species, we assumed that monitored animals demonstrated behaviors representative of their larger populations. Caribou, wolves, and grizzly bears were fit with ST-10 or ST-14 satellite collars (Telonics, Mesa, USA) and wolverines were monitored with very high frequency (VHF) radiocollars (Telonics, Mesa, USA). Caribou, wolves, bears, and wolverines were monitored from April 1996 to December 2000, June 1997 to August 1999, May 1995 to June 1999, and March 1996 to January 2000, respectively.

Season Designations

Arctic ecosystems are temporally and spatially dynamic. Behavior and resource selection by ungulates and carnivores vary according to the seasonal availability and use of food, breeding, birthing, and rearing habitats. We used our understanding of the 4 species to identify what we assumed were ecologically relevant seasons. The majority of location data for caribou, grizzly bears, and wolves, were collected for nonwinter periods (April–November). Furthermore, caribou and wolves migrated south of the study area during winter. For those 3 species, we limited our analyses to periods of the year that animals were active and occurred across the study area (15 April–31 October). Wolverines ranged within the study area and were active throughout the year; therefore, we modeled resource selection for that species during the summer and winter.

The 349,000 (±95,000) caribou of the Bathurst herd migrate annually from forested areas in the southern Northwest Territories toward calving grounds near Bathurst Inlet (Gunn et al. 1997). Based on that pattern, we defined 3 seasons for our resource selection analyses. We considered the northward spring migration and calving of caribou to occur from 15 April to 14 June, the post-calving period as 15 June to 31 August, and the southern autumn migration as 1 September to 31 October.

Wolves occupied distinct summer and winter ranges (Walton et al. 2001). During summer, wolves denned and reared pups in tundra located north of treeline. Winter movements reflected the southern migration of Bathurst caribou into forested areas outside our study area. The seasonal shift was defined for each radiocollared wolf according to the date of long-distance movements (>50 km) from or towards den sites. The median departure date from summer ranges in 1997 and 1998 was 26 October and 3 November, and the median arrival date in 1998 and 1999 was 1 May and 18 April (Walton et al. 2001). Thus, the spring and autumn season encompassed those periods during which wolves moved from or to the caribou winter range from denning habitats.

We used past research on the dietary patterns of grizzly bears to identify 4 time periods that likely correlated with seasonal changes in resource selection (Gau et al. 2002). The spring season, defined as den emergence to 20 June, represented the period when bears fed primarily on caribou, arctic ground squirrels (*Spermophilus parryii*) and overwintered fruit. Early summer was defined by a diet of emergent vegetation (21 June–31 July). Ripening of berries and the southward migration of caribou led to greater consumption of those foods during late summer (1 August–9 September). In autumn, bears fed primarily on caribou and ground squirrels (10 September–denning; Gau et al. 2002).

Wolverines hunt caribou and scavenge carcasses (Mulders 2000). We defined 2 seasons according to the presence or absence of caribou across the range of collared wolverines. From 8 May to 29 September, locations from collared caribou overlapped the home range (95% kernel) of all wolverine locations (Worton 1989). We considered a second season (winter) as the period where caribou occurred outside the range of monitored wolverines.

Resource and Human Disturbance Variables

Using past research and our knowledge of the study area and species, we identified a number of resource (i.e., habitat) and human disturbance variables we assumed were useful in modeling the responses of caribou, bears, wolves, and wolverine to the central Arctic environment. As with most studies conducted at such broad spatial and temporal scales, the variables, as presented in a GIS, are only surrogates for functional components of habitats related to foraging, scavenging, denning, or avoidance behaviors.

Vegetation Composition.—Vegetation habitat variables were derived from a supervised classification of 8 overlapping Landsat Thematic Mapper images covering an area of approximately 200,000 km^2 (Matthews et al. 2001). The original map represented 22 land and water classes. Terrestrial classes were identified following image enhancement and field investigations and were based on broad vegetation types or plant communities and modifying features such as terrain or soil. Classification accuracy for the study area ranged from 51 to 82% among cover types (Matthews et al. 2001). To reduce the dimensionality of statistical models and increase overall accuracy of the map, we combined the 22 original land cover classes into 14 classes of similar types (Table 1). Our models included only those recombined classes that were assumed to support forage (i.e., excluding water, rock dominated or burned classes).

We developed selection models that integrated vegetation resources at 2 spatial scales: patches and collections of patches found across the larger study area. We defined a patch as a single or homogeneous collection of pixels representing 1 cover type. At this scale, we queried the percentage use of each cover type found across the reclassified satellite map (25 × 25 m pixels). We recognized that the large study area and the north-to-south ecological gradient resulted in variation in the distribution and clustering of patches. Therefore, we generated a second set of variables quantifying the density of patches representing the regional variation in the availability of each cover type across the broader study area (Johnson et al. 2004*b*).

We used a pattern analysis technique, 3-term local quadrat variance, to identify the distributional patterns of each land cover type. First, we randomly placed 10 north-to-south transects across each cover type. Transect length varied according to the distribution of each type and ranged from 170 to 295 km. We then used an overlapping moving window, consisting of 3 terms or blocks, to calculate the variance in pixel (i.e., patch) occurrence along each transect. The variance was repeatedly calculated for each transect following incremental increases in block size. When plotted, peaks in variance corresponding with block size indicate scales of patchiness (Dale 2000). We plotted the median variance for the 10 sample transects and identified the major peak in variance as 1 scale at which availability of vegetation differed beyond that of individual patches (Johnson et al. 2004*b*). We used that scale (i.e., distance) to identify the size of a rectangular moving window that was applied to a binary image of each land cover type to calculate and map the density of pixels (i.e., patches) across the study area. Because of computational constraints, these analyses were conducted at a pixel resolution of 100 × 100 m.

Human Disturbance.—We identified producing mines, mines under development, mineral exploration areas, camps servicing winter roads, outfitter camps, and communities as human disturbance features. To increase sample sizes, we grouped producing mines, mines under development, communities, and winter road camps and assumed that those developments acted as major disturbance features. We buffered each discrete point feature to represent the larger area potentially influencing the movements and habitat use of the 4 species. Based on our observations of the spatial extent of those features, we chose a 1,000 m buffer for major disturbances and a 500 m buffer for outfitter camps. Outfitters often hunt caribou from lake shorelines; therefore, we buffered lakeshores 5 km inland when situated within 20 km of a hunt camp. Exploration rights and activities (e.g., geophysical surveys and mapping, drilling, mobile camps, helicopter traffic) extend over large mineral claims; therefore, it was difficult to quantify the exact location and area potentially influenced by these activities (Department of Indian Affairs and Northern Development 2001; Government of Northwest Territories 2001, 2002). As an approximation of the area of mineral exploration activities potentially impacting monitored animals, we invoked a 10,000 m buffer around the reported point location of the mineral claim. We did not consider the responses of the 4 monitored species to subsistence hunting and fishing.

We attributed individual disturbance features only for months or years during which human activity was recorded. Winter road camps were in operation until 1 May of each year (Tibbitt to Contwoyto Winter Road Joint Venture, 2001, Tibbitt to Contwoyto winter road project description report, Department of Indian Affairs and Northern Development, Yellowknife, Northwest Territories, Canada, unpublished report). Depending on time of year and company, outfitters accommodated fishing, hunting, or both fishing and hunting. Fishing was considered the primary activity from 7 July to 14 August and hunting from 15 August to 1 October. We used the Government of Northwest Territories Parks and Tourism Recreation Operator Database, company advertisements, and personal communication with guide outfitters to identify the location, primary service, and operating times of outfitter camps. The location of mineral extraction, development, and exploration varied across the study period (1996–2000). We used the most reliable and recent data to identify the geographic location and year of activity for mining developments (Department of Indian Affairs and Northern Development 2001; Government of Northwest Territories 2001, 2002).

Interspecific Interactions.—We hypothesized that the distribution of wolves and bears was correlated with the availability of caribou and that the movements and behavior of wolverines was influenced by the presence of wolves, bears, and caribou (Magoun 1987, Heard and Williams 1992, Mulders 2000, Gau et al. 2002). Starting with caribou, we in turn modeled and generated maps of habitat selection for each species. Those maps then served as spatially explicit covariates to evaluate the strength of interspecific interactions. We assumed that predator's affinity for caribou was stronger than caribou's avoidance of risk-prone habitats. Thus, we first modeled selection of habitats by caribou and used those maps to infer interactions with the predator species.

Statistical Definition of Resource Selection

We used resource selection functions (RSF) to quantify the relationship between the observed distribution of the 4 species and variables representative of habitats and human disturbance (Table 1). A RSF is any mathematical function that is proportional to the probability of use of a resource or habitat (Manly et al. 2002). Typically, a RSF consists of a number of coefficients (β_i) that quantify selection for or avoidance of some environmental feature. Coefficient sign and strength is a result of differential variation in the distribution of each environmental feature measured at a sample of animal locations and a comparison set of random sites. Where an animal's observed use of a resource is greater than availability (i.e., random sites) we infer selection. If use is less than availability we conclude that the animal avoided that resource or environmental feature. We used a GIS to apply the RSF coefficients to our spatial data and generated maps of the relative value of habitats for each species across the study area for each biologically defined season.

We used conditional fixed-effects logistic regression to estimate coefficients for our RSF analyses (Manly et al. 2002). The primary advantage of fixed-effects logistic regression is that it allowed us to statistically control for effects that characterized clustered use and availability data (Pendergast et al. 1996, Hosmer and Lemeshow 2000). In this application, we clustered the fixed-effects regression on each animal location to control for temporal and spatial variation in resource availability. Each animal location was paired with 5 randomly selected comparison sites that quantified the availability of

Table 1. Variables used to model resource selection by caribou, wolves, grizzly bears, and wolverines monitored from May 1995 to January 2000 across the Canadian central Arctic.

Variable	Description
Resource Variables	
Esker density/patch[a]	Sparsely vegetated sand and gravel esker complexes
Forest density/patch	Continuous or discontinuous forested areas of dwarf white spruce, black spruce, and tamarack
Heath rock density/patch	Open mat heath tundra interspersed with bedrock and boulders
Heath tundra density/patch	Closed mat of heath found on moderate to well drained soils on upland areas
Lichen veneer density/patch	Windswept, dry, flat topography covered with a continuous mat of lichen
Low shrub density/patch	Extensive areas of low birch and willow found on moist well-drained soils
Peat bog density/patch	Mosaic of uplands and lowlands with fens, bogs, mixed-wood forest, and peatlands
Riparian shrub density/patch	Active stream courses or areas of water seepage with a shrub layer of birch, willow, and alder
Rock association density/patch	Large areas of windswept bedrock or boulders with little vegetation cover
Sedge association density/patch	Wetland complexes of wet sedge meadow and drier hummock sites
Occurrence of caribou	Predicted likelihood of encountering caribou
Occurrence of grizzly bear	Predicted likelihood of encountering a grizzly bear
Occurrence of wolf	Predicted likelihood of encountering wolves
Human Disturbance Factors	
Major developments[b]	Operating mines, communities, winter road camps
Mineral explorations	Areas of mineral exploration activities
Outfitter camps	Seasonal guide-outfitter camps

[a] Vegetation was modeled as the percent area of land cover patches and the mean density of land cover types.

