EFFECTS OF PETROLEUM OPERATIONS IN ALASKAN WETLANDS: A CRITIQUE

by
Roger A. Post

Technical Report No. 90-3

Alaska Department of Fish & Game
Division of Habitat

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EXECUTIVE SUMMARY

INTRODUCTION

Management, restoration, and preservation of North American wetlands are currently being debated in the United States with growing support for a national goal of "no net loss" of the country's remaining wetlands. The petroleum industry's view of this issue as it affects arctic-tundra wetlands was expressed in early 1989 when Dr. R.G.B. Senner completed a report entitled *Effects of Petroleum Operations in Alaskan Wetlands* for ARCO Alaska, Inc. and BP Exploration (Alaska) Inc. The Alaska Department of Fish and Game has found Dr. Senner's report does not accurately portray the ecological and socioeconomic values of arctic-tundra wetlands. Our review of scientific literature related to wetland functions and the ecology of arctic species supports the following findings.

- Tundra wetlands share many of the attributes of temperate wetlands, and the differences between individual types of temperate wetlands are as great as the differences between temperate and arctic wetlands.
- The majority of species of arctic wildlife are ultimately controlled by the availability of their habitats in the same way that wildlife species are controlled in other regions of the globe.
- Managing wetlands by monitoring fish and wildlife populations is neither feasible nor wise in the face of developmental impacts.
- Habitat protection is a cost-effective approach for maintaining fish and wildlife populations.

ARCTIC-WETLAND FUNCTIONS: COMPARISON WITH OTHER WETLANDS

Although quantitative differences in individual functions occur between wetlands regardless of location, arctic wetlands do not qualitatively differ from wetlands in other regions.

Arctic wetlands share most of the hydrologic functions characteristic of temperate-zone wetlands.

- Arctic wetlands generally are not sites of discharge or recharge for subpermafrost aquifers, but suprapermafrost groundwater can influence wetland communities below arctic slopes in ways comparable to aquifer discharge in temperate regions.
- The complex of ponds, lakes, tundra, and beaded drainages of the Coastal Plain regulates runoff through storage in the active layer, depression storage, detention, and velocity reduction and by slow release of water to streams over extended periods, similar to temperate wetlands during summer.

- Tundra vegetation insulates thaw-unstable, ice-rich soils, which prevents thermal erosion; the tundra mat insulates and stabilizes the bottoms of thaw lakes; and emergent aquatic vegetation may reduce wave erosion in large arctic lakes.

Arctic-tundra wetlands are reasonably productive and can transform or retain sediment, nutrients, and toxicants similar to many temperate wetlands.

- Arctic-tundra wetlands inhibit generation of inorganic particulates by maintaining the thermal equilibrium of ice-rich, thaw-unstable soils in the watersheds of tundra systems.

- At breakup, streams flood adjacent tundra creating extensive wetland complexes that provide sites for suspended solids to settle, and sediment is trapped by riparian wetlands along large arctic rivers with mountain headwaters.

- Microbes and plants contribute to nutrient and contaminant retention or transformation in tundra wetlands since arctic-tundra species are adapted to low temperatures, are biologically active even under harsh conditions, and respond to nutrient input.

- Tundra ponds show chemical responses to nutrient input, reach temperatures as high as 16°C, have a high ratio of sediment surface to water volume, contain fine inorganic and organic sediment, and experience wind-driven circulation that oxygenates sediment.

- Nutrient concentrations may vary by an order of magnitude between adjacent microhabitats, a characteristic ensuring that waterborne nutrients and contaminants contact a variety of potential reaction sites during periods of high water.

Net primary production, nutrient export, and food-chain support are important functions of arctic wetlands and are qualitatively similar to those of temperate regions.

- Tundra production is remarkably high, approximately one-half that of temperate grasslands, and supplies the energy (plant biomass) on which animals exist.

- Nutrient export is an important function of arctic wetlands.

- Arctic-tundra wetlands support food chains, both through the herbivore-based trophic system from living plant tissues to rodents and ungulates and their predators and through the detritus-based trophic system from dead plant tissue to invertebrates to shorebirds and their predators.

From the standpoint of fish and wildlife resources, the habitat function of wetlands is their preeminent value.

- In Alaska, subsistence uses of wetlands by Alaska Natives provide an additional reason to value wetland habitats.

- Species-habitat relationships for arctic wetlands are discussed elsewhere in this critique.

Few places on the globe possess the untrammeled expanses of arctic landscapes. These landscapes and the wetlands they contain provide recreation and heritage values.

- Recreational values include the opportunity to experience solitude, wilderness, and adventure and to view wildlife.
- River float trips, backpacking (and similar uses), sport hunting, and unreported (estimated) private activity in the Arctic National Wildlife Refuge accounted for an estimated 1,289 person-use days in wetlands of the Arctic Coastal Plain during 1989.
- The recreational value of arctic wetlands is also represented by their production of wildlife that supports recreational activity elsewhere.

THE "VACANT-HOTEL HYPOTHESIS": A MYTH

Senner postulates that the availability of arctic-wetland habitats does not control animal abundance and believes arctic habitats are not fully stocked with fish and wildlife. We refer to the concept, which we reject, as the "Vacant-Hotel Hypothesis." Since the Vacant-Hotel Hypothesis holds that animal numbers do not decrease as arctic habitat is lost, it requires that factors controlling fish and wildlife populations operate independently of animal density and provides the basis for testing the hypothesis.

Population ecology provides general evidence that most or all factors controlling animal populations act in ways influenced by animal densities.

- Many population ecologists do not accept the existence of density-independent factors.
- The superabundant resources and lack of density-dependent predation rates assumed by the Vacant-Hotel Hypothesis are unlikely for the majority of predator and prey species inhabiting arctic wetlands.
- The effects of increased density brought about by habitat loss may differ by species and the dynamics of affected populations and could include reduced birth rates, increased mortality, or emigration to suboptimal habitat.
- Even if weather were accepted to act in a density-independent fashion on at least some arctic species, the Vacant-Hotel Hypothesis would remain unconfirmed if other factors influenced populations in a density-dependent manner.

The majority of the evidence indicates that migratory birds in the Arctic respond to their environment in the same way that birds do elsewhere.

- Except for several species having long incubation and fledging periods (e.g., tundra swans and loons), variation in the length of the breeding season does not control reproductive success for most waterbirds on the North Slope.
- For waterbirds nesting only in the Arctic, tundra wetlands are crucial regardless of waterbird densities elsewhere.
- Low nest density over the huge area of the Coastal Plain represents large waterfowl production.
- The Arctic's seasonally-rich wetlands provide stable water levels for waterfowl displaced from the Prairie Region by drought.

Despite the importance of habitat loss and other factors operating on waterbird populations outside the Arctic, there is no evidence that these factors alone control their populations.

- Territorial behavior in some North Slope shorebird species controls the total number of nests by excluding surplus individuals from breeding, growth rates of young shorebirds vary related to weather and food availabilty, and predators destroy eggs and young of shorebirds.
- Breeding conditions are important determinants of waterfowl populations for arctic-nesting species.
- The distribution of shorebird migration routes, migration timing, and wintering areas reduces the probability that catastrophe will simultaneously affect all arctic-nesting species during migration and wintering.
- Habitat-conservation efforts in countries supporting overwintering shorebirds should not be discounted or rendered ineffective by allowing unnecessary losses of breeding habitat in the Arctic.
- Sea ducks, abundant arctic breeders, winter in marine waters; the availability of staging and wintering habitat is not an issue for these species.

Tundra is a mosaic of microhabitats with greatly differing prey densities and structural characteristics of significance to waterbirds.

- Wetlands near the coast of the Beaufort Sea have relatively higher values to some waterfowl and shorebirds than do inland wetlands.
- Although availability of post-nesting and traditionally used habitats have not been conclusively shown to limit waterfowl populations, displacement of individuals to suboptimal habitats likely would adversely affect their energy balance and survival.
- Shorebird use of wetland habitats is affected by fidelity to birth sites and previous nest sites, which may offer advantages to returning birds and argues against the notion that displacement of shorebirds has no potential effect on shorebird numbers.

Food is a limiting aspect of waterbird habitat in the Arctic.

- Territoriality allocates limited food resources in waterfowl and loons.
- Territoriality and the evolution of both a conservative and an opportunistic breeding strategy among shorebirds can be interpreted as evidence of resource competition.
- It is difficult to reconcile the existence of negative energy budgets in nesting and post-nesting birds with the superabundance of resources required by the Vacant-Hotel Hypothesis.

Studies of avian predators provide evidence that the availability of resources found within their habitats and territoriality strongly influence their breeding density, underscoring the importance of habitat availability.

- The role of food in limiting the abundance of avian predators in arctic-tundra wetlands is clear; most species show strong relationships between breeding density, reproductive output, and prey availability.

- The availability of nest sites affects breeding densities of predaceous birds such as the peregrine falcon and the gyrfalcon.

- Most avian predators breeding in arctic wetlands are territorial, occupy all suitable habitat, and exclude surplus individuals from breeding.

Evidence from arctic mammals indicates a complex system of biotic interactions that does not support the assumptions of density-independent controls over populations and superabundant resources inherent in the Vacant-Hotel Hypothesis.

- Lemmings are important herbivores that exhibit density-dependent mortality and reproduction and affect species such as mammalian predators that may not otherwise show obvious limitation by density-dependent factors.

- Moose occupy riparian wetlands on the North Slope, are almost entirely dependent upon these high-value habitats, and exhibit density-dependent changes in birth rates and death rates in response to their nutritional status.

- Population control in caribou is complex and includes density-dependent mechanisms such as predation, nutrition, and social behavior.