[b] Disturbance was modeled as the distance of animal and random locations from the nearest facility.

habitat resources and the random distance to the nearest edge of a buffered disturbance feature. For logistic regression, the addition of 0s adds little to the explanatory variables' information content when they exceed the number of 1s by a factor of 2 to 5 (King and Zeng 2001*a*,*b*). The number of random locations satisfied the tradeoff between data collection costs and slight increases in the precision of model parameters.

For each animal location, we sampled comparison sites from within a circle that was centered on the preceding location, and had a radius equal to the 95th percentile movement distance for that particular relocation interval (e.g., 48 hr, 2 day) for that species (Fig. 2, 3; Arthur et al. 1996). Resource selection occurs at a number of behavioral scales (Johnson et al. 2002*a*), but

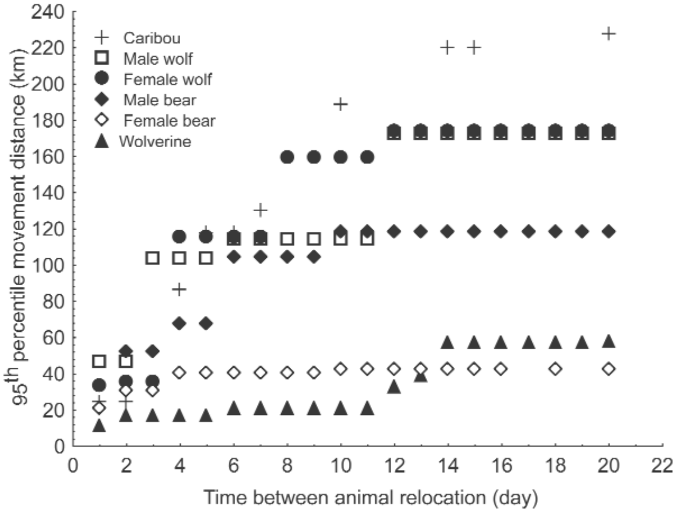

Figure. 2. Availability radii applied to resource selection analyses for caribou, wolves, grizzly bears, and wolverines monitored across the Canadian central Arctic (1995-2000). Each radius was calculated as the 95th percentile of movement distances for all locations of a particular relocation interval.

Table 2. Accuracy and number of relocations for caribou, wolves, grizzly bears, and wolverines collared from 1995–2000 across the Canadian central Arctic.

Species Season	Error radius[a] 125 m	150 m	350 m	1,000 m
Caribou				
Spring migration and calving	0	233	275	118
Post-calving	0	197	337	208
Autumn migration	0	107	102	58
Wolf				
Spring/autumn	4	65	135	235
Denning	172	295	666	1,313
Grizzly bear				
Spring	0	536	539	307
Early summer	0	551	633	335
Late summer	0	485	582	362
Autumn	0	285	431	322
Wolverine				
Caribou available	205	0	0	0
Caribou unavailable	305	0	0	0

[a] Error radius of 125 m was assumed for conventional radiotelemetry from aircraft, whereas errors of 150, 350, and 1,000 m corresponded with satellite collar locations of classes 3, 2, and 1, respectively (Leptich et al. 1994, Ballard et al. 1995).

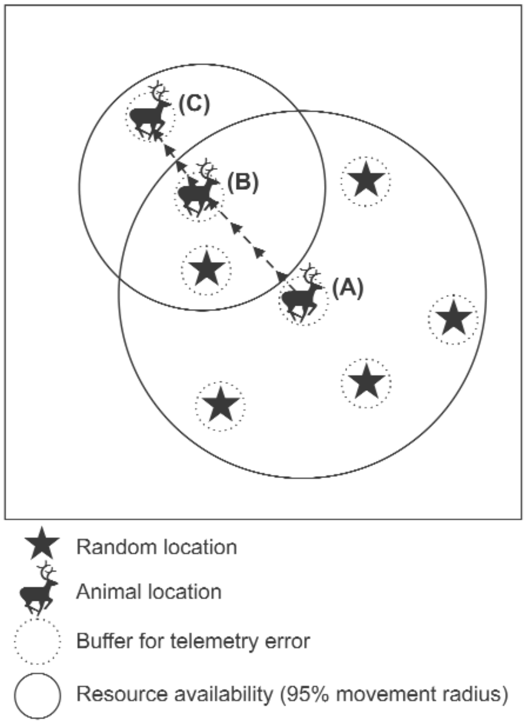

Figure. 3. Resource selection function sampling design for used and available resources and distance from disturbance features for caribou, wolves, grizzly bears, and wolverines monitored across the Canadian central Arctic (1995-2000). The radius of the full circle centered on location A represents availability for the focal location B and was calculated as the 95th percentile movement distance for that species and relocation interval. Following measurement of attributes under the error polygons (open circles) for used and random locations, location B then becomes the centre point for the availability window for location C. For each availability window, the fixed-effects logistic regression contrasts attributes at each animal location with 5 random locations indicated by the star symbol.

for simplicity we considered these resource-selection models to be representative of the range of behaviors the 4 species demonstrated over their mean relocation interval. Mean time between relocation was 226.7 ± 16.6 (SE), 78.5 ± 8.4, 52.4 ± 1.2, and 411.7 ± 48.1 hr, for caribou, wolves, bears, and wolverines, respectively.

We pooled animal locations for each seasonal model across independently monitored individuals. Pooling sacrificed an analysis of inter-animal variability in resource selection, but provided sample sizes sufficient to build complex models (Marzluff et al. 2004). Clustering animal locations statistically controlled for differences among animals.

We used a logit link function to relate resource or human disturbance variables to the dependent variable consisting of animal and random locations (Table 1). Resource covariates were measured as the percent area of vegetation by type, mean vegetation density by type, and the mean predicted occurrence (i.e., odds ratio) of interacting species. We measured the effect of disturbance as the distance of each animal or random location from the buffered boundary edge of the nearest human disturbance feature. We chose distance over density as the metric of response, because disturbance features were distributed at low densities and we could not objectively define the size of the moving window necessary for density calculations. We sampled attributes from within (resources) or the distance from (disturbance) an error polygon centered on each focal location with a radius equal to the accuracy expected for the collar type and location quality (Table 2, Fig. 3; Leptich et al. 1994, Ballard et al. 1995).

We assumed log-linear relationships between resource covariates (i.e., vegetation, interspecific interactions) and observed habitat selection, and, based on previous work, nonlinear responses by monitored animals to human disturbances (Carroll et al. 2001, Boyce and Waller 2003, Johnson et al. 2004*a*). Thus, variables for major disturbances, mineral exploration sites, and outfitter camps were each fit as 2-term Gaussian (i.e., squared) functions. The extra term allowed us to model nonlinear avoidance or selection responses as distance to human facilities decreased.

Given the low density of human facilities across the study area, we assumed that at some distance animal behavior and habitat selection would no longer be influenced by human activities. To statistically control for this threshold, we held the distance values (i.e., disturbance covariates) constant for use and random locations where the disturbance feature occurred outside the respective availability radius. Here, we assumed that our definition of availability was functionally related to an animal's response to a human disturbance. Clustered samples with the same value for a covariate are uninformative for estimation of that particular coefficient (Hosmer and Lemeshow 2000). This allowed the cluster to represent habitat effects, but statistically remove disturbance effects for animal locations that were at extreme distances from human facilities.

Model Selection

We used an information-theoretic approach to guide model development and selection (Anderson et al. 2000). We employed a 2-step process where initially we developed a set of candidate models that provided ecologically plausible explanations for the selection patterns of the monitored animals exclusive of disturbance features. Those models contained independent variables representative of land cover and the occurrence of other species. We then used the Akaike Information Criterion (AIC) difference adjusted for small sample sizes (AIC_c Δ), and Akaike weights (*w*) to evaluate and choose the most parsimonious model (i.e., 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 each model is the best from the set of proposed models (Anderson et al. 2000). Following selection of the most parsimonious of the habitat models, we included and evaluated all combinations of terms for the disturbance covariates. Although our approach could be considered a best subsets evaluation (King 2003), thoughtful generation of a few plausible resource and disturbance variables resulted in relatively few models.

Selection of the final model for mapping habitat change was not strictly a function of parsimony. Previous studies of carnivores monitored across other geographic locations suggested that some species might demonstrate selection for, not avoidance of human facilities (Johnson et al. 2004*a*). Attractants can alter the distribution of carnivores resulting in human–animal interactions and population sinks for some areas (e.g., campsites, garbage dumps) that are identified as selected habitats. Our modeling approach and the focus of this work was premised on avoidance as an indicator of disturbance. Thus, we required the final model to have a relatively low AIC_c and a convex Gaussian disturbance term indicative of avoidance of a disturbance feature.

The AIC provides evidence for selection of the most parsimonious model, but does not permit evaluation of discriminatory performance (Pearce and Ferrier 2000). We used *k*-fold cross validation to evaluate predictive success of each selected model (Boyce et al. 2002). The *k*-fold procedure was performed 5 times withholding 20% of the data for each iteration. We used a Spearman-rank correlation to assess the relationship between predicted occurrence for withheld animal locations and their frequency within 10 equally sized classes of predicted values (e.g., 0 to 0.1, 0.11 to 0.2…0.91–1.0; Boyce et al. 2002). A predictive model will have a strong mean correlation indicating a greater number of withheld locations in higher ranked classes representative of more strongly selected habitats. We used 95% confidence intervals to assess the strength of effect of each predictor covariate. Selection or avoidance cannot be inferred from covariates with confidence intervals that approach or overlap 0. We used the Pregibon $\Delta\ \beta$ and leverage (i.e., hat) statistics and the Hosmer and Lemeshow $\Delta\ \chi^2$ statistic to identify cases and clusters that had a large influence on the parameters of the model (Hosmer and Lemeshow 2000). We used tolerance scores to assess variables within each model for excessive collinearity (Menard 2001).

Spatial Representation of Resource Selection and Measured Disturbance

Predictions generated with conditional fixed-effects logistic regression are a relative measure of habitat selection, not a true probability of animal occurrence. Therefore, we used the odds ratio as a relative measure of habitat quality (Menard 2001):

$$\text{Odds ratio} = \exp(\beta_1 x_1 + \beta_2 x_2 + \ldots + \beta_i x_i) \quad (1)$$

We populated Equation 1 with coefficients ($\beta_1 \ldots \beta_i$) from the regression models and applied that equation to each raster GIS surface ($x_1 \ldots x_i$) used to sample the animal and random locations. Before generating predictive maps for the RSF equations, we rescaled the GIS surfaces to accommodate vegetation covariates that were modeled using percentage composition and mean density of cover types.

For ease of interpretation and further analysis we grouped all predicted values (i.e., odds ratios) into 4 classes we qualitatively defined as poor-, low-, good-, and high-quality habitat (Fig. 4). The terminology is subjective, but recognizes the increasing strength of habitat selection within each class. We used quartiles calculated for each species by season odds ratio map to categorize the continuous surfaces (Knick and Dyer 1997, Erickson et al. 1998, Carroll et al. 2001). The upper quartile represented the most strongly selected and presumably the most valuable habitats, the lower quartile represented the least valuable habitats. We produced habitat maps at a pixel resolution of 100 × 100 m (Fig. 4).

Quantifying Changes in Habitat Effectiveness

For each resource selection model, we generated maps that depicted the distribution of poor-, low-, good-, and high-quality habitat. Disturbance coefficients were applied to those maps in 3 ways, with each of the "scenarios" providing an alternative measure of habitat effectiveness. Here, disturbance coefficients, both modeled and assumed, degraded the effectiveness (i.e., odds ratio) of proximal vegetation resources.

For the first scenario, modeled disturbance, we applied the coefficients for disturbance features generated following the construction and assessment of various fixed-effects logistic regression models. Because we fit nonlinear disturbance terms, concave disturbance functions forced us to spatially represent only that portion of the relationship that reflected avoidance of human use facilities (e.g., Fig. 5). We determined the peak of that curve by holding the corresponding resource covariates at their mean and plotting the change in the odds ratio as a function of distance from the nearest disturbance feature. When mapping the RSF (Equation 1) we allowed each GIS disturbance surface, which represented the distance from any location on the study area to a disturbance feature, to vary only over the maximum distance at which avoidance was observed. Beyond that maximum, pixels were held constant at the distance observed at the peak of the curve.

The second scenario, no disturbance, mapped the distribution of habitats after controlling for avoidance responses of monitored animals (Mace et al. 1999, McDonald and McDonald 2002). Here, we used the GIS to modify each disturbance surface to represent a constant distance equal to the observed peak where resource selection, when mapped, was strongest relative to avoidance of disturbance features. The no disturbance scenario served as a control to measure the change in the area of the 4 habitat classes according to avoidance responses demonstrated by monitored animals.

We recognized that the small sample of collared animals, in combination with relatively few disturbance features and an extremely large study area, resulted in some uncertainty in the measured disturbance responses. Therefore, we developed a third scenario, assumed disturbance, which was based on hypothetical, not modeled, disturbance coefficients and zones of influence. Values were guided by the published literature and our knowledge of the study area (Kasworm and Manley 1990, Thurber et al. 1994, Nellemann and Cameron 1996, Dyer et al. 2001, Nellemann et al. 2001). We acknowledge that the hypothetical disturbance coeffi-

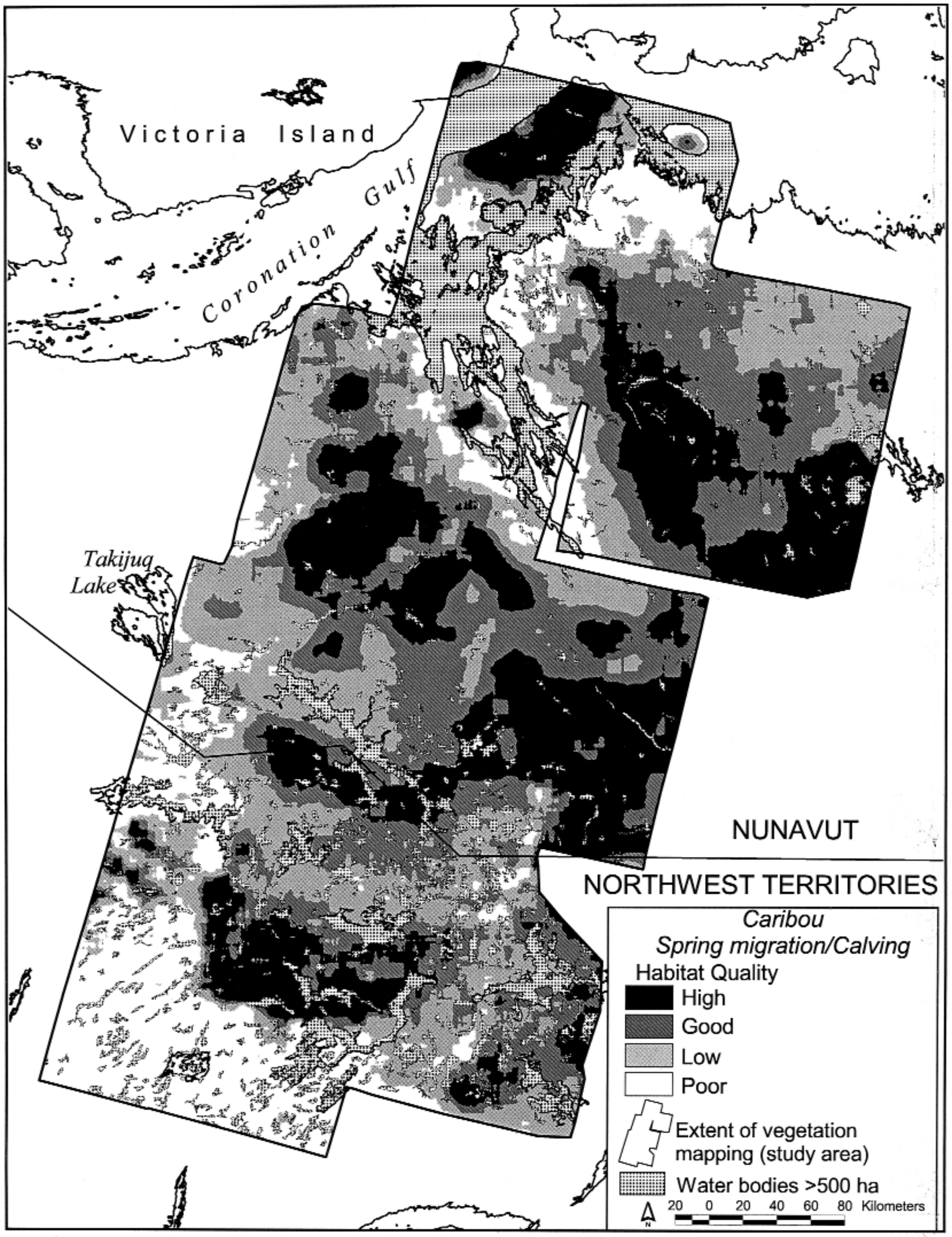

Figure. 4. Example of a map displaying predicted quality of habitats for caribou during the spring migration and calving season, across the Canadian central Arctic, 2000. Habitat quality was predicted with a resource selection function consisting of covariates for vegetation density and major developments.

cients are likely only approximations of effects, but this approach is consistent with past efforts for similar species (Schoen et al. 1994, Dixon 1997, Suring et al. 1998).

Coefficients for major disturbances represented a 95 and 50% reduction in habitat effectiveness within a cumulative zone of influence of 1 and 5 km, respectively. Mineral exploration sites effected a hypothetical 50% reduction in the value of habitats found within a 10 km radius of the assumed development site, and a 25% reduction within a 5 km zone around that buffered area. Habitat effectiveness within areas influenced by recreation outfitters was reduced by 10%. We attributed a 1 km buffer to the 29 km all-season road and reduced all habitats within that area by 95%. We applied the hypothetical disturbance coefficients and zones of influence to the maps for which we held disturbance constant (i.e., no disturbance). Because we could not statistically control for the correlation among disturbance effects, we did not compound (i.e., multiply) the effects of multiple coefficients at the same location. Where zones of influence overlapped, the coefficient with the strongest effect was applied. As with the modeled disturbances, we report the net decrease in the area of high- and good-quality habitat and increase in poor-quality habitat after adjusting for avoidance of human facilities.

RESULTS

From 1995 to 2000 biologists monitored 28 barren-ground caribou, 23 wolves, 81 grizzly bears, and 38 wolverines (n = 1,635, 2,885, 5,368, and 288 animal locations, respectively; Table 2). Collectively, those data allowed us to develop seasonal resource-selection models for each species representing responses to vegetation resources, interspecific interactions, and human disturbances.

Caribou

For the spring migration and calving season the most parsimonious resource model consisted of covariates for vegetation density (AIC w = 0.924). When combined with the disturbance covariates, the most parsimonious model contained nonlinear terms for major developments and mineral exploration sites (Table 3). However, we observed a near linear positive relationship between distance to mineral exploration sites and caribou occurrence and thus selected the next most parsimonious model as our final predictive equation. That model contained covariates for vegetation density and a nonlinear term for distance to major developments which demonstrated a convex relationship with a peak at 33 km (Fig. 5A). Caribou occurrence was positively related to areas dominated by lichen veneer, heath tundra, and low shrub and negatively related to riparian shrub (Table 4). A mean Spearman rank correlation of 0.844 (P = 0.002) across 5 cross-validation samples indicated that the final model had good predictive capacity.

During the post-calving season, vegetation quantified at both the patch and density scales were better predictors of caribou occurrence than models consisting of independent sets of those covariates (AIC w = 1.0). The most parsimonious resource-disturbance model contained terms for major developments, mineral explorations, and outfitter camps (Table 3). However, apparent selection for outfitter camps forced us to choose a less parsimonious, but highly predictive model ($\bar{r}_s$ = 0.842, P = 0.002). With the exception of density of riparian shrub, coefficients suggested relatively weak selection for vegetation, but avoidance of forested areas. Caribou demonstrated strong avoidance of major developments, but confidence intervals overlapping zero indicated a less conclusive effect for mineral exploration sites (Table 4, Fig. 5A).

Resource selection during autumn migration was best modeled using covariates for patches and density of vegetation (AIC w = 0.793). When including disturbance covariates, the most parsimonious model contained terms for mineral exploration sites and outfitter camps (Table 3). However, the measured responses were relatively small and imprecise, peaking at distances of 6 and 4 km, respectively (Fig. 5A). As with the other seasons, the model demonstrated good predictive performance ($\bar{r}_s$ = 0.763, P = 0.010). Caribou selected patches of lichen veneer and avoided areas dominated by sedge, peat bog, rock, and heath tundra (Table 4).

We observed considerable interseason variability in the measured or assumed effects of disturbance on the availability of habitats for caribou. During the spring migration and calving, and autumn migra-

Table 3. Number of model parameters (k), differences in Akaike's Information Criterion (AIC$_c$) scores (Δ) and AIC$_c$ weights (w) for candidate resource-disturbance models for caribou monitored from April 1996 to December 2000 across the Canadian central Arctic. Inclusion of resource covariates was determined using separate AIC model selection processes.