- Muskox populations are controlled in a density-dependent manner by social behavior such as emigration and by the effects of nutrition on the age of first reproduction and conception rate in female muskoxen.

- Polar bears produce significantly more cubs per den in land dens than those on the sea ice, which is important because female bears surviving to breeding age and entering the breeding population each year approximately equal the annual loss of breeding females in the Beaufort Sea population.

- Unexploited wolf populations appear to be regulated by the interaction of social factors and nutrition, density-dependent responses of wolves to their environment, in particular to food resources.

- In unexploited populations adult males may regulate brown bear abundance in a density-dependent manner by killing other bears; however, fragmentation of landscapes used by brown bears may lead to their extirpation because they cannot adapt to large-scale habitat modification and human habitation and require extensive freedom of movement to reach necessary resources.

HABITAT-BASED RESOURCE MANAGEMENT: A RATIONAL ALTERNATIVE TO MEASURING POPULATION-LEVEL IMPACTS

Senner believes that regulatory agencies should not require mitigation beyond careful design and siting of oilfield facilities until the cumulative impacts of wetlands fills demonstrably reduce fish and wildlife populations on Alaska's North Slope. We favor offsetting developmental impacts through habitat management. The relative merits of these management systems should be considered in the debate over wetlands policies as applied to arctic-tundra wetlands.

Managing the impacts of development on arctic-tundra wetlands by monitoring fish and wildlife populations is not practical for reasons of cost, lack of appropriate indicator species, difficulty of estimating populations, and difficulty of statistically separating multivariate causes of population fluctuation.

- Incremental wetland loss acts chronically and diffusely to reduce the total area of habitat available, not only to fish and game species used for human consumption but to all components of the biological community, reducing potential maximum populations.
- Population-based management of wetland fills would shift the burden of proof for habitat protection from the private to the public sector and would be beyond government's current or conceivable fiscal capacility.
- Natural population fluctuations combined with errors of population estimation reduce the statistical probability of detecting the effects of habitat loss on populations until the losses are dramatic, which would permanently cap populations at the levels where the effects of habitat loss are demonstrated.
- Allowing large declines in arctic species as tests of impacts of development would unjustifiably risk animal populations.
- Economics would limit monitoring to at most several "indicator species" representing the herbivore-based and the detritus-based trophic systems; however, potential indicators do not meet suitable selection criteria.
- Populations of animals existing at the carrying capacities of their environments must decline as wetland habitats are lost because their densitites cannot be increased in remaining habitats.

Wetland management based on habitat protection is a rational, cost-effective alternative to population-based management of developmental impacts.

- Habitat-based management is predicated on identification and protection of high-value habitats so that necessary development can be directed into those areas having less value for fish and wildlife.
- Gravel fill in arctic wetlands diminishes the areas of natural ecosystems, buries nutrient reservoirs such as organic matter, and may otherwise alter ecosystem character.
- Resource managers can maintain arctic ecosystems by identifying significant functions impaired by necessary development, by determining appropriate mitigation to maintain these functions and values, and by ensuring that mitigation procedures are properly and successfully executed by developers.
- Those who profit from siting development in wetlands would largely bear the costs of habitat management by incorporating required mitigation features in project design and construction.

- Partial or complete fill removal from abandoned sites increases the probability that adequate soil moisture will be present to promote colonization by native species, restoring at least some of the ecological values lost when the fill was originally placed.

- Positive habitat value can be obtained even from out-of-kind compensation or partial restoration as compared to the alternative of sterile gravel pads.

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INTRODUCTION

Management, restoration, and preservation of North American wetlands are currently being debated in the United States with growing support for a national goal of "no net loss" of the country's remaining wetlands. Alaska's wetlands, particularly those of the Arctic Coastal Plain, site of present and anticipated future oil and gas development, figure prominently in this policy debate. The petroleum industry brought discussion of arctic-tundra wetlands to the fore in early 1989 when Dr. R.G.B. Senner, an industry consultant, completed a report entitled *Effects of Petroleum Operations in Alaskan Wetlands* (Senner 1989) for ARCO Alaska, Inc. and BP Exploration (Alaska) Inc. The latter company subsequently prepared a profusely illustrated brochure, "Alaska Wetlands & Energy Development," summarizing the report for public relations purposes. Widespread distribution of both documents has occurred, including circulation to members of Congress and to participants of the Coastal Zone 89 Symposium held in Charleston, South Carolina. Because the fate of Alaska's wetland resources may be influenced by these documents, governmental agencies having advisory or regulatory responsibilities for Alaskan wetlands should assess their accuracy and provide independent assessments to policy makers. The Alaska Department of Fish and Game has assessed Dr. Senner's report and has found it does not accurately portray the ecological and socioeconomic values of arctic-tundra wetlands.

Senner states that arctic-tundra wetlands have fewer values than temperate wetlands, as well as diminished value as wildlife habitat; estimates cumulative wetland losses in Alaska from petroleum development and other causes; discusses the petroleum industry's mitigation practices on Alaska's North Slope; and discusses the industry position on current and proposed public policies for regulation of wetland fills. His overall thrust is that current industry practice adequately mitigates wetland losses; thus, he concludes no further regulation of wetland fills is necessary on Alaska's North Slope. Senner supports his position by rejecting the concept that habitat limits the abundance of arctic-wetland species and extends his argument to suggest biological resources be managed by monitoring wildlife populations rather than by protecting wetland habitats. In his view, habitat loss should continue until governmental agencies demonstrate that such loss has caused wildlife populations to decline.

Conversely, we show that tundra wetlands share many of the attributes of temperate wetlands and that the differences between individual types of temperate wetlands are as great as the differences between temperate and arctic wetlands. Contrary to Senner's assertion that North Slope habitat does not limit abundances of arctic-wetland species, we find examples of such limitation in the scientific literature, the majority of which either does not support or is clearly inconsistent with Senner's view of species-habitat relationships. Further, we find that population-based wetland management is neither feasible nor wise in the face of developmental impacts and conclude that habitat protection is a cost-effective approach for maintaining fish and wildlife populations.

While differences of opinion on scientific issues are to be expected based on differing interpretations of available evidence, we believe *Effects of Petroleum Operations in Alaskan Wetlands* is seriously flawed in ways other than mere misinterpretation of evidence. Specifically, the report fails to review important references concerning the ecology of tundra wetlands, places excessive reliance on a single paper (Robertson 1987) not well founded in the technical literature of arctic hydrology, cites references in support of conclusions when the references do not address the conclusions, uses strained or nonstandard definitions of ecological terms and concepts, uses unsupported assertions as the basis for technical arguments, and fails to differentiate between the wide variety of arctic-tundra wetlands. Because serious flaws are present in Senner's report, the scope for potential rebuttal is broad. Necessarily, we have had to concentrate our review on a few major subjects crucial for understanding the functions, values, and mangement of arctic wetlands and the fish and wildlife resources they support. Thus, the following critique of the ideas and conclusions presented by Senner addresses three major topics: functions of arctic wetlands, habitat as a limiting factor for arctic-wetland species, and habitat-based versus population-based wetland management.

ARCTIC-WETLAND FUNCTIONS: COMPARISON WITH OTHER WETLANDS

Senner (1989) and development interests in Alaska have stated that the wetlands of Alaska's North Slope do not perform most of the functions performed by wetlands elsewhere. The validity of this assertion is important because national initiatives for wetland preservation and restoration have incorporated the concepts of wetland function and acreage for measuring wetland losses and applying appropriate mitigation (The Conservation Foundation 1988:3). Senner cites Robertson (1987) in comparing arctic wetlands to deserts and states that arctic wetlands generally lack "values relating to groundwater recharge and discharge, flood storage and desynchronization, erosion protection, sediment trapping, nutrient retention and removal, aquatic habitats supporting significant fisheries, and active outdoor recreational use" and thus are similar to deserts. In a related vein, he also implies that permafrost makes arctic wetlands qualitatively different from temperate or tropical wetlands and states that "without permafrost to trap rain and meltwater, most of the Arctic Coastal Plain would probably not be a wetland." Finally, and most importantly, Senner believes that the availability of wetland habitats in the Arctic does not influence the abundance or productivity of the wildlife species found in those habitats. Because these views single out arctic-tundra wetlands as uniquely deficient in the functions and values usually associated with wetland ecosystems and are at variance with accepted ecological principles, we searched relevant scientific literature for evidence substantiating Senner's position but found little. The majority of the literature that we examined, subsequently presented in detail in this critique, leads us to conclude that arctic wetlands as a whole perform the same wetland functions as temperate wetlands.

As a consequence of our literature review, we can assess several of Senner's general statements at the outset. First, our preceding conclusion concerning the functions of arctic wetlands removes the basis for Senner's "desert paradox," earlier stated by Robertson (1987). The Robertson paper, presented at a coastal zone conference, provided a description of Alaska's arctic coast based on a review of the literature; made a series of largely unsubstantiated assertions that arctic wetlands do not perform most of the functions associated with temperate wetlands and thus are comparable to deserts; and stated the petroleum-industry perspective on developmental impacts affecting the coastal environment. Since Robertson's assertions about wetland functions are unfounded, as we will show in this section of our critique, we also reject Senner's arguments for arctic wetlands being comparable to deserts on any basis other than relatively low annual precipitation (Pruitt 1978:12). Low precipitation in arctic wetlands interacts with low rates of evapotranspiration and permafrost to retain water on or near the surface of the ground (Hobbie 1984) in bogs or fens (Mitsch and Gosselink 1986:287-315) where it is available to the biota. Arctic wetlands have a continuous supply of moisture that allows vigorous primary and secondary productivity. As a result, plant cover in tundra wetlands of the Low Arctic ranges from 80 to 100% (Bliss 1981). Plant and invertebrate growth is driven by 24-hour sunlight, attracts birds, and makes breeding and production in the

Arctic worth the cost of migration for many species. In contrast, for most of the year moisture is not available to desert biota because evapotranspiration greatly exceeds precipitation (Crawford and Gosz 1986). When moisture is available, it flows from the soil, through plants, and into the atmosphere, with a linked flow of nutrients and energy driving a pulse of primary and secondary production in the desert ecosystem (Crawford and Gosz 1986). Thus, arctic-tundra wetlands greatly differ from deserts despite similarities in precipitation.