Season Model	k	AIC$_c$ Δ_i	AIC$_c$ w_i
Spring migration and Calving			
Mineral exploration[a]	3	138.59	<0.001
Major development	3	127.13	<0.001
Vegetation density[b]	11	16.31	<0.001
Vegetation density + mineral exploration	13	15.99	<0.001
Vegetation density + major development[c]	13	0.32	0.460
Vegetation density + major development + mineral exploration	15	0	0.540
Post-calving			
Major development	3	115.02	<0.001
Mineral exploration	3	108.74	<0.001
Outfitter camp	3	66.58	<0.001
Vegetation patch + vegetation density	21	52.19	<0.001
Vegetation patch + vegetation density + major development	23	48.99	<0.001
Vegetation patch + vegetation density + mineral exploration	23	44.58	<0.001
Vegetation patch + vegetation density + major development + mineral exploration[c]	25	39.66	<0.001
Vegetation patch + vegetation density + outfitter	23	16.46	<0.001
Vegetation patch + vegetation density + major development + outfitter	25	6.80	0.029
Vegetation patch + vegetation density + mineral exploration + outfitter	25	4.31	0.101
Vegetation patch + vegetation density + major development + mineral exploration + outfitter	27	0.00	0.870
Autumn migration			
Major development	3	80.93	<0.001
Mineral exploration	3	67.63	<0.001
Outfitter	3	60.11	<0.001
Vegetation patch + vegetation density + major development	21	37.44	<0.001
Vegetation patch + vegetation density	19	34.07	<0.001
Vegetation patch + vegetation density + major development + mineral exploration	23	28.35	<0.001
Vegetation patch + vegetation density + mineral exploration	21	25.47	<0.001
Vegetation patch + vegetation density + major development + outfitter	23	6.73	0.023
Vegetation patch + vegetation density + major development + mineral exploration + outfitter	25	3.25	0.133
Vegetation patch + vegetation density + outfitter	21	2.81	0.166
Vegetation patch + vegetation density + mineral exploration + outfitter[c]	23	0.00	0.677

[a] All disturbance covariates were parameterized as Gaussian (squared) functions.

[b] Vegetation density and vegetation patch represented all vegetation covariates present across the seasonal range of monitored caribou.

[c] Model used to predict reduction in habitat quality resulting from disturbance.

tion seasons our modeled disturbance coefficients resulted in a relatively small reduction in the availability of high-quality habitats (Table 5). When applied to the zones of influence, hypothetical disturbance coefficients revealed a slightly larger reduction of 2.5 and 5.2% in the availability of high-quality habitats for the before mentioned seasons. Habitat quality was most severely reduced by disturbance during the post-calving season; modeled coefficients effected a 37% reduction in high-quality and an 84% increase in low-quality habitats (Table 5).

Wolf

We used sets of covariates for patch and vegetation density to model wolf-resource relationships and included a covariate derived from the spatial extrapolation of the caribou selection models. During spring and autumn, resource use was best represented by a model consisting of covariates for vegetation patches and density (AIC w = 0.711). The next most parsimonious model included the former and a covariate for caribou occurrence (AIC w = 0.289). The resource-disturbance model with the largest AIC w included nonlinear terms for major developments and mineral exploration sites, with coefficients suggesting selection for mineral exploration areas (Table 6, 7). The next most parsimonious model indicating

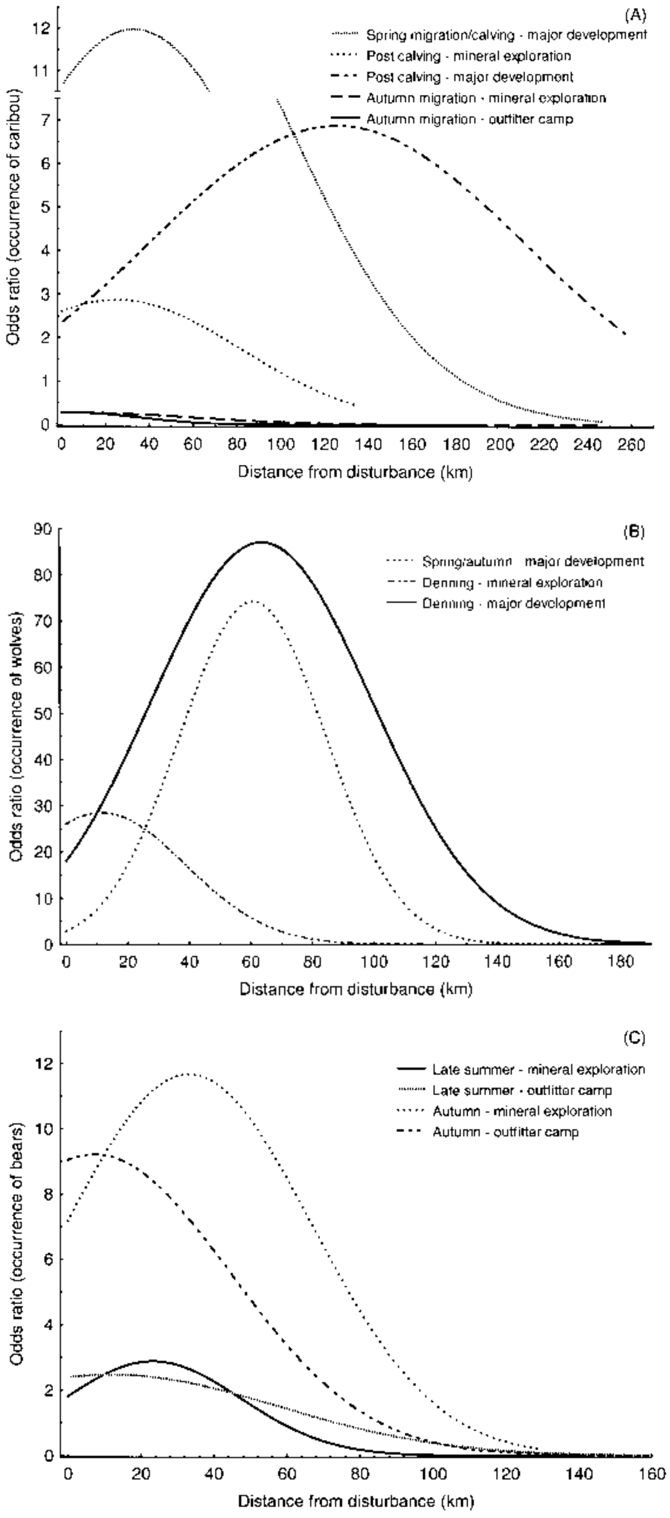

Figure. 5. Plots representing the likelihood of occurrence of monitored (A) caribou, (B) wolves, and (C) grizzly bears relative to disturbance features found across the Canadian central Arctic (1995-2000). Animal occurrence was allowed to vary with distance from disturbance features while other disturbance and vegetation covariates were held at their mean values.

Table 4. Coefficients (β) and 95% confidence intervals from seasonal resource-selection models for caribou of the Canadian central Arctic monitored from April 1996 to December 2000.

	Spring migration and calving		Post-calving		Autumn migration	
Covariate	β	95% CI	β	95% CI	β	95% CI
Esker density	–6.30	–15.84–3.24	2.32	–6.41–11.04	–8.70	–24.13–6.73
Esker patch	NI[a]	NI	<–0.01	–0.02–0.02	–0.02	–0.07–0.04
Forest density	–1.97	–5.81–1.87	–7.77	–14.09– –1.45	0.82	–1.89–3.54
Forest patch	NI	NI	0.03	<–0.01–0.06	<0.01	–0.01–0.02
Heath rock density	0.95	–1.47–3.37	–0.21	–2.26–1.85	–1.37	–4.77–2.04
Heath rock patch	NI	NI	0.01	0.01–0.02	0.01	<0.01–0.02
Heath tundra density	4.73	2.54–6.92	0.10	–1.78–1.98	–4.14	–7.20– –1.08
Heath tundra patch	NI	NI	0.01	0.01–0.02	0.01	<0.01–0.02
Lichen veneer density	8.48	6.30–10.66	1.79	–1.09–4.66	–0.87	–5.59–3.85
Lichen veneer patch	NI	NI	–0.01	–0.02–<0.01	0.02	0.01–0.04
Low shrub density	4.43	0.89–7.97	–7.60	–16.50–1.31	NI	NI
Low shrub patch	NI	NI	–0.01	–0.05–0.03	NI	NI
Peat bog density	–2.37	–13.97–9.23	4.81	–3.12–12.74	–8.68	–16.66– –0.70
Peat bog patch	NI	NI	0.05	0.01–0.10	–0.01	–0.04–0.03
Riparian shrub density	–10.84	–17.86– –3.81	10.10	5.64–14.56	1.58	–2.57–5.73
Riparian shrub patch	NI	NI	–0.04	–0.08– –0.01	0.01	–0.01–0.03
Rock density	1.94	0.61–3.28	–1.51	–2.84– –0.19	–7.49	–12.40– –2.58
Rock patch	NI	NI	0.01	<0.01–0.01	0.02	<–0.01–0.04
Sedge density	1.28	–1.92–4.47	1.08	–1.60–3.76	–9.94	–15.33– –4.54
Sedge patch	NI	NI	0.01	<0.01–0.02	0.01	<–0.01–0.03
Major development	0.01	<–0.01–0.02	0.02	<0.01–0.03	NI	NI
Major development[b]	<–0.01	<–0.01– –0.01	<–0.01	<–0.01–<0.01	NI	NI
Mineral exploration	NI	NI	0.01	–0.01–0.02	<0.01	–0.02–0.02
Mineral exploration[b]	NI	NI	<–0.01	<–0.01–<–0.02	<–0.01	<–0.01–<0.01
Outfitter camp	NI	NI	NI	NI	<0.01	–0.02–0.03
Outfitter camp[b]	NI	NI	NI	NI	<–0.01	<–0.01–<–0.01

NI: Not included; covariate excluded during model selection process or absent from range of monitored caribou.

[b] Squared second term for nonlinear Gaussian function.

Table 5. Seasonal change in the availability of habitats for caribou across the Canadian central Arctic, 1996–2000. Disturbance was held constant (No disturbance) and compared to resource selection maps modified with disturbance coefficients modeled from relocation data (Modeled disturbance), and maps with hypothetical disturbance coefficients and zones of influence (Assumed disturbance).

		Disturbance scenarios				
		No disturbance	Modeled disturbance		Assumed disturbance	
Season	Habitat quality	Area (km^2)	Area (km^2)	% change	Area (km^2)	% change
Spring migration and Calving						
	Poor	31,063	31,174	0.36	34,796	12.02
	Low	41,658	41,720	0.15	40,755	–2.17
	Good	43,558	43,470	–0.20	41,831	–3.96
	High	44,970	44,886	–0.19	43,867	–2.45
Post-calving						
	Poor	17,099	31,485	84.13	20,350	19.01
	Low	25,807	37,291	44.50	27,688	7.29
	Good	43,883	45,555	3.81	43,314	–1.30
	High	74,461	46,919	–36.99	69,898	–6.13
Autumn migration						
	Poor	43,801	43,823	0.05	45,335	3.50
	Low	41,217	41,290	0.18	43,409	5.32
	Good	39,839	39,808	–0.08	37,986	–4.65
	High	36,393	36,329	–0.18	34,520	–5.15

avoidance behaviors contained covariates for vegetation and major developments. That model had relatively poor predictive power ($\bar{r}_s = 0.605$, $P = 0.062$). Wolves demonstrated strong selection for forested areas and avoided locations dominated by peat bogs and lichen veneer (Table 7). Major developments were strongly avoided to a distance of 61 km (Fig. 5B). Exclusion of the covariates for major developments resulted in a more predictive selection model and indicated that our final model was sufficient for representing wolf-resource relationships, but failed to capture some dimension of the disturbance response ($\bar{r}_s = 0.675$, $P = 0.034$).

The most parsimonious resource model for the denning season consisted of covariates representing vegetation at the patch and density scales (AIC $w = 0.657$). As with spring and autumn, a model containing a covariate for caribou occurrence was ranked second (AIC $w = 0.343$). A disturbance model with terms for major developments,

Table 6. Number of model parameters (*k*), differences in Akaike's Information Criterion (AIC_c) scores (Δ) and AIC_c weights (*w*) for candidate resource-disturbance models for wolves monitored from June 1997 to August 1999 across the Canadian central Arctic. Inclusion of resource covariates was determined using separate AIC model selection processes.

Season	Model	*k*	$AIC_c\ \Delta_i$	$AIC_c\ w_i$
Spring and autumn				
	Outfitter camp[a]	3	64.62	<0.001
	Mineral exploration	3	49.06	<0.001
	Major development	3	41.33	<0.001
	Vegetation patch[b] + vegetation density + outfitter	21	39.84	<0.001
	Vegetation patch + vegetation density	19	38.47	<0.001
	Vegetation patch + vegetation density + mineral exploration + outfitter	23	28.59	<0.001
	Vegetation patch + vegetation density + mineral exploration	21	26.54	<0.001
	Vegetation patch + vegetation density + major development + outfitter	23	16.26	<0.001
	Vegetation patch + vegetation density + major development[c]	21	13.38	0.001
	Vegetation patch + vegetation density + major development + mineral exploration + outfitter	25	3.24	0.165
	Vegetation patch + vegetation density + major development + mineral exploration	23	0.00	0.834
Denning				
	Outfitter camp	3	422.33	<0.001
	Major development	3	389.34	<0.001
	Mineral exploration	3	377.60	<0.001
	Vegetation patch + vegetation density	19	150.00	<0.001
	Vegetation patch + vegetation density + outfitter	21	103.37	<0.001
	Vegetation patch + vegetation density + major development	21	101.01	<0.001
	Vegetation patch + vegetation density + mineral exploration	21	73.84	<0.001
	Vegetation patch + vegetation density + major development + outfitter	23	63.10	<0.001
	Vegetation patch + vegetation density + major development + mineral exploration[c]	23	40.09	<0.001
	Vegetation patch + vegetation density + mineral exploration + outfitter	23	28.22	<0.001
	Vegetation patch + vegetation density + major development + mineral exploration + outfitter	25	0.00	1.000

[a] All disturbance covariates were parameterized as Gaussian (squared) functions.

[b] Vegetation Density and Vegetation Patch represented all vegetation covariates present across the seasonal range of monitored wolves.

[c] Model used to predict reduction in habitat quality resulting from disturbance.

Table 7. Coefficients (β) and 95% confidence intervals from resource-selection models for wolves of the Canadian central Arctic monitored from June 1997 to August 1999.

	Spring and autumn		Denning	
Covariate	β	95% CI	β	95% CI
Esker density	–7.49	–27.73–12.76	11.38	4.27–18.49
Esker patch	0.02	–0.03–0.07	0.03	0.01–0.05
Forest density	12.54	0.25–24.83	1.36	–3.49–6.20
Forest patch	–0.01	–0.05–0.04	0.02	<0.01–0.05
Heath rock density	4.89	1.36–8.42	5.68	4.14–7.22
Heath rock patch	<–0.01	–0.01–<0.01	<–0.01	<–0.01–<0.01
Heath tundra density	2.71	–1.03–6.46	4.56	2.95–6.18
Heath tundra patch	<0.01	–0.01–0.01	<0.01	<0.01–0.01
Lichen veneer density	–12.65	–22.17– –3.13	–7.04	–11.31– –2.77
Lichen veneer patch	<0.01	–0.03–0.04	0.03	0.01–0.04
Peat bog density	–26.54	–50.23– –2.86	7.77	–0.46–16.01
Peat bog patch	0.12	–0.01–0.24	0.01	–0.04–0.05
Riparian shrub density	–2.10	–9.56–5.36	1.64	–1.64–4.93
Riparian shrub patch	0.02	–0.03–0.06	0.01	–0.01–0.03
Rock density	–5.80	–11.63–0.03	–3.32	–5.32– –1.32
Rock patch	0.02	<0.01–0.04	0.02	0.01–0.02
Sedge density	–7.19	–13.51– –0.87	–1.56	–4.13–1.02
Sedge patch	0.03	0.01–0.04	0.03	0.02–0.03
Major development	0.11	0.05–0.16	0.10	0.03–0.07
Major development[a]	<–0.01	<–0.01–<–0.01	<–0.01	<–0.01–<–0.01

[a] Squared second term for nonlinear Guassian function.

mineral exploration sites, and outfitter camps had the lowest AIC score, but indicated selection for outfitter camps (Table 6, 7). The next most parsimonious model, exclusive of the covariates for outfitter camps, indicated that wolves avoided major developments and mineral exploration sites, instead selecting patches of esker and portions of the study area where esker complexes were abundant (Table 7). Heath rock, heath tundra, and lichen veneer also were important predictors of wolf occurrence. The final resource-selection model was predictive ($\bar{r}_s$ = 0.719, P = 0.020).

Relative to a scenario where we held disturbance constant, the large coefficient for avoidance of major developments suggested that during spring and autumn poor-quality wolf habitat increased by 32% and good- and high-quality habitats decreased by 25% (Table 8). Our assumed disturbance functions included a larger range of effects, but were more conservative when predicting habitat loss. Using these values, we recorded 5, and 3% losses in the total area of high- and good-quality habitat with 7 and 4% increases in the two less valuable classes. Effects of disturbance were less pronounced during denning. Modeled coefficients for major developments and mineral exploration sites suggested a 13% decrease in high-quality and a 16% increase in poor-quality habitats (Table 8). Our hypothetical disturbance scenario revealed a 5% loss of high-quality habitat for wolves during the denning season.

Grizzly Bear

During spring, observed movements of monitored grizzly bears were best modeled using covariates for vegetation density and patches and the occurrence of caribou (AIC w = 0.764). The model had good predictive capacity, but human disturbances did not have a discernible effect ($\bar{r}_s$ = 0.692, P = 0.023). The next most parsimonious model included covariates for the effects of mineral exploration, but its AIC score differed by nearly 4 points (Table 9). Distribution of grizzly bears was negatively correlated with the predicted occurrence of caribou, forested and peat bog habitats, but was positively related to portions of the study area dominated by the esker, lichen veneer, and heath tundra habitat types, and patches of riparian shrub (Table 10).

Table 8. Seasonal change in the availability of habitats for wolves across the Canadian central Arctic, 1997–1999. Disturbance was held constant (No disturbance) and compared to resource selection maps modified with disturbance coefficients modeled from relocation data (Modeled disturbance), and maps with hypothetical disturbance coefficients and zones of influence (Assumed disturbance).

		Disturbance scenarios				
		No disturbance	Modeled disturbance		Assumed disturbance	
Season	Habitat quality	Area (km^2)	Area (km^2)	% change	Area (km^2)	% change
Spring and Autumn						
	Poor	31,742	41,768	31.59	33,971	7.02
	Low	37,561	39,288	4.60	39,204	4.37
	Good	44,503	39,980	–10.16	43,158	–3.02
	High	47,443	40,215	–15.24	44,917	–5.32
Denning						
	Poor	35,025	40,554	15.79	37,952	8.36
	Low	38,830	40,702	4.82	38,894	0.16
	Good	41,655	40,220	–3.44	40,900	–1.81
	High	45,739	39,774	–13.04	43,504	–4.89

The most parsimonious resource model for the early summer season included terms for vegetation modeled at the patch and density scales and caribou occurrence (AIC w = 0.993). The addition of disturbance covariates resulted in several models with lower AIC scores (Table 9); however, covariates for major developments and mineral exploration sites suggested selection for, rather than avoidance of people and associated facilities. The next most parsimonious and final selection model was exclusive of disturbance effects. Coefficients for that model were similar to those generated for the spring season and suggested little use of portions of the study area frequented by caribou and selection for esker and low shrub habitats (Table 10). Our final model demonstrated excellent prediction ($\bar{r}_s$ = 0.896, P < 0.001).

During late summer, the resource model with the lowest AIC score contained covariates for vegetation density and patches (AIC w = 0.682). The next most parsimonious model contained an additional term representing a positive response of bears to caribou occurrence (AIC w = 0.284). Inclusion of disturbance effects resulted in a final model with covariates for vegetation, mineral exploration sites, and outfitter camps

Table 9. Number of model parameters (*k*), differences in Akaike's Information Criterion (AIC_c) scores (Δ) and AIC_c weights (*w*) for candidate resource-disturbance models for grizzly bears monitored from May 1995 to June 1999 across the Canadian central Arctic. Inclusion of resource covariates was determined using separate AIC model selection processes.

Season Model	*k*	$AIC_c\Delta_i$	AIC_cw_i
Spring			
Mineral exploration[a]	3	56.91	<0.001
Major development	3	56.81	<0.001
Caribou + vegetation density[b] + vegetation patch + major development + mineral exploration	26	7.85	0.015
Caribou + vegetation density + vegetation patch + major development	3	4.14	0.096
Caribou + vegetation density + vegetation patch + mineral exploration	24	3.62	0.125
Caribou + vegetation density + vegetation patch[c]	22	0.00	0.764
Early summer			
Outfitter camp	3	232.31	<0.001
Major development	3	227.65	<0.001
Mineral exploration	3	214.64	<0.001
Caribou + vegetation patch + vegetation density + outfitter	24	13.55	<0.001
Caribou + vegetation patch + vegetation density[c]	22	13.07	<0.001
Caribou + vegetation patch + vegetation density + major development + outfitter	26	8.55	0.005
Caribou + vegetation patch + vegetation density + major development	24	7.86	0.007
Caribou + vegetation patch + vegetation density + mineral exploration + outfitter	26	1.38	0.167
Caribou + vegetation patch + vegetation density + major development + mineral exploration + outfitter	28	0.88	0.216
Caribou + vegetation patch + vegetation density + mineral exploration	24	0.42	0.270
Caribou + vegetation patch + vegetation density + major development + mineral exploration	26	0.00	0.334
Late summer			
Major development	3	198.28	<0.001
Outfitter camp	3	189.88	<0.001
Mineral exploration	3	175.76	<0.001
Vegetation patch + vegetation density + major development	23	31.86	<0.001
Vegetation patch + vegetation density + major development + outfitter	25	29.32	<0.001
Vegetation patch + vegetation density	21	28.96	<0.001
Vegetation patch + vegetation density + outfitter	23	26.39	<0.001
Vegetation patch + vegetation density + major development + mineral exploration	25	2.40	0.122
Vegetation patch + vegetation density + mineral exploration	23	1.20	0.222
Vegetation patch + vegetation density + major development + mineral exploration + outfitter	27	0.94	0.253
Vegetation patch + vegetation density + mineral exploration + outfitter[c]	25	0.00	0.404
Autumn			
Major development	3	86.82	<0.001
Outfitter camp	3	83.80	<0.001
Mineral exploration	3	81.83	<0.001
Caribou + vegetation patch + vegetation density + major development + outfitter	26	6.89	0.009
Caribou + vegetation patch + vegetation density	22	6.54	0.011
Caribou + vegetation patch + vegetation density + outfitter	24	6.22	0.013
Caribou + vegetation patch + vegetation density + major development	24	5.62	0.017
Caribou + vegetation patch + vegetation density + major development + mineral exploration + outfitter	28	1.38	0.141
Caribou + vegetation patch + vegetation density + mineral exploration	24	0.17	0.258
Caribou + vegetation patch + vegetation density + mineral exploration	24	0.17	0.258
Caribou + vegetation patch + vegetation density + major development + mineral exploration	26	0.07	0.271
Caribou + vegetation patch + vegetation density + mineral exploration + outfitter[c]	26	0.00	0.280

[a] All disturbance covariates were parameterized as Gaussian (squared) functions.