Second, wetland ecosystems are defined by soil, hydrology, and vegetation (Cowardin 1979, Zoltai 1988), not by the mechanisms that form and maintain them; therefore, Senner's claim that permafrost wetlands are fundamentally different from other wetlands is not supported. It is true that in the absence of permafrost many North Slope wetlands would not exist. It is also true that permafrost influences the development of particular wetland types through interaction with climate, relief, animals, vegetation, and hydrology (Tarnocai and Zoltai 1988). Nevertheless, wetlands are created and maintained by a variety of physical mechanisms (Maltby 1986:29-33). In each case, altering or removing the parameters enabling or responsible for a wetland's existence likely would also eliminate the wetland. For example, pocosin wetlands in North Carolina (Mitsch and Gosselink 1986:46-47) would not be wetlands if North Carolina were not so flat in the region where pocosins occur, and temperate wetlands created by aquifer discharge to basins or slopes (Larson et al. 1988) would soon disappear if discharge ceased. Thus, the role of permafrost in wetland maintenance is no different than "hardpan" or other less permeable layers beneath temperate wetlands.

Having briefly addressed several of Senner's general assertions, we discuss major functions of arctic-tundra wetlands in this portion of our critique. The discussion centers on the effectiveness (*sensu* Adamus 1983) of these wetlands in performing a given function rather than the opportunity (*sensu* Adamus 1983) for a given wetland or group of wetlands to provide the function to the limit of its effectiveness. For example, knowledge that a certain class of wetlands effectively removes pollutants from water says nothing about the opportunity of a specific wetland to do so, since the opportunity is dependent upon the presence of a source of pollutants. Likewise, we do not address the social significance (*sensu* Adamus 1983) of individual wetlands, because a wetland's social value to some extent is dependent upon its location and relationship to human populations. In aggregate, however, wetlands are tremendously valuable to human society (Maltby 1986:12-27), as may be inferred from the following discussion of wetland functions.

Origin and Distribution of Arctic Wetlands

The Arctic has been defined as the region lying poleward of 66° 33'N (Young 1989), as the region lying north of the polar timberline (Pruitt 1978:2, Dahl 1986, Tarnocai and Zoltai 1988, Young 1989), or as "the treeless zone with a southern boundary approximately coincident with the mean summer position of the arctic front" (Chapin and Shaver 1985*a*). The latter two definitions to some extent overlap with "tundra," although tundra also includes naturally treeless alpine areas as well as ice-free areas of the Antarctic (Wielgolaski 1986). Bliss (1981) further subdivided the north-polar region into the Low Arctic and High Arctic and into vegetation types described as tundra, polar semi-desert, and polar desert. The High Arctic encompasses the Canadian Arctic Archipelago (excepting the most southerly portion of Baffin Island) as well as a portion of the Canadian mainland northwest of Hudson Bay and the most northerly portion of Alaska (e.g., Pt. Barrow and vicinity), whereas the Low Arctic lies between the High Arctic and the taiga, encompassing nearly all of Alaska's North Slope and a broad band of the northern Canadian mainland (Bliss 1981). In general, polar semi-desert and polar desert characterize the vegetation of the High Arctic, although wet sedge-moss tundra also occurs in patches (Chapin and Shaver 1985*a*). Some authors have identified a Mid-Arctic Region approximately coincident with the distribution of polar semi-desert vegetation (Tarnocai and Zoltai 1988), but we use the terminology of Bliss (1981) in this critique. Tundra vegetation, often underlain by peat and providing 80 to 100% ground cover, characterizes the Low Arctic (Bliss 1981). Many arctic-tundra sites are wetlands.

Arctic-tundra wetlands form because permafrost is a relatively impermeable barrier to water movement into the ground, confining flow to a shallow "active layer" or zone of seasonal thaw (Kalff 1968); because precipitation, although low, is sufficient to maintain soil moistures ranging from standing water to moist (Hobbie 1984, Chapin and Shaver 1985*a*); and because low temperatures reduce rates of evapotranspiration (Ryden 1981, Hobbie 1984). This contrasts with conditions present in much of the High Arctic where precipitation is lower than that of the Low Arctic (Carter et al. 1987) and where thaw of the active layer is deeper due to lack of vegetative cover (Chapin and Shaver 1985*a*). Consequently, soil moisture in the High Arctic ranges from moist to very dry during summer, which favors polar semi-desert or polar desert vegetation rather than wet tundra (Chapin and Shaver 1985*a*), except in localized sites of poor drainage (Bliss 1981). Alaska's Arctic Coastal Plain, by virtue of its primarily Low Arctic location and low relief, thus is a broad expanse of tundra wetlands.

Hydrologic Functions

The hydrology of wetlands is in one sense their most important attribute (Mitsch and Gosselink 1986:55) since wetland hydrology is "the driving force behind wetland formation" (Tiner 1989). Water not only forms wetlands but interacts with them in various ways. These interactions produce what may be termed the hydrologic functions of wetlands: aquifer discharge and recharge, flow regulation, and erosion control. Hydrologic functions are part of overall ecosystem processes and, as such, are intimately linked to such things as fish and wildlife habitat (Sather and Smith 1984) and water quality (Kadlec 1987). For example, Tarnocai and Zoltai (1988) state that arctic wetlands "are vital to water storage in an environment that is generally water-poor after the first few weeks of the spring melt." Knowledge of these functions in arctic-tundra wetlands is necessary if their habitat and other values are to be maintained.

Aquifer Discharge and Recharge: Senner (1989) discusses aquifer discharge and recharge as hydrologic functions of temperate wetlands (some, but not all [Adamus and Stockwell 1983]) that are not performed by arctic (i.e., continuous-permafrost) wetlands. We agree that arctic wetlands generally are not hydrologically connected to subpermafrost aquifers (for example, see Ford and Bedford 1987) and thus are not sites of discharge or recharge for these aquifers. This should not be construed to mean that groundwater and subsurface flow are absent. Taliks (unfrozen zones) may be present under waterbodies that do not freeze to the bottom during winter (Carter et al. 1987). Hobbie (1980*b*) cites a thaw depth of 60 m beneath Imikpuk Lake, and "significant unfrozen zones underlie the Colville River and other large rivers" (Dingman et al. 1980). Williams and van Everdingen (1973) also describe "unfrozen alluvial aquifers beneath the Colville River and nearby terraces at Umiat" and large springs and icings in the Brooks Range that "issue from fault zones in which limestone of the Lisburne group is brought into contact with other rocks and from solution-enlarged fractures in the limestone." Similar phenomena occur on the Seward Peninsula of Alaska (Williams and van Everdingen 1973). Nevertheless, alluvial aquifers are associated with large rivers, and springs largely occur outside the Arctic Coastal Plain. More generally, Woo (1986) states, "In continuous permafrost areas, suprapermafrost groundwater provides the most common source for subsurface flow." We examine the role of suprapermafrost groundwater in arctic-tundra wetlands in the following paragraphs.

Groundwater flow is a function of the cross-sectional area of the zone of flow, hydraulic conductivity of the medium, and hydraulic gradient (Darcy's law) (Mitsch and Gosselink 1986:71). These factors tend to be low in permafrost wetlands (Roulet and Woo 1986*a*). Suprapermafrost groundwater occupies the active layer (Woo 1986), a zone typically less than 1 m thick in arctic lowlands (Carter et al. 1987). The small thickness of the active layer and the short period of time when it is thawed place major quantitative constraints on lateral groundwater flow. Likewise, significant hydraulic gradients are unlikely in the flat expanse of Alaska's Arctic Coastal Plain, limiting conceivable groundwater flows. Nevertheless, subsurface flows have been measured at arctic sites where slopes are present. At one site in the High Arctic, subsurface flow was one order of magnitude smaller than surface flow in spring (snowmelt period), but in summer the magnitudes of surface and subsurface runoff were similar (Woo and Steer 1986). At a low-arctic site, subsurface flow was about 10% of total discharge from the study slope, based on data for the entire field season (Roulet and Woo 1988). Similar measurements within an adjacent low-arctic wetland where the hydraulic gradient did not exceed 2% showed that subsurface flow was about two orders of magnitude less than surface flow, based on data for the entire field season (Roulet and Woo 1988). These studies indicate that suprapermafrost groundwater plays a quantitatively minor role in runoff from arctic wetlands.

Qualitatively, however, suprapermafrost groundwater may be an important determinant of wetland communities. At Woo and Steer's (1986) sparsely vegetated high-arctic site, which presumably was largely polar desert based on a general map by Bliss (1981), vegetated areas appeared to form where water was most abundant, either from "late-lying snowbanks or by a resurgence of groundwater flow at the foot of slopes or at slope concavities." Woo (1986) cites literature indicating that localized wet locations below concave slope segments receive greater and longer-lasting supplies of meltwater (presumably some of which is subsurface flow) than other areas, permitting tundra vegetation to develop at many high-arctic sites that are otherwise barren. Similarly, Woo et al. (1981) studied the catchment of a high-arctic lake where both surface and subsurface flows from slopes delivered water to the lake. Surface flow tended to follow boggy strips; presumably these wetlands were also sites of subsurface flow as summer progressed and thaw depths increased. This example of one wetland (the boggy strips) delivering water to another (the lake) by flow of suprapermafrost groundwater contains parallels to aquifer recharge and discharge in nonpermafrost areas. The situation at low-arctic sites is less clear. Although Roulet and Woo (1986*a,b*) characterize subsurface discharge from a low-arctic fen as insignificant (from a hydrological perspective), they also state that the fen itself could not exist without inflow from a lake via a small pond lying upslope. Overbank flow from the pond into the fen occurred for approximately one month in early summer (Roulet and Woo 1986*a*). Roulet and Woo (1986*a*, 1986*b*, 1988) did not report whether or not subsurface flow from the pond entered the fen or what role this potential source might have had in maintaining the wetland community after surface flow ceased by replenishing soil moisture lost to evapotranspiration. Movement of suprapermafrost groundwater appears qualitatively important for allowing wetlands to develop in the High Arctic, but its role in wetland formation and maintenance in the Low Arctic may be small or limited to areas below slopes with significant hydraulic gradients. Similarities to the aquifer-discharge and -recharge functions in nonpermafrost wetlands can be found in at least some arctic wetlands.

In comparing the aquifer-discharge and -recharge functions of arctic and temperate wetlands, it is important to realize that many temperate wetlands (e.g., perched wetlands) perform neither function (Mitsch and Gosselink 1986:71). Recent studies have refuted the idea that all wetlands recharge groundwater. It now appears that in many temperate areas uplands are more important for recharge than are wetlands (Adamus and Stockwell 1983, Sather and Smith 1984). In the Temperate Zone, as elsewhere, wetlands form in depressions in level basins or form on slopes in the absence of groundwater discharge by retaining surface flow (Mitsch and Gosselink 1986:55-87, Larson et al. 1988). Temperate wetlands underlain by substrates of low permeability are similar to wetlands underlain by permafrost because neither type is hydrologically connected to aquifers lying beneath the layers of low permeability and thus do not recharge those aquifers. For wetlands hydrologically connected to aquifers, recharge and discharge cannot occur simultaneously at a given location and time, although variation by season and location within a wetland is possible (Mitsch and Gosselink 1986:67-72, Larson et al. 1988). Aquifer discharges in riverbeds, lakes, or other aquatic environments may not form vegetated wetlands, but even where temperate wetlands are formed by such discharges, wetland values such as maintenance of fish and wildlife habitats, public water supply, irrigation, livestock watering, and recreation derive from the presence of water rather than from any specific water source. For this reason, we view aquifer discharge as much a mechanism of wetland formation as a hydrologic function of wetlands.

The mutually exclusive nature of the discharge and recharge functions illustrates the invalidity of differentiating arctic and temperate wetlands by comparing the summed attributes of <u>all</u> temperate wetlands with those of arctic wetlands. Many of these attributes are mutually exclusive or inversely correlated (Adamus and Stockwell 1983); therefore, few wetlands perform all functions (Larson et al. 1988). We can say that arctic wetlands do not perform quantitatively large discharge or recharge functions and, in this respect, are similar to some temperate wetlands and dissimilar to others. Because some arctic wetlands perform small, shallow, but qualitatively important discharge or recharge functions via suprapermafrost groundwater, similarities to temperate wetlands possessing those functions are apparent.

<u>Flow Regulation</u>: Flood storage and flood-peak desynchronization are related wetland functions describing the capacity of wetlands to store water and release it over an extended period of time and thus to ameliorate flood events (Adamus and Stockwell 1983, Larson et al. 1988). These functions reduce peak flows at downstream locations in watersheds containing significant wetland area, producing moderate flows of longer duration than would otherwise occur. Senner, again drawing on Robertson (1987), contends that frozen-arctic wetlands do not regulate surface flow during spring runoff and even when thawed during summer, have "only minimal capacity for water uptake," "provide little or no storage for floodwaters," and have "minimal capacity for damping extremes in runoff flows." In contrast, he states that temperate wetlands have these properties, as well as those of coastal protection. More seriously, Senner quotes Ford

and Bedford (1987) who state, "Peak flows in permafrost-dominated catchments tend to be higher and base flows lower than in adjacent permafrost-free catchments, suggesting that overall, high-latitude wetlands do not play an important role in streamflow regulation." These authors thoroughly reviewed the hydrology of Alaskan wetlands, and their views deserve careful consideration. Although frozen ground prevents most absorption of runoff during spring "breakup" (Carter et al. 1987), other mechanisms of flow regulation exist in arctic wetlands. These mechanisms also influence streamflow at other times, such as by supplying water during periods of low precipitation; therefore, we describe this topic as "flow regulation" to encompass the range of conditions occurring throughout the year.

Specific studies of arctic hydrology document the role of arctic wetlands in the dramatic breakup process. This process occurs because snow accumulates throughout the arctic winter, a 9-month period, with relatively little loss to melting (Woo 1986) or sublimation (Woo et al. 1981). (Woo [1986] does report significant sublimation at several high-arctic sites in Canada.) When rising air temperature finally initiates melting of the snow mass, loss of snow cover is rapid because incoming short-wave radiation is near its maximum, and runoff is very high (Kane and Carlson 1973). Frozen ground in arctic wetlands at the time of maximum snowmelt limits their capacity to take up water; however, several mechanisms may operate to depress peak flows. Tundra soils generally comprise an organic mat of varying thickness overlaying mineral soil horizons (Everett et al. 1981). Surficial organics may enter winter relatively dry or become dehydrated during winter through upward transport of water vapor into the snowpack (Slaughter and Kane 1979, Kane et al. 1981). During snowmelt, these materials can take up meltwater (Carter et al. 1987). For example, dehydrated moss took up approximately one-half of the meltwater at a subarctic site underlain by permafrost (Kane et al. 1981). In a low-arctic fen, "The subsurface storage capacity available at the time of snowmelt is dependent on the previous fall's water content of the peat" (Roulet and Woo 1986*b*). Based on thermal profiles, Roulet and Woo (1986*a*) estimated that 4 $mm \cdot day^{-1}$ penetrated frozen peat for 2 days at a low-arctic site. Even at high-arctic sites where organic material may be absent or sporadic (Everett et al. 1981), ice-free void space is created in frozen soil over the winter from the temperature-induced upward flux of water vapor (Woo and Steer 1983), and initial meltwater can penetrate frozen soil through cracks and voids, especially if the soil has a low moisture content (Woo 1986). Although the hydraulic conductivity of frozen soil is low, a temperature-induced, downward pore-pressure gradient may develop as meltwater enters the soil, further facilitating uptake of moisture (Woo 1986). Eventual freezing of infiltrated meltwater and formation of basal ice at the snow-ground interface releases sufficient latent heat to raise soil temperature to 0°C by the time snow cover disappears, which accelerates subsequent thawing of the active layer and increases its potential capacity for water storage (Woo 1986). Although these mechanisms demonstrate that some meltwater is taken up by the soil of arctic wetlands during breakup, most snowmelt appears as runoff in the Arctic (Ryden 1981). Tundra streams receiving this runoff are classified as having a "wetland" streamflow regime characterized by "a pronounced spring freshet," "water retention in ponds and organic soils," and summer flow attenuation (Woo 1986). These characteristics point to more important regulatory mechanisms for snowmelt runoff than immediate uptake by the soil.

The complex of ponds, lakes, tundra, and beaded drainages of the Coastal Plain provides flow regulation through detention, retention (depression storage [Woo 1986]), and velocity reduction. Detention occurs when water enters a wetland faster than it is released, retention occurs "when water is held in a wetland and never returns to surface flow," and "velocity reduction occurs when dense wetland vegetation increases the frictional drag" on flowing water (Larson et al. 1988). The mechanisms are not strongly dependent upon thawed ground and thus can operate effectively at breakup. Each of these mechanisms reduces flood peaks and spreads flow over longer periods of time. For example, at a study site containing over 100 ponds near Barrow, 83% of the snowmelt appeared as runoff one year but only 51% appeared the following year (M.C. Miller et al. 1980). Most of this storage apparently was retention, because pond outflow ceased when water levels dropped. The retention capability of arctic wetlands was further demonstrated by Marsh and Woo (1979). They found less runoff and greater evaporation for a small, boggy basin than for basins with proportionately less wetland area at a high-arctic site. Finally, Woo (1986) provides evidence that arctic-wetland slopes have more hummocky surfaces than non-wetland slopes and thus have a higher probability of requiring large depression (retention) storage before runoff occurs.

Once tundra ponds and the troughs of frost polygons fill with meltwater and satisfy depression storage, water runs off to streams and lakes, and "coastal tundra is largely covered with water" (Dingman et al. 1980). At this time, detention storage and velocity reduction by microtopographic features and tundra vegetation presumably can moderate peak flows, based on physical principles; however, we are unaware of specific studies addressing these mechanisms of flow regulation on the Arctic Coastal Plain during breakup. At a Canadian low-arctic fen where input from overbank flow from a lake exceeded *in situ* snowmelt by a factor of 3, detention storage and resistance to flow appeared to moderate streamflow only slightly during breakup (Roulet and Woo 1986*a*). In this case, once the limited storage capacity of the fen was exceeded, it effectively conveyed basin runoff to the basin outlet (Roulet and Woo 1988). Nevertheless, it is important to note that evaporative losses from the fen were greater than precipitation inputs (during a year of low rainfall), and storage showed a net increase (Roulet and Woo 1986*a*). Hobbie (1984) expresses his opinion that studies of well-defined watersheds may not accurately reflect the situation where "surface flow" (as opposed to streamflow) may predominate during breakup. He believes most precipitation in these areas is retained and lost to evaporation during summer rather than appearing as runoff. Based on the preceding evidence, it appears some arctic-tundra wetlands retain a significant proportion of annual precipitation (M.C. Miller et al. 1980, Hobbie 1984, Roulet and Woo 1986*a*), but others may not have sufficient storage capacity to strongly moderate breakup flows (Roulet and Woo 1986*a*, 1988), especially where the flows derive from larger drainage basins. In this respect, arctic-tundra wetlands are similar to small peatland watersheds in temperate regions where 66% of annual runoff can appear at snowmelt (Bay 1969) and where high water tables in winter (Moore 1981, Ryden 1981) limit storage capacity in spring.