[b] Vegetation Density and Vegetation Patch represented all vegetation covariates present across the seasonal range of monitored bears.

[c] Model used to predict reduction in habitat quality resulting from disturbance.

(Table 9). However, the model was a poor predictor of our withheld sample of cross-validation locations ($\bar{r}_s = 0.492$, $P = 0.142$). Bears avoided forested areas, demonstrated weak selection for portions of the study area dominated by the riparian and low shrub habitat types, and strong selection for patches of esker (Table 10). Model coefficients suggested that mineral exploration sites had a moderate negative influence on habitat

Table 10. Coefficients (β) and 95% confidence intervals from resource-selection models for grizzly bear of the Canadian central Arctic monitored from May 1995 to June 1999.

	Spring		Early summer		Late summer		Autumn	
Covariate	β	95% CI	β	95% CI	β	95% CI	β	95% CI
Esker density	4.45	–2.12–11.02	14.11	7.53–20.69	1.98	–4.90–8.86	11.46	2.90–20.03
Esker patch	0.01	<0.01–0.03	0.01	–0.01–0.02	0.05	0.03–0.06	0.02	<–0.01–0.04
Forest density	–9.92	–18.49– –1.36	–32.24	–46.32– –18.16	–9.06	–14.70– –3.42	–4.15	–7.88– –0.43
Forest patch	0.04	0.01–0.07	0.08	0.04–0.11	0.02	<–0.01–0.04	<0.01	–0.02–0.02
Heath rock density	1.48	–0.09–3.05	–0.60	–2.15–0.96	0.49	–1.07–2.06	3.07	1.22–4.92
Heath rock patch	0.01	<0.01–0.01	<0.01	<–0.01–0.01	<0.01	<–0.01–0.01	<–0.01	–0.01–<0.01
Heath tundra density	4.05	2.29–5.82	–0.62	–2.23–0.99	–0.82	–2.48–0.85	0.57	–1.52–2.65
Heath tundra patch	<0.01	<–0.01–0.01	0.01	0.01–0.01	0.01	<0.01–0.01	0.01	0.01–0.01
Lichen veneer density	5.93	2.91–8.95	–0.20	–2.83–2.42	1.71	–0.88–4.29	2.21	–0.59–5.01
Lichen veneer patch	<0.01	<–0.01–0.01	–0.01	–0.02–<0.01	–0.01	–0.02–<0.01	–0.01	–0.02–<0.01
Low shrub density	2.69	1.12–4.25	1.86	0.33–3.38	1.58	0.13–3.02	2.12	0.12–4.13
Low shrub patch	0.01	<–0.01–0.01	0.01	0.01–0.02	0.01	0.01–0.02	0.02	0.01–0.02
Peat bog density	–9.29	–16.75– –1.83	–0.57	–8.01–6.87	4.62	–0.53–9.77	11.58	5.10–18.07
Peat bog patch	0.01	–0.03–0.05	0.05	0.01–0.09	0.01	–0.02–0.03	–0.03	–0.07–<0.01
Riparian shrub density	–1.15	–4.00–1.70	2.67	–0.35–5.69	2.98	0.49–5.47	0.07	–2.92–3.07
Riparian shrub patch	0.01	–0.01–0.03	0.01	<0.01–0.03	0.02	0.01–0.03	0.01	<–0.01–0.02
Rock density	2.07	0.52–3.61	–0.65	–1.89–0.59	–1.10	–2.70–0.50	0.93	–1.06–2.93
Rock patch	<0.01	<–0.01–0.01	0.01	<0.01–0.01	<0.01	<–0.01–0.01	<–0.01	–0.01–0.01
Sedge density	–0.48	–3.45–2.49	–1.61	–4.44–1.21	–0.34	–3.16–2.49	1.94	–1.84–5.71
Sedge patch	<0.01	<–0.01–0.01	0.01	0.01–0.02	0.01	0.01–0.02	0.01	<–0.01–0.01

use to a distance of 23 km, while the coefficients for outfitter camps were smaller having an effect over a distance of 12 km (Fig. 5C).

During autumn, grizzly bears demonstrated a positive response to caribou, and, as with the other seasonal models, to covariates for vegetation density and patches (AIC $w = 0.646$). Our final set of resource-disturbance models was characterized by small AIC weights suggesting considerable model selection uncertainty. The most parsimonious model contained covariates for caribou occurrence, vegetation and mineral exploration, and outfitter camps (Table 9). Habitat selection was strongly influenced by occurrence of caribou and the prevalence of the esker, heath rock, low shrub, and peat bog vegetation types (Table 10). Monitored bears avoided mineral exploration sites and outfitter camps, but wide confidence intervals suggested that the latter relationship was statistically uncertain. Predictive performance of that model was excellent ($\bar{r}_s = 0.814$, $P = 0.004$).

Our scenario of assumed disturbance effects suggested that habitat loss for grizzly bears was most extreme during late summer and autumn, where we measured 12 and 11% reductions in the total availability of high- and good-quality habitats, respectively (Table 11). Modeled responses of bears to mineral exploration sites and outfitter camps suggested an even larger impact. For autumn, we identified a 34% increase in the area of poor-quality habitats and a reduction of nearly 21% of high- and good-quality habitats to low- and poor-quality habitats. During late summer, model coefficients suggested a nearly 18% decrease in the total availability of good- and high-quality habitats. We did not observe much evidence for a relationship between grizzly bear movements and avoidance of human disturbance factors during spring and early summer.

Wolverine

During winter, when caribou were absent from the range of monitored wolverines, the most parsimonious model included covariates for vegetation density and patches (Table 12). Disturbance features were largely absent from the range of monitored wolverines; therefore, we could not reliably model these effects. Coefficients suggested

Table 11. Seasonal change in the availability of habitats for grizzly bears across the Canadian central Arctic, 1995–1999. Disturbance was held constant (No disturbance) and compared to resource selection maps modified with disturbance coefficients modeled from relocation data (Modeled disturbance), and maps with hypothetical disturbance coefficients and zones of influence (Assumed disturbance).

		Disturbance scenarios				
		No disturbance	Modeled disturbance		Assumed disturbance	
Season	Habitat quality	Area (km^2)	Area (km^2)	% change	Area (km^2)	% change
Spring	Poor	41,815	NA	NA	47,820	14.36
	Low	40,179	NA	NA	37,425	–6.85
	Good	39,540	NA	NA	36,886	–6.71
	High	39,716	NA	NA	39,119	–1.50
Early summer						
	Poor	41,179	NA	NA	46,787	13.62
	Low	40,282	NA	NA	38,971	–3.25
	Good	39,893	NA	NA	37,863	–5.09
	High	39,896	NA	NA	37,628	–5.68
Late summer						
	Poor	30,722	39,835	29.66	37,281	21.35
	Low	41,375	40,175	–2.90	40,324	–2.54
	Good	45,037	40,655	–9.73	42,254	–6.18
	High	44,116	40,585	–8.00	41,391	–6.18
Autumn						
	Poor	30,651	41,190	34.38	36,632	19.51
	Low	41,738	40,362	–3.30	40,557	–2.83
	Good	44,680	39,842	–10.83	42,392	–5.12
	High	44,180	39,855	–9.79	41,670	–5.68

that occurrence of wolverines was correlated with patches of heath rock and rock association, and areas dominated by sedge and a low density of lichen veneer, heath rock, and heath tundra patches (Table 13). The cross validation procedure suggested that the final selection model was highly predictive of a withheld sample of wolverine locations ($\bar{r}_s$ = 0.905, $P < 0.001$).

We hypothesized that wolverines would scavenge kills from other carnivores and hunt caribou when present. Therefore, we generated models for summer that included covariates representative of the occurrence of caribou, wolves, and bears. Our most parsimonious model consisted of covariates for vegetation density indicating a strong relationship between wolverine occurrence and the sedge habitat and little use of areas dominated by heath rock, heath tundra, and lichen veneer (Table 12, 13). However, similar AIC values suggested considerable model-selection uncertainty. Alternative models could include terms for wolf, caribou, and bear occurrence with little reduction in parsimony; wolverines were positively associated with those species. Prediction was excellent for the vegetation density model

Table 12. Number of model parameters (*k*), differences in Akaike's Information Criterion (AIC$_c$) scores (Δ) and AIC$_c$ weights (*w*) for candidate resource selection models for wolverines monitored from March 1996 to January 2000 across the Canadian central Arctic.

Season	Model	*k*	AIC$_c$ Δ_i	AIC$_c$ w_i
Winter				
	Vegetation patch[a]	9	155.06	<0.001
	Vegetation density	9	12.89	0.002
	Vegetation patch + vegetation density[b]	17	0.00	0.998
Summer				
	Wolf + vegetation patch	10	162.27	<0.001
	Vegetation patch	9	161.89	<0.001
	Bear + vegetation patch	10	159.87	<0.001
	Bear + caribou + wolf + vegetation patch	12	156.63	<0.001
	Caribou + vegetation patch	10	155.81	<0.001
	Bear + caribou + wolf + vegetation patch + vegetation density	20	15.16	<0.001
	Caribou + vegetation patch + vegetation density	18	10.81	0.002
	Bear + vegetation patch + vegetation density	18	10.73	0.002
	Wolf + vegetation patch + vegetation density	18	10.49	0.002
	Vegetation patch + vegetation density	17	8.41	0.005
	Bear + caribou + wolf + vegetation density	12	4.72	0.034
	Bear + vegetation density	10	1.68	0.155
	Caribou + vegetation density	10	1.62	0.160
	Wolf + vegetation density	10	0.49	0.281
	Vegetation vensity[b]	9	0.00	0.360

[a] Vegetation Density and Vegetation Patch represented all vegetation covariates present across the seasonal range of monitored wolverines.

[b] Model used to predict reduction in habitat quality resulting from disturbance.

Table 13. Coefficients (β) and 95% confidence intervals from resource-selection models for wolverines of the Canadian central Arctic monitored from March 1996 to January 2000.