Following breakup, the previously discussed mechanisms of low-magnitude streamflow regulation by arctic wetlands become more pronounced. The active layer rapidly increases in depth in early summer (Dingman et al. 1980) allowing a commensurate increase in storage capacity (Woo and Steer 1986). Increased storage capacity allows the active layer to retain or transport incident precipitation until the suprapermafrost water table rises to the surface, at which time surface flow occurs on slopes (Woo et al. 1981, Roulet and Woo 1986*b*, Roulet and Woo 1988, Kane and Hinzman 1988). On the flat Coastal Plain near Barrow, Brown et al. (1968) found that the active layer retained nearly all incident precipitation during dry summers. Even during the third consecutive wet year at this site (close to maximum precipitation for the region) only 46% of summer-storm precipitation appeared as runoff. In the Foothills Region of the North Slope, Kane and Hinzman (1988) studied a small (2.2 km^2) permafrost watershed and found that the highly-organic upper 10 cm of the active layer varied in unfrozen soil moisture (e.g., from <5 to about 90% by volume at 5 cm) in response to snowmelt and precipitation. Stream-discharge peaks occurred less frequently and lasted longer than precipitation events. These investigators concluded that "summer runoff events are controlled by the antecedent moisture conditions of the organic layer . . . ." Likewise, Roulet and Woo (1986*b*) found that a low-arctic fen effectively regulated runoff through water absorption by peat when the water table was low and concluded that fens "can regulate runoff in a manner commonly depicted for the temperate latitude wetlands" during summer. Woo and Steer (1983) studied subsurface flow on a high-arctic slope. Although they found surface flow was 2.5 times greater than subsurface flow during the study period, the slower delivery time for subsurface flow fed by suprapermafrost groundwater could "maintain base flow in arctic streams for a large part of summer." Similarly, Woo et al. (1981) reported that only heavy rainstorms supplied "sufficient moisture to raise the water table above the ground surface" at a high-arctic site, thus demonstrating the flow-regulating characteristics of the active layer on permafrost slopes. These results indicate significant short-term storage, subsurface transport, or dissipation through evapotranspiration occurring in the active layer of tundra wetlands, acting to regulate summer streamflow.

Arctic-tundra wetlands further moderate summer streamflow by depression and detention storage, as well as resistance to flow. For example, rainfall runoff from a system of tundra ponds near Barrow rarely occurs and is dependent upon the ponds being refilled by heavy rainfall (M.C. Miller et al. 1980). These ponds are small, contained in ice-wedge polygons, and shallow. Pond extent varies from entire polygons at breakup to only the central depressions after a dry summer (M.C. Miller et al. 1980). Available depression storage is inversely related to pond extent at the time of rainfall, which is in turn dependent upon antecedent conditions. Flow regulation by tundra ponds thus is similar to flow regulation by the active layer. Precipitation is retained or moves as subsurface flow (if a hydraulic gradient is present) until the water table is raised above the surrounding ground surface and overbank surface flow or outflow to a defined channel occurs. Detention storage and resistance to surface flow would operate at such times. On slopes, exceptionally heavy precipitation or precipitation falling when antecedent moisture is high can also produce surface flow (Woo and Steer 1983, 1986). Surface flow in the High Arctic often occurs on vegetated wetland strips -- snowpatch fens (Tarnocai and Zoltai 1988) -- where thaw depths are less than in surrounding barren terrain. The suprapermafrost water table can surface at the upper edge of such strips only to drop below the surface at the lower edge (Woo and Steer 1983). Small-scale detention storage and resistance to surface flow could occur on these wetland strips. Arctic lakes and surrounding catchments also show a capacity for flow regulation, even where surface flow is present. At a high-arctic site, a 20-hour lag between initiation of precipitation and peak outflow from a lake demonstrated flow regulation by the lake and surrounding slopes (Woo et al. 1981) from a combination of effects including detention. Long unit-area recession times (time flow remains elevated after a flood peak, adjusted for drainage area), up to 10,000 times those recorded for temperate latitudes, are characteristic of high-latitude wetland drainages (Ford and Bedford 1987) and can be interpreted as evidence of detention storage regulating flow. Brown et al. (1968) attributed long recession times at their study site near Barrow to "very low slopes and numerous sites for surface detention . . . ." Ford and Bedford (1987) attributed long recession times for generalized high-latitude sites to "storage and slow release by peats with high-water retention capabilities . . . and . . . low evapotranspiration rates . . . ." Regardless of the specific mechanisms invoked to explain long recession times, wetlands act to maintain summer flows in arctic-tundra streams through surface or near-surface release of water over extended periods of time.

Although Ford and Bedford (1987) find high-latitude wetlands relatively unimportant in streamflow regulation, this is true only in the gross sense that the majority of annual precipitation appears as runoff during the snowmelt period (Kane and Carlson 1973, M.C. Miller et al. 1980, Woo and Steer 1986). On a finer scale, arctic wetlands show considerable influence on streamflow during most of the snow-free period, as shown in the preceding discussion, and should be recognized as similar to many temperate-latitude wetlands in this regard. Ford and Bedford's (1987) referenced summary conclusion is an overgeneralization of site-specific studies from interior Alaska that does not adequately reflect the complexity of permafrost hydrology documented in the body of their paper and does not necessarily extend to all high-latitude wetlands, particularly those of the arctic continuous-permafrost zone. Specifically, the studies upon which they based their conclusion were conducted in the Subarctic Region in an area of discontinuous permafrost. Slaughter and Kane (1979), cited by Ford and Bedford (1987), reported higher peak flows and lower base flows in a permafrost-dominated catchment than in an adjacent catchment nearly free of permafrost. The study area was in the Caribou-Poker Creeks Research Watershed near Fairbanks, Alaska. Other cited studies of permafrost hydrology, such as Haugen et al. (1982 [in Ford and

Bedford 1987]) and Dingman (1966, 1971 [in Ford and Bedford 1987]), also were conducted in this drainage and in the nearby Glenn Creek watershed. Citing Dingman and Koutz (1974) elsewhere in their paper, Ford and Bedford (1987) state, "In discontinuous permafrost regions, aspect can determine the presence or absence of permafrost, which in turn determines the distribution of wetlands." Dingman and Koutz (1974), however, did not discuss wetlands *per se*, rather they discussed permafrost as a determinant of vegetation types. The predominant type on the permafrost portion of their study area was black spruce (*Picea mariana*)-thick moss on steep north-facing slopes (average slope for entire area was 18%). Site-specific investigation would be required to identify these slopes as wetlands. Because not all areas underlain by permafrost are wetlands, the characteristics of specific permafrost catchments do not necessarily apply to wetlands in general. In fact, for the permafrost catchment described in Slaughter and Kane (1979), wetlands were nearly absent (Dr. Douglas L. Kane, Professor of Civil Eng. and Water Resour., Univ. of Alaska, Fairbanks, pers. comm.). Thus, the characteristics of low base flow and high peak flows in the permafrost catchment described by these authors were due to the presence of a thick organic layer on steep slopes acting as a "shallow, highly responsive aquifer" overlying permafrost (Slaughter and Kane 1979), rather than the presence of wetlands. Having reached this conclusion, we also reject Senner's (1989) arguments on streamflow regulation. Rather, we endorse Woo's (1986) conclusion that hydrologic processes in permafrost regions differ from those of temperate regions only in intensity, not in fundamental character.

In summary, streamflow regulation is a function of arctic wetlands. Such regulation is relatively ineffective during the snowmelt period (Roulet and Woo 1986*b*), because of frozen ground and sudden release of roughly one-half of annual precipitation; nevertheless, a number of mechanisms (e.g., limited infiltration, depression storage, detention storage, surface roughness) affect the magnitude and timing of breakup flows. During summer, flow regulation by arctic wetlands becomes more effective. Thaw thickens the active layer, and evapotranspiration lowers the water table. Both events increase the capacity of wetlands to store precipitation. Regulation of flow is evident when wetlands trap and hold incident precipitation, lowering hydrographic peaks. Continuous or very large storms can overwhelm wetland storage capacity resulting in rapid runoff (Roulet and Woo 1986*a,b*), a situation also reported for temperate-latitude bogs (Bay 1969). Long recession times following hydrographic peaks are again evidence of short-term streamflow regulation by arctic wetlands. Although groundwater discharge may regulate streamflow through provision of base flows in permafrost-free areas, tundra streams on Alaska's North Slope are entirely fed by surface or near-surface wetland discharge. Thus, wetlands must regulate streamflow (and water quality) in tundra systems, although potentially via different mechanisms than in permafrost-free areas.

Erosion Control: Although Senner discusses the role of permafrost wetlands in terms of "erosion control," others discuss "shoreline anchoring and dissipation of erosion forces" (Sather and Smith 1984, Robertson 1987) or "sediment regulation and shoreline anchoring" (Larson et al. 1988). Erosion control could equally well be considered a water quality function because erosion degrades water quality, but we include erosion control with hydrologic functions since flowing water is an erosive force. Senner makes the point that temperate-zone wetlands provide erosion protection along streams, rivers, and coasts and around lakes. He then states that permafrost wetlands do not have this function because they are subject to thermal erosion, citing coastal erosion rates along the Beaufort Sea as evidence for his position. Although exposed soil surfaces such as coastal bluffs, river banks, and thermokarst lake edges thermally erode (Carter et al. 1987), such erosion is largely confined to areas where natural forces (e.g., river flow) have cut or removed the overlying vegetative mat (Walker et al. 1987). This is demonstrated by the known adverse effects of vegetation disturbance or removal (Hok 1969, Radforth 1972, Lawson et al. 1978, Walker et al. 1987). For example, Lawson (1986) studied surface disturbance at former drill sites in the National Petroleum Reserve - Alaska (NPR-A). He noted that the most severe impacts resulted from removal of tundra vegetation and soil, initiating a process of thermal degradation and erosion that lasted more than 30 years in ice-rich, thaw-unstable materials. Natural revegetation of disturbed sites did not occur until they became partially stable. Revegetation in turn further stabilized surficial materials, and development of an organic mat hastened thermal equilibration of the disturbed areas. Lawson's observations illustrate the importance of tundra vegetation for preventing thermal erosion of thaw-unstable, ice-rich materials on Alaska's North Slope, a subject thoroughly reviewed by Walker et al. (1987). Arctic-tundra wetlands thus reduce the instability of the majority of the Coastal Plain because "Vegetation and the associated peat layer are important in maintaining the thermal regime of perennially frozen sediments" (Walker et al. 1987:10).

Another aspect of mechanical and thermal erosion related to wetlands is natural formation of thaw lakes and thermokarst topography when permafrost thaws and the ground surface subsides. Anthropogenic disturbances can create similar features (Walker et al. 1987). Some wetlands dissipate mechanical erosive forces and anchor shorelines because aquatic vegetation and shallow water absorb wave energy (Adamus and Stockwell 1983); however, the opportunity for wave generation and consequent erosion to occur is greatest on open waters that extend at least 2 km from the wetland edge (Larson et al. 1988). On the Coastal Plain, *Carex aquatilis* and *Arctophila fulva* are "dominant vascular plants" in freshwater habitats, forming belted patterns around ponds and lakes with *A. fulva* occurring optimally in water depths of 20 to 45 cm and *C. aquatilis* occurring at depths less than 30 cm (Bergman et al. 1977). Large coastal-plain lakes such as those studied by Derksen et al. (1981) may be many km long and generate waves capable of mechanical erosion. Many of these waterbodies also contain *Arctophila* and *Carex* wetlands, which may anchor shorelines and dissipate mechanical erosive forces.

Thermal erosion, however, plays a major role in the thaw-lake cycle (Bergman et al. 1977). These lakes are oriented with their long axes perpendicular to the direction of prevailing wind (Carter et al. 1987). Carter et al. (1987) describe formation mechanisms for oriented thaw lakes. Sublittoral shelves of sunken tundra mat quickly form on the downwind sides of thaw lakes, insulate the underlying permafrost, and damp storm waves. Winds on the Coastal Plain are generally from the ENE or WSW; thus, sublittoral shelves form along opposite sides of thaw lakes with deep water between the shelves extending to the lake ends. Thaw is retarded in the directions of prevailing winds but proceeds unabated in directions perpendicular to prevailing winds. In addition, hydrodynamic theory predicts maximum littoral drift will occur near oriented-lake ends, creating sediment-supply deficits and increasing basin elongation. Conceivably, emergent wetland vegetation could slow littoral drift at lake margins, thus affecting lake evolution. Even if this speculative mechanism is not operative, the sunken organic mat of the sublittoral shelves is derived from wetland vegetation and insulates lake-bottom materials. Thus, it is likely emergent vegetation and submerged mats respectively function to slow shoreline hydraulic (mechanical) erosion and thermally stabilize bottom sediment in thaw lakes.

Summary: Arctic wetlands share the hydrologic functions characteristic of temperate-zone wetlands with the exception of aquifer discharge and recharge. In this respect, arctic wetlands are similar to perched temperate wetlands, which also are not hydrologically connected to aquifers. Qualitatively important suprapermafrost-groundwater flows occur in arctic wetlands as does flow regulation, particularly during summer. Arctic-tundra wetlands stabilize sediment and anchor shorelines and, more importantly, maintain the thermal equilibrium of ice-rich soils. With regard to hydrologic functions, arctic wetlands do not differ from temperate-zone wetlands to a greater extent than individual temperate-zone wetlands differ from each other.

Water Quality Functions

The important hydrologic functions of wetlands strongly influence their water quality functions (Kadlec 1987). Hydrologic factors such as water depth, velocity, and discharge, and the spatial and temporal variation in these factors, affect sediment and nutrient transport, alteration, and retention in wetlands. Biological processes also strongly influence the water quality functions of wetlands. From an ecosystem perspective, the effects of wetlands on water quality result from interaction of hydrologic, chemical, and biological factors (see Mitsch and Gosselink 1986). In this sense, we could defer discussion of water quality functions until most other functions had been addressed. Nevertheless, many biological processes, such as nutrient uptake by plants and chemical transformations by microbial populations, are linked to water quality, and these processes are best presented prior to discussion of wetland productivity and nutrient export. For these reasons, we discuss the water quality functions of arctic-tundra wetlands immediately following hydrologic functions.

Sediment Retention: Senner (1989), citing Robertson (1987), states that temperate-zone wetlands remove pollutants, excess nutrients, and sediment from water whereas North Slope wetlands "can provide these functions only to a limited extent during the brief arctic summer." Robertson states, "Tundra streams are very clear and contain little sediment to be trapped." He interprets this characteristic of tundra streams as evidence tundra wetlands fail to trap sediment (i.e., they lack the opportunity to function in this manner). Robertson also dismisses the value of riparian wetlands associated with larger rivers on the North Slope for sediment trapping because the ground is frozen during breakup when the wetlands are flooded with turbid water. We disagree. Fundamentally, significant natural generation of suspended solids can occur only during the open-water season in the Arctic, although some natural (e.g., loess from river deltas [Walker et al. 1980]) and anthropogenic sources (e.g., road dust [Benson et al. 1975]) of airborne particulates are present in winter. Thus, as in temperate latitudes, the period of sediment generation largely coincides with the period of sediment removal. Furthermore, sediment removal is a function of settling time and quiescence of the waterbody. Settling times are measured in hours in reasonably calm water, such as might occur in flooded tundra or waterbodies with emergent vegetation. For example, Environmental Protection Agency (EPA) tests on placer-mine effluent showed that 3 hours of quiescent settling reduced settleable solids to 0.2 $mg{\bullet}L^{-1}$ (from Federal Register 53[100]:18764-19817). Longer settling times remove finer particles; however, even these times are measured in days (R&M 1982).

The clarity of tundra streams is evidence for sediment trapping and stabilization (i.e., mantling ice-rich mineral soils and providing thermal stability) by tundra wetlands, thus providing source water with potentially low levels of inorganic suspended solids. Tundra ponds near Barrow have extremely low concentrations of dissolved silica (Prentki et al. 1980), perhaps indicative of low input of mineral particulates. We further note that the physical structure of tundra streams, particularly the smaller drainages, consists of a series of "beads" (small thermokarst ponds) connected by narrow, deep channels. At breakup, beaded streams flood adjacent tundra creating extensive wetland complexes (Bergman et al. 1977). Later in summer, when beaded streams are confined to their channels and discharges may be intermittent (Bergman et al. 1977), water velocities are typically very low on the flat Coastal Plain. Finally, as ice cover forms on tundra wetlands, wind-driven circulation is eliminated and resuspension of sediment becomes unlikely. Thus, beaded drainages and the network of tundra ponds and lakes provide ample opportunity for quiescent settling of particulates.

Sediment can also be trapped by riparian wetlands along large arctic rivers such as the Colville (Walker 1983) and Sagavanirktok, even during breakup, because thawed ground is not necessary to trap sediment. The Sagavanirktok River has a braided pattern and a broad floodplain with many vegetated and unvegetated islands. Vegetated terraces border the active floodplain. At breakup, turbid water covers the floodplain, inundating the complex of channels, islands, and riparian wetlands. Zones of low water velocity are created by the increased cross-sectional area of the inundated floodplain, frictional resistance of flooded vegetation, and low wetland gradients, allowing settling of particulates. As river discharge diminishes, pools in high-water channels and microtopographic depressions retain water, trapping sediment. Field observations of riparian wetlands in the Sagavanirktok system by the Alaska Department of Fish and Game have verified that sediment trapping occurs as evidenced by deposits of fine material in a rehabilitated gravel pit (Winters 1990). Similarly, the Colville River, the North Slope's largest and most burdened by sediment, terminates in a delta covered with "tapped" (channel-connected) lakes and old channels that trap large amounts of sediment (Walker 1978). Deposition of sediment in the Colville Delta from annual breakup flooding can reach depths of more than 25 cm at specific locations (Walker 1983). Arctic-tundra wetlands therefore function to inhibit generation of inorganic particulates by maintaining the thermal equilibrium of ice-rich, thaw-unstable materials in the watersheds of tundra systems and to remove and stabilize suspended solids in the floodplains of large arctic rivers with mountain headwaters.