	Winter		Summer	
Covariate	β	95% CI	β	95% CI
Esker density	4.60	−22.45–31.65	0.03	−32.39–32.46
Esker patch	−0.02	−0.05–0.02	NI	NI
Forest density	5.46	−41.58–52.50	−5.98	−68.98–57.03
Forest patch	0.04	−0.03–0.10	NI	NI
Heath rock density	−17.94	−24.07– −11.82	−18.97	−26.44– −11.50
Heath rock patch	0.01	0.01–0.02	NI	NI
Heath tundra density	−12.87	−17.93– −7.81	−20.33	−27.01– −13.65
Heath tundra patch	<0.01	<−0.01–0.01	NI	NI
Lichen veneer density	−16.88	−23.99– −9.78	−14.93	−23.18– −6.69
Lichen veneer patch	0.01	−0.01–0.02	NI	NI
Riparian shrub density	−7.41	−19.71–4.90	−15.03	−31.27–1.21
Riparian shrub patch	0.03	−0.01–0.05	NI	NI
Rock density	7.25	−1.82–16.32	1.88	−10.18–13.94
Rock patch	0.03	0.02–0.05	NI	NI
Sedge density	36.06	24.96–47.16	42.43	28.26–56.61
Sedge patch	0.01	<−0.01–0.01	NI	NI

NI: Not included; covariate excluded during model selection.

($\bar{r}_s = 0.903$, $P < 0.001$).

Application of our hypothetical zones of influence and disturbance coefficients resulted in a relatively small reduction in the availability of high-quality habitats for wolverines. The potential impacts were most severe during summer, when caribou were present across the range of the monitored wolverines. We predicted a 2.6% increase in the amount of low-quality habitat and a 2.4% decrease in high-quality habitat (Table 14).

Summary of Results

The AIC weights suggested uncertainty in model selection for some species by season combinations, and 2 of 11 models had low predictive performance. Model results indicated that human disturbances influenced animal distribution, but responses to types of disturbance were inconsistent across seasons and species. The covariate mineral exploration site was most frequently included in our models, but major developments had the strongest negative influence on habitat selection. For bears and wolves, some seasonal models suggested selection for human facilities.

Our hypothetical zones of influence and corresponding disturbance coefficients also suggested variable impacts. Measured habitat loss was most extreme for grizzly bears and wolves followed by caribou and wolverine. Vegetation density or vegetation density in combination with percentage of vegetation patches typically were the most parsimonious combination of covariates for modeling species occurrence.

Seasonal reductions in habitats were greatest for caribou during post-calving where responses of collared animals to human disturbance features suggested a 37% decrease in the area of high-quality habitat. Across seasons, grizzly bears and wolves demonstrated the strongest avoid-

Table 14. Seasonal change in the availability of habitats for wolverines across the Canadian central Arctic, 1996–2000. Disturbance was held constant (No disturbance) and compared to resource selection maps with hypothetical disturbance coefficients and zones of influence (Assumed disturbance).

		Disturbance scenarios		
		No disturbance	Assumed disturbance	
Season	Habitat quality	Area (km^2)	Area (km^2)	% change
Winter	Poor	40,623	41,610	2.43
	Low	39,983	39,710	−0.68
	Good	40,452	40,396	−0.14
	High	40,191	39,534	−1.64
Summer	Poor	39,834	40,878	2.62
	Low	39,797	39,639	−0.40
	Good	39,772	39,884	0.28
	High	41,848	40,849	−2.39

ance and thus the greatest overall reductions in the availability of high-quality habitats. Modeled responses suggested a maximum conversion of nearly 15% of high-quality habitats for wolves during the denning season and 9.8% for bears during autumn. We only modeled assumed responses for wolverines and measured a 2.4% decrease in high-quality habitats during summer.

DISCUSSION

Our study is the first to quantify the cumulative effects of multiple sources of human disturbance as they relate to habitat displacement for sensitive Arctic wildlife. Industrial development is of considerable concern, but assessment of impacts across the Arctic has been constrained largely to facilities associated with petroleum extraction. With few exceptions, researchers have focused on the oilfield region near Prudhoe Bay, Alaska, and the potential impacts on calving caribou (Cronin et al. 1998). However, a massive increase in exploration and development activities across the Canadian central Arctic, spurred by the first discovery of diamond deposits in 1991, has broadened the geographic range of possible impacts. Although most tundra ecosystems are still relatively pristine, our research demonstrates that human presence and associated infrastructure have the potential to disrupt the movements and reduce the availability of high-quality habitats for caribou, wolves, grizzly bears, and wolverines that inhabit the study area.

We defined an impact as the reduction in the use of habitats ranked on a relative scale from poor- to high-quality. Change in ranking was the product of coefficient strength and the area over which we measured a response. The distribution of resources interacted with avoidance behaviors to moderate or amplify disturbance-related changes in habitat quality. We deliberately chose few habitat rankings to facilitate interpretation (Knick and Dyer 1997, Erickson et al. 1998, Carroll et al. 2001) and smooth errors inherent in the GIS data. The alternative, a continuous surface of odds ratio values, would provide a more detailed evaluation of changes in habitat quality (McDonald and McDonald 2002), but also a false perception of precision in our final maps.

Considering the large areas over which monitored animals moved we thought it implausible that avoidance would occur in a linear fashion to distances of several 100 km (Kasworm and Manley 1990, Thurber et al. 1994, Nellemann and Cameron 1996, Dyer et al. 2001, Nellemann et al. 2001; Fig. 2). Thus, we modeled nonlinear responses assuming an asymptotic disturbance effect: avoidance behaviors decreased gradually as distance from a human facility increased until that facility no longer influenced resource selection. As demonstrated in the declining slopes (Fig. 5), the decreasing likelihood of occurrence with distance from a facility, after some threshold, probably resulted from the low density of disturbance features and our failure to saturate the study area with collared animals. Although non-collared animals may have occurred across those areas, our models reported coefficients that suggested avoidance. A similar sampling issue was reported by other researchers modeling disturbance across large study areas (Carroll et al. 2001, Boyce and Waller 2003).

Our results suggested that wolves and grizzly bears were most impacted by human disturbances throughout the year, and that caribou demonstrated a strong seasonal response. The 37% decrease in high-quality post-calving habitats may be attributed to strong avoidance of major developments over a large area. Other researchers have reported avoidance behaviors of caribou at finer spatial and temporal scales. Nellemann and Cameron (1996, 1998) found that caribou density was inversely related to road density, and that caribou avoided high-quality habitats within 4 km of roads and oilfield production facilities at Prudhoe Bay. Woodland caribou in northern Alberta demonstrated avoidance of areas within 1,000 m from oil and gas wells and within 250 m from seismic lines, accounting for a 22–48% decrease in habitat availability (Dyer et al. 2001). Across Norway, incremental developments have resulted in a 70% reduction in the availability of undisturbed reindeer habitats (Nellemann et al. 2003). Given these examples and others, there is a large body of compelling evidence to support the assertion that caribou have a negative response to human disturbances (Harrington and Veitch 1991, Vistnes and Nellemann 2001, Dyer et al. 2002, Mahoney and Schaefer 2002, Reimers et al. 2003). However, the following caveats apply: implications to vital rates and ultimately to populations are not well studied or understood (Wolfe et al. 2000); caribou can adjust behaviorally to accommodate some levels of disturbance (Johnson and Todd 1977, Duchesne et al. 2000, Colman et al. 2001); and disturbance responses do not always infer considerable energetic costs (Tyler 1991).

Carnivore populations have demonstrated extreme sensitivity to the presence of humans. Across North America and Europe, wolf, grizzly bear, and wolverine populations have declined in distribution and abundance (Corsi et al. 1999, Carroll et al. 2001, Vangen et al. 2001, Mattson and Merrill 2002). In most circumstances, declines are directly linked to uncontrolled trapping and hunting, defense of life or property, or concerted efforts to extirpate populations that compete with human interests. Disturbance-related reductions in habitat availability have a less direct effect on population productivity, but should be minimized where resources are limiting. As with our study, researchers have documented avoidance responses of carnivores that may restrict the use of habitats that might otherwise confer reproductive or survival benefits (Thurber et al. 1994, Mace and Waller 1996).

Several of our models suggested selection of habitats in the vicinity of human facilities. Collared wolves demonstrated weak selection for mineral exploration sites and strong selection for outfitter camps. During early summer, the most parsimonious model for bears included coefficients of a small magnitude for mineral exploration sites. This behavior may have been in response to food attractants. Problem wolverines were managed at 1 of the diamond sites (BHP Diamonds Inc., 2001, Environmental agreement annual report 2001, Yellowknife, Northwest Territories, Canada, unpublished report) and across other areas of the Arctic, human presence has attracted and resulted in mortality of grizzly bears (Follman and Hechtel 1990). Where resources and habitats are not limiting, mortality from hunting, trapping, or removal of problem animals can be additive rather than compensatory (Krebs et al. 2004). McLoughlin et al. (2003) performed an aspatial PVA for tundra grizzly bears and reported that risk of extinction was low, but even a small increase in mortality of adults through hunting or management actions could lead to a substantial increase in the risk of decline. Although we did not have sufficient data to present the population implications of human-carnivore interactions, prudent conservation planning would include measures to limit attractants of bears, wolves, and wolverines to development facilities (McLellan et al. 1999, Johnson et al. 2004*a*).

Our failure to model a strong avoidance response to each source of disturbance does not confirm the absence of an impact. Monitored animals ranged over a large area with a low density of human facilities, we collared only a small proportion of each population, and, as a result, some models were constructed using relatively few animal relocations (Table 2). Such limitations in our data may lead to small effects and imprecise coefficients and models may not generalize well to the population or the larger study area. Also, we cannot dismiss the possibility that we identified spurious relationships. General trends in movements could lead to apparent, but erroneous avoidance or selection of facilities. In an effort to control for such results, we adopted a conservative modeling approach. We used conditional fixed-effects regression to eliminate the influence of locations that occurred at extreme distances from a disturbance feature, we accepted only models that conformed to the predicted convex response function, and we did not attempt to fit models where a response was implausible. As an example, the range of monitored wolverine did not encompass many disturbance features, thus, avoidance effects would likely be spurious. Acknowledging the limitations of our data and approach and considering the scope of the question, our results should be considered informative, but preliminary. Further research at a range of behavioral scales and using a number of experimental and observational approaches is essential for refuting or confirming and understanding additional and similar effects.

Although we are confident that observed patterns of avoidance are an approximation of a real effect, we recognize the limitations of our data and the possibility of false negatives. Holding modeled disturbance effects constant and applying predetermined coefficients allowed us to easily assess the simple "footprint" impacts associated with current all-season roads, mines, exploration, and outfitter facilities. Similar approaches were used to assess the cumulative impacts of human actions on the availability of habitats for grizzly bears (Schoen et al. 1994, Dixon 1997, Suring et al. 1998). For our analyses, we assumed that disturbance was consistent for all species across all seasons, and that the magnitude of effect was within the range of responses reported in the published literature. The results, however, are likely sensitive to those values: increasing the zone of influence and coefficient will reduce the area of high-quality habitats.

Results suggested less extreme effects, but were consistent with impacts attributed to the modeled coefficients. Although not empirically based, the analysis of assumed disturbance is easily replicated and may serve as a simple tool to evaluate a range of development impacts where information for actual animal responses is lacking. Future information can be used to modify the magnitude of effects and zones of influence, update the locations and status of disturbance features, and recalculate the risk assessment.