Nutrient Uptake and Contaminant Removal: Senner states that low temperatures, a "relative paucity of fine sediment," and a lack of inflow from upstream sources limit the ability of arctic wetlands to remove or alter contaminants or excess nutrients and thus to purify water. These assertions are not supported by the literature. While low temperatures can reduce chemical reaction rates, tundra ponds near Barrow reach temperatures as high as 16°C (Hobbie 1980*a*), averaging from 5° to 9°C during the summer (Alexander et al. 1980), and show chemical responses to nutrient input. For example, Hobbie (1980*a*) reports that when dissolved reactive phosphorus (DRP) enters tundra ponds, "it quickly moves to the sediment where much of it is sorbed onto a dense hydrous iron complex" and concludes "that chemical reactions in surface sediments, especially those reactions involving iron, set the concentration of DRP in the water and in this way control the productivity of the ponds." (This is also true of other environments where iron is abundant.) Specifically, the phosphate-buffering intensity for Barrow pond sediments is 50 to 250 times greater than that reported for a temperate-latitude site (Prentki et al. 1980). This buffering capacity for phosphate is evidence that arctic-tundra wetlands remove excess phosphorus from inflowing water. Further evidence for this function is provided by the annual phosphorus budget for tundra ponds. Less than 1 mg $P \cdot m^{-2} \cdot yr^{-1}$ is lost from the ponds, or about "0.003% of the 25 g $P \cdot m^{-2}$ present in the top 10 cm of . . . sediments" (Prentki et al. 1980). A portion of the phosphorus lost from tundra ponds is recovered by the wetland system since "As meltwater moves across the watershed, phosphorus is . . . removed from the ponds and resorbed by the terrestrial soils" (Prentki et al. 1980).

Fine inorganic and organic sediment is abundant in arctic-tundra wetlands. Both types of sediment are known to adsorb pollutants in temperate regions (Sather and Smith 1984). Near Prudhoe Bay, inorganic carbonate sediment is found in ponds and alkaline wet tundra as surface deposits several millimeters thick (Walker et al. 1980). Tundra ponds near Barrow are characterized by a layer of highly organic sediment from 18 to 30 cm thick "underlain by a layer of mixed organic matter and sand" over "layers of sand and lenses of buried peat at a depth of 40 to 60 cm" (Prentki et al. 1980). The uppermost bottom sediments of these tundra ponds had a mean particle size of 0.5 mm (Prentki et al. 1980). Further definition is provided by Butler et al. (1980) who describe two types of sediments in the pond areas free of macrophytes: "fine, unconsolidated sediments" and "irregularly spaced peaty sediments." Surface sediments from tundra ponds near Barrow contain from 68 to 84% organic matter, but organic content is as low as 18% at a depth of 8 to 9 cm (Prentki et al. 1980). Likewise, Prentki et al. (1980) described the organic sediments in tundra ponds as iron-rich peats and stated, "pond chemistry is controlled by the events in the sediments." Contact between ions and the organic substrate is enhanced in shallow ponds by ion exclusion from freezing ice, forcing ions into the sediment. This mechanism may account for elevated cation concentrations in interstitial water of tundra ponds relative to concentrations in the overlying water column (Prentki et al. 1980).

Outside tundra ponds, tundra soils most commonly are made up of hemic materials, partially decomposed plant matter resistant to mechanical disintegration (Gersper et al. 1980). Fibric materials, slightly decomposed plant matter, are common in surface horizons; but sapric materials, fine-particled, highly decomposed, easily disintegrated plant matter, occur as inclusions in other soils or make up the entire active layer in dryer microsites (Gersper et al. 1980). Organic material has a high cation exchange capacity (CEC) in terrestrial systems (Buckman and Brady 1969:90-91,144-146), a characteristic that facilitates chemical reactions and retains nutrients. Gersper et al. (1980) report a similar function in arctic wetlands. They found an average CEC of 55 meq•$(100g)^{-1}$ for tundra-meadow soils, a value "well above that of most mineral soils." Anions such as phosphate and cations such as ammonium are both adsorbed by the organic mat of tundra wetlands during snowmelt runoff (Chapin et al. 1980*b*). Like pond sediments, tundra soils contain fine particles (e.g., sapric soils) as well as mineral soils exposed at the surface by frost boils (Walker et al. 1980). Mineral soils also occur on river bars and low terraces adjacent to rivers (Walker et al. 1980) and thus are present in riparian wetlands. In addition, tundra soils are highly variable over short lateral distances in response to microtopography (Gersper et al. 1980), a characteristic ensuring that waterborne nutrients and contaminants contact a variety of potential reaction sites during periods of high water. Thus, we see no relative paucity of fine sediment in tundra ponds, which is where contaminants and nutrients are likely to end up if not immobilized elsewhere, and no shortage of mineral or organic substrates in tundra wetlands.

Tundra ponds have a high ratio of sediment surface to water volume (Prentki et al. 1980), and wind-driven circulation contributes to oxygenation of the sediment (Butler et al. 1980, Miller et al. 1980). These factors ensure contact between waterborne pollutants and the substrate and support sediment respiration. Biological activity in pond sediments can degrade pollutants. For example, Barsdate et al. (1980) presumed biological degradation of hydrocarbon compounds with fewer than 13 carbon atoms was responsible for their disappearance 5 years after an experimental oil spill in a tundra pond. Kadlec and Kadlec (1978) reviewed literature indicating that microbial processes removed hydrocarbons from a shallow marsh. Wetlands also remove other contaminants from the water, for instance toxic metals (Kadlec and Kadlec 1978). Anaerobic sediments (below the oxidized layer) permit "conversion of soluble forms of heavy metals to insoluble forms," and plants can take up metals and store them in tissues (Sather and Smith 1984). Since arctic wetlands contain aerobic sediments, anaerobic sediments (below 1 to 2 cm in deepwater areas [Prentki et al. 1980]), and plants (Alexander et al. 1980, Tieszen et al. 1980), contaminant removal should occur in the same manner as documented for temperate wetlands.

Microbial populations, epipelic algae, phytoplankton, and macrophytes contribute to nutrient and contaminant retention or transformation in tundra wetlands since arctic-tundra species are adapted to low temperatures and are biologically active even under harsh conditions. For example, cold adaptations in tundra microflora permit respiration at temperatures as low as -7.5°C and fungal growth at 0°C (Flanagan and Bunnell 1980). Mosses and lichens can photosynthesize at more than 50% of their maximum rates at 0°C (Chapin and Shaver 1985*a*). Vascular plants such as *Carex aquatilis* (an aquatic sedge) can photosynthesize at temperatures as low as -4°C; *Carex* shows "significant respiration and translocation of carbohydrates" as well as "significant root elongation near 0°" (Alexander et al. 1980). In addition, tundra graminoids show physiological adaptations to the arctic environment that may facilitate uptake of nutrients. *Dupontia fisheri*, for instance, "maintains 35% of its 20°C phosphate absorption rate at 1°C," and shoot production is positively correlated with soil phosphorus availability (Chapin et al. 1980). Although algae in tundra ponds generally function at less than optimum temperatures for maximum photosynthesis, low temperatures may also depress herbivore grazing and respiration losses, thus compensating for reduced gross production so that algal biomass and net production may be relatively insensitive to temperature (i.e., if gross production [photosynthesis], grazing rates, and respiratory losses are all directly related to temperature over a given range, the balance between gains and losses may remain relatively constant over the same range) (Alexander et al. 1980). Conversely, photosynthetic rates in rooted aquatics are limited primarily by low light intensity rather than by temperature (Alexander et al. 1980). Nevertheless, the *Carex* leaf angle is optimized for absorbing incident radiation, and the continuous daylight of high-latitude summer allows positive net photosynthesis to occur from mid-June until early August (Alexander et al. 1980).

Arctic soils generally exhibit low nutrient availability, but concentrations may vary by an order of magnitude between adjacent microhabitats (Chapin and Shaver 1985*a*). Plants growing in environments where nutrients are not readily available often grow slowly, tolerate stress, and maximize root:shoot ratios and mycorrhizal associations (Chapin 1980). Consequently, belowground biomass of arctic plants is often high, although this may also be influenced by low root temperatures (Chapin and Shaver 1985*a*). Since nutrient availability is generally low in the Arctic, one might expect that tundra vegetation would show a response to added nutrients. In fact, arctic wetlands do show a biological response to phosphorus and nitrogen (Tieszen et al. 1980), the two most common components of anthropogenic nutrient enrichment (Mackenthun 1969). *Sphagnum* wetlands in Alaska have been shown to respond to added nitrogen and phosphorus with increased biomass (Sanville 1988). Plants adapted to infertile soils often respond by increasing tissue concentrations of nutrients (luxury consumption) rather than substantially increasing growth rates (Chapin 1980), but arctic plants exhibit species-specific responses to nutrient inputs (Chapin and Shaver 1985*b*). In mixed communities of tundra vegetation, nutrient enrichment increases the "dominance of rapidly growing species" (Chapin and Shaver 1985*a*) suggesting that arctic wetlands assimilate nutrients by increasing growth rates in some species and concentrating nutrients in plant tissues of other species. For example, phosphorus added to tundra ponds increased planktonic nitrogen uptake and photosynthetic rate (Prentki et al. 1980). Chronic and intense fertilization of *Dupontia* stands increased their density and their leaf-area index but presumably had little effect on leaf photosynthetic rates, because *Dupontia*'s photosynthetic structures normally operate at near optimal capacities at rates comparable to those of similar growth forms in temperate regions (Tieszen et al. 1980). Low concentrations of inorganic phosphorus and other inorganic nutrients appear to limit microfloral "growth rates in some mictotopographic units" (Bunnell et al. 1980), which further indicates that excess nutrients can be assimilated by tundra wetlands.