Comparison of results with past research at alternative and similar scales can provide a relative measure of model consistency and logical inference. Unfortunately, there are few studies of the movements, habitat selection patterns, and disturbance responses of central Arctic wildlife. Our results do, however, meet some general expectations: we observed decreased use of habitats within a widely reported threshold distance of 500 m to 5 km of a disturbance, and avoidance responses were greatest for major developments associated with the highest level of human activities (Czech 1991, Nellemann and Cameron 1998, Vistnes and Nellemann 2001, Mahoney and Schaefer 2002, Frid 2003).

Information on the broad-scale habitat use patterns and foraging habits of Bathurst caribou is sparse. Griffith et al. (1999) conducted field investigations across the calving grounds and found that female caribou used lichen heath and moist shrub vegetation associations. In our study, the most parsimonious model for the spring migration and calving season included large, relatively precise coefficients for the lichen veneer and low shrub habitat types.

Habitat selection by wolves during the denning season was most strongly related to patches and large-scale prevalence of eskers. Those glaciofluvial features consist of loose unfrozen gravels, a substrate suitable for excavating dens across a landscape dominated by permafrost and exposed bedrock. McLoughlin et al. (2004) used the same data with different techniques and scales of analyses, and also reported selection by wolves for eskers during the denning season. Other field investigations also have revealed that soil conditions are an important consideration for tundra wolves during den site selection (Heard and Williams 1992).

Relative to the patterns of habitat selection we modeled, McLoughlin et al. (2002*b*) used the same sample of collared bears and reported use of esker habitats as den sites. During autumn, when some proportion of activity should relate to dens, we also noted selection for areas dominated by esker complexes. Using these data, but different scales and methods of analysis, McLoughlin et al. (2002*a*) identified selection for esker, lichen veneer, and several habitat classes that fell within our more broadly defined sedge and riparian shrub habitat types. In general, our results agreed. Fecal samples and observations of feeding grizzly bears within our study area indicated that caribou was the dominant diet item during all seasons except early summer (Gau et al. 2002). Percent occurrence and volume of caribou recorded in feces was greatest during autumn. Our most parsimonious selection model for autumn contained a coefficient indicating strong selection by bears for areas we predicted as having a high likelihood of caribou occurrence. However, we also reported a relatively small coefficient suggesting avoidance of caribou-occupied areas during spring.

Diet analyses revealed that 62% of wolverine stomachs collected across our study area contained caribou and 11% of stomachs contained muskox (*Ovibos moschatus*; Mulders 2000). Remains of large mammals also were prevalent in the stomachs of wolverines trapped across Alaska and the Yukon, but not to the extent noted for central Arctic animals (Rausch and Pearson 1972, Magoun 1987). Accordingly, we modeled behavior that suggested wolverines interacted with wolves, caribou and bears. Those interactions were strongest during the period caribou were available across the range of collared wolverines. Ours is the first study of habitat selection by tundra-dwelling wolverines, and thus there is little information to further corroborate model results at the scales of analysis we pursued.

The logic of the risk assessments and our inferences to habitat quality is dependent on a link between the coefficients generated with our selection models and the value of habitats to the 4 species. We assumed that the disproportionate use of resources correlated with animal fitness. Considering that the results of resource selection studies often are congruent with more detailed and mechanistic site investigations, that assumption appears valid for some cases (Johnson et al. 2002*b*). However, as demonstrated by species such as the grizzly bear, we may observe strong selection for a food resource associated with human habitation that ultimately results in decreased survival (Delibes et al. 2001, Mattson and Merrill 2002). Furthermore, apparent resource selection may be confounded by animal density or territoriality (VanHorne 1983, Hobbs and Hanley 1990, Garshelis 2000). Selected habitats may not contain the most abundant or nutritious resources nor confer the greatest population benefits.

Scale of observation and definition of resource availability also are important considerations when building RSF models and interpreting results. We parameterized vegetation at 2 spatial scales, the patch and region, and used observed animal movements to define availability. Although this is a progressive approach for resource selection studies (Cooper and Millspaugh 1999, Rushton et al. 2004) variation in relocation schedules and consequently a redefinition of available resources will have implications for model selection and interpretation (Apps et al. 2001, Boyce et al. 2003). As an example, a more frequent relocation interval would lead to a reduction in availability radii and a reduced zone of influence for human disturbances. Given the range of movements observed for collared animals (Figure 2) we are confident that the scale of observation and resulting resource selection models represented broad regional responses, the focus of this work. Resource selection studies are not without limitations, but the technique can provide useful guidance to conservation and management where model coefficients and resulting maps are carefully interpreted and inferences are constrained to the sample data (Hobbs and Hanley 1990, Fielding and Bell 1997, Garshelis 2000, Johnson et al. 2004*c*).

A decrease in "good" habitat is not easily translated into absolute consequences such as changes in fecundity, recruitment, adult survival, and carrying capacity. Although long-term changes in a wildlife population's distribution can have consequences for ecosystem processes and human use of the land, resource planning and land-use decisions are best served by information that relates a potential or current development to direct changes in animal abundance (Bergerud et al. 1984, Gill et al. 2001). Such causal relationships can be difficult to establish given that most conservation efforts are focused on mobile long-lived species that often are impacted indirectly by a development only across a portion of their annual range. The absence of experimental tools and requisite data for demographically-based landscape-scale analyses have led to correlative studies relating changes in behavior to disturbance (Hargrove and Pickering 1992). Measured responses include abandonment of habitats or ranges, avoidance of particular areas, barrier effects, short-term physiological or behavioral reactions, and altered movements (Smith and Cameron 1985, Harrington and Veitch 1991, Mahoney and Schaefer 2002, Frid 2003, Nellemann et al. 2003).

Models of habitat suitability, capability, and selection are commonly applied to studies of disturbance, but often yield measures of net habitat loss or decreases in a limiting nutritional factor such as digestible energy (Dixon 1997, Suring et al. 1998). Such estimates should be considered naïve. Simple removal of resources is only meaningful when animals are strongly dependent on discrete irreplaceable features of the landscape and their life-history provides little opportunity for adaptation. Natural or anthropogenic disturbances may lead to a reduction in the availability of a resource, but the species of concern may have considerable plasticity in foraging habits that allow for adjustments to an altered environment (Mattson et al. 1991, Kasbohm et al. 1998). Ultimately, we should strive to identify the mechanistic relationships between habitats and population productivity (Boyce and McDonald 1999). An understanding of such linkages may allow us to detect thresholds of disturbance after which we can expect an unacceptable risk to population viability, decrease in distribution, or decline in population productivity. Population viability analyses and energetics modeling are approaches applicable to such questions (Gurney et al. 1996, Reed et al. 2002, Parker 2003).

CONSERVATION AND MANAGEMENT IMPLICATIONS

Currently, land-use managers are attempting to assess the effects of unprecedented levels of industrial development across the Canadian Arctic. In the future, we will likely see new diamond and gold mines and possibly an all-weather road connecting Yellowknife to a deep-water port on the Arctic coast (Government of Northwest Territories 1999). Major projects such as these require regulatory approval from federal and territorial governments. As in other countries, approval is contingent on the completion of an environmental assessment which must include cumulative effects (Walker et al. 1987, Dixon and Montz 1995, Canadian Environmental Assessment Agency 2003). Identification of cumulative effects ensures that incremental impacts resulting from the combined influences of past, present, and future development activities are quantified and evaluated (McCold and Saulsbury 1996). Although cumulative effects analysis is a relatively intuitive concept, its structure, mechanisms, and role within the environmental assessment process have received considerable criticisms (Parry 1990, Kennett 1999, Davey et al. 2000).

Cumulative effects often are inadequately represented during project evaluations (Burris and Canter 1997). They are not immediately associated with the time and place of a proposed action and, therefore, it may be difficult to define the extent of impacts (McCold and Saulsbury 1996). Also, lack of consistent and general methods has limited the ability of proponents and regulators to effectively quantify effects and their significance (Dixon and Montz 1995). We view predictive resource selection modeling as a general approach with broad applicability to cumulative effects analyses and more challenging regional environmental assessments. The approach is based on accepted statistical theory, and methods, data, and results are easily documented and relatively transparent. Furthermore, geographic and temporal range of animal data can be evaluated for bias, precision of coefficient estimates can be determined, and numerous methods are available to assess model fit and predictive capacity (Fielding and Bell 1997, Pearce and Ferrier 2000, Manly et al. 2002). Although our application is specific to wildlife, predictive models and risk assessments are valid for any terrestrial, aquatic, stationary or mobile species whose distribution can be related to environmental covariates (Austin and Meyers 1996, Cowley et al. 2000).

Results of our research can contribute to the development of a regional environmental assessment for sensitive wildlife that will assist with the preparation and review of project-specific cumulative effects analyses. Small-scale maps generated from resource-selection models are an excellent tool for visualizing animal–habitat relationships and sensitive areas (Fig. 4; Abbitt et al. 2000, Johnson et al. 2004*c*). When analyzed with a GIS, maps provide a consistent measure by which to assess the effects of proposals from different resource sectors over large geographic areas. Proponents may use selection coefficients to situate or time ephemeral and permanent mining activities to reduce the level of disturbance across important seasonal habitats. Regulators may restrict development or demand remediation based on the total area of impact and associated high-quality habitats. Recognizing the uncertainty in predicting the pace of development and the impacts to the environment, RSF models and maps could serve as the foundation for scenarios representing a range of development intensities or variation in disturbance effects (Peterson et al. 2003).

When applying these results, it is important to consider the uncertainty inherent within our models and the limitations of the data upon which they were constructed. As with all spatial modeling exercises of this scope, follow-up monitoring and analysis should be an essential part of the process (Conroy et al. 1995, Mladenoff et al. 1999, Carroll et al. 2001). We recommend further studies to validate and refine the modeled avoidance responses. Monitoring should occur at a number of scales of observation, from the behavior of individual animals in the vicinity of a disturbance (Smith and Cameron 1985, McLellan and Shackleton 1989, Bradshaw et al. 1997) to multi-year changes in the distribution and size of populations (Mahoney and Schaefer 2002, Nellemann et al. 2003). Currently, resource inventory and disturbance data for the Northwest Territories and Nunavut are limited and not readily available. Vegetation maps should be assessed, and, where necessary, improved, and standardized spatial databases of development activities should be constructed and regularly updated; data gathering, review, synthesis, and availability are key outcomes of regional environmental assessments (Davey et al. 2000). A representative regional environmental assessment would incorporate the needs of all potentially sensitive biota. It may be necessary to construct additional models for species that occupy ecological niches that differ from caribou, wolf, grizzly bear, and wolverine.

Of greatest value to understanding ecological relationships and conserving sensitive wildlife is the further development of methods that relate habitat use to population demographics (Franklin et al. 2000). A mechanistic understanding of that relationship will aid in the definition of critical thresholds of disturbance, permit better evaluation of the significance of effects, and increase the confidence with which regulatory agencies use models to make difficult decisions with considerable economic consequences. In the absence of such understanding, development decisions with inherent ecological risk should be conservative, adaptive, and guided by the best available information integrated to represent a dynamic system with feedbacks, interactions, and scalar effects (Ludwig et al. 1993, Lister 1998).

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