Wetlands can assimilate nitrogen for long periods of time because they are the most important sites of denitrification by microbial populations (Adamus and Stockwell 1983). Anaerobic conditions within the substrate are necessary for denitrification (Kadlec and Kadlec 1978). Denitrification releases nitrogen gas to the atmosphere, removing it from the aquatic and terrestrial environments. Tundra ponds near Barrow, like wetlands in temperate regions, exhibit denitrification. Nitrogen removal by this mechanism is relatively low: 2.8 mg $N{\bullet}m^{-2}{\bullet}yr^{-1}$ (Prentki et al. 1980). Wet meadows in the same area lose nitrogen by denitrification at a rate of 3.4 mg $N{\bullet}m^{-2}{\bullet}yr^{-1}$ (Gersper et al. 1980). Denitrification rates appear to be nutrient limited and increased 4-fold in tundra soils with added glucose and phosphorus (Prentki et al. 1980). This response indicates that arctic wetlands can remove excess nutrients. Despite loss of dissolved inorganic nitrogen (DIN) by denitrification, tundra ponds showed a net DIN gain of 10.5 mg $N{\bullet}m^{-2}{\bullet}yr^{-1}$ and a dissolved organic nitrogen (DON) gain of 69.6 mg $N{\bullet}m^{-2}{\bullet}yr^{-1}$ for a total of about 80 mg $N{\bullet}m^{-2}{\bullet}yr^{-1}$. This gain is small (0.0004%) compared to the 219 g $N{\bullet}m^{-2}$ "in the top 10 cm of sediment" (Prentki et al. 1980) but demonstrates that tundra ponds function for nitrogen uptake.

Ammonia concentrations in tundra-pond water generally are much greater than nitrate concentrations. In pond sediments, both DON and ammonia occur in much higher concentrations than nitrate (Prentki et al. 1980). Sufficient ammonia is present to supply the needs of phytoplankton, but based on the primary productivity of epipelic algae and macrophytes, which exceeds that of phytoplankton by several orders of magnitude, epipelic algae and macrophytes are much more significant for DIN uptake, requiring about 12 mg $N \cdot m^{-2} \cdot day^{-1}$ and 18 mg $N \cdot m^{-2} \cdot day^{-1}$, respectively (Prentki et al. 1980). *Carex* appears to turn over all the ammonia in root-zone interstitial water each day (Hobbie 1980*a*), implying rapid regeneration of ammonia from decomposition of organic matter (Prentki et al. 1980). Anthropogenic phosphorus and nitrogen entering tundra ponds likely would promote nutrient uptake by benthic algae and rooted vegetation in a similar manner, potentially acting to purify water.

Although the opportunity for individual wetlands to purify water is generally not discussed in this critique, it is clear that arctic-tundra wetlands often receive water from "upstream" sources. For instance, the seasonal snowmelt and inundation of the Coastal Plain in June and early July (Hobbie 1980*b*) fill tundra ponds and other wetlands (M.C. Miller et al. 1980) as well as the network of tundra streams that overflow into adjacent wetlands (Bergman et al. 1977). These water sources carry nutrients or (potentially) pollutants into the wetlands. Water also enters tundra wetlands as precipitation, slope runoff, and subsurface discharge and as flow from anthropogenic sources (e.g., sewage treatment facilities). Drilling fluids released from reserve pits by seepage or regulated discharge have elevated inorganic ion and hydrocarbon concentrations in both sediments and the water column in wetlands adjacent to drill pads on Alaska's North Slope (West and Snyder-Conn 1987, Woodward et al. 1988), illustrating that such wetlands do have the opportunity to perform water quality functions. Spills of hazardous or toxic substances from improper storage or disposal within the Prudhoe Bay "Lease Tract Area" (Brad Fristoe, Environ. Eng., Alaska Dep. of Env. Conserv., Fairbanks, pers. comm.) also originate on wetland fills and may enter wetlands on Alaska's North Slope, although the extent of tundra contamination from spills of hazardous waste is unknown at this time. If Robertson (1987) were correct that these wetlands have no value for water purification, Senner would be presenting a strong argument against wetland fills, because in his view wetlands could not ameliorate the adverse effects of pollutants generated on or by such fills.

Natural sources of nutrients are also present in the tundra. For example, Prentki et al. (1980) reported retained spring runoff as an important source of DON for tundra ponds. Rainfall was the major source of DIN for the ponds. Likewise, dissolved unreactive phosphorus is carried into tundra ponds by annual runoff, and DRP may be trapped there as well (Prentki et al. 1980). Dry deposition of particulates is another potential source of nutrient (Kadlec 1987) or contaminant input for wetlands. For example, loess deposition downwind from the Sagavanirktok River Delta near Prudhoe Bay forms marl deposits, making affected wetlands alkaline rather than acidic like many other North Slope wetlands (Walker et al. 1980).

Dust from roads (Benson et al. 1975, Brown and Berg 1980) and pads can also deposit contaminants in wetlands. Finally, we note that many temperate-zone wetlands do not receive water from upstream sources (e.g., aquifer discharge areas, bogs, prairie potholes, etc.) in the sense that "upstream" means input by a discrete stream channel. These temperate wetlands may be fed by diffuse surface drainage, precipitation, or groundwater discharge.

Summary: Arctic-tundra wetlands purify water by trapping sediment and by transforming or retaining nutrients and toxicants. In this respect, arctic wetlands are similar to many temperate wetlands. Arctic wetlands, just as temperate-zone wetlands that receive river, stream, or surface discharge, have finite capacities for sediment, nutrient, and toxicant removal. For example, it would be ludicrous to suggest swamps and marshes along the Mississippi River produce sparkling clear, pure water at the river's mouth despite the beneficial influences of these wetlands. Likewise, the vegetated floodplains of arctic rivers cannot remove all suspended solids and pollutants that might be present during massive breakup flooding. Wetlands associated with large arctic rivers do retain a portion of peak flows, whether the substrate is frozen or not, trapping sediment by physical settling and potentially purifying retained water. The Colville River Delta, with seasonal inundation recharging lakes and other wetlands that are not connected to the river, and with "tapped" lakes (Walker 1978) connected to the river, probably functions for water purification much like temperate-zone deltas. Finally, Hobbie (1980*a*) states, "When compared to the daily production of other ecosystems the [tundra] ponds are reasonably productive." If we take productivity as one indicator of a wetland's capacity for water purification, then arctic ponds are limited in this capacity only by the short summer season, not by lack of the functional capability. Vascular plants, plankton, and soil microflora of arctic-tundra wetlands either respond, or have the potential to respond, to nutrient input with increased growth. The period of high productivity coincides with the period of potential nutrient or contaminant input, enhancing the water-purification function of these wetlands.

Production and Export Functions

Wetlands are often productive habitats (Sather and Smith 1984) where plant biomass can exceed that produced by fertilized upland crops (Larson et al. 1988). This production supports food chains of heterotrophic organisms, which is an inherent function of all wetlands (Sather and Smith 1984). Heterotrophs consuming organic material produced in wetlands may be found within those wetlands or at locations "downstream" from the sites of production, although the nutrient-export function is less well established than is the typically high net primary productivity of wetlands (Sather and Smith 1984). Heterotrophic consumption constitutes the secondary productivity of wetlands, a characteristic Sather and Smith (1984) regard as well established. Senner (1989) does not directly discuss the production and export functions of arctic-tundra wetlands except to argue that Alaska's North Slope is not productive waterfowl habitat when compared to other arctic sites such as the Yukon-Kuskokwim Delta or subarctic sites such as the Yukon River Flats. Nevertheless, net primary production, nutrient export, and food-chain support are important functions of arctic wetlands that merit discussion in the following paragraphs.

Net Primary Production: Low temperature indirectly limits productivity in arctic ecosystems through its influence on length of growing season, availability of nutrients, and presence of permafrost (Chapin and Shaver 1985*a*). Nevertheless, tundra plants are well-adapted to growth at low temperatures (Alexander et al. 1980, Chapin et al. 1980*a*, Tieszen et al. 1980, Chapin and Shaver 1985*a*) with photosynthetic rates similar to those of comparable growth forms (e.g., grasslands [Chapin et al. 1980*a*]) in temperate regions (Tieszen et al. 1980, Young 1989). Net primary productivity in arctic wetlands thus is limited by the short growing season (McNaughton and Wolf 1973, Chapin et al. 1980) rather than rates of photosynthesis. Within the tundra environment near Barrow, aboveground productivity of vascular plants increases as soil moisture increases along a gradient from high polygon centers to stream and pond margins (P.C. Miller et al. 1980), consistent with the general pattern seen in arctic communities (Chapin and Shaver 1985*a*). For example, *Arctophila* (an emergent aquatic grass) exhibited highest aboveground production, and *Dupontia* (a grass of wet tundra meadows) showed highest belowground production among the vegetation types studied by P.C. Miller et al. (1980). The effects of moisture on primary production in the tundra environment may be related to transport of nutrients to roots or to nutrient availability rather than direct physiological requirements for water (Chapin and Shaver 1985*a*). Gross primary production averaged over all vegetation types for a typical year near Barrow was about 465 gdw•m^{-2} while net primary production was about 230 gdw•m^{-2} (P.C. Miller et al. 1980). Production is divided between aboveground and belowground components. At Barrow, the belowground component of net primary production is greater than the aboveground component for each vegetation type except *Arctophila* stands and, when averaged over all types, is 3 times greater than aboveground production (P.C. Miller et al. 1980). High root-to-shoot ratios of tundra graminoids facilitate growth in an environment of low nutrient availability (Chapin et al. 1980*a*), enhancing the productivity of tundra wetlands. Tundra production, while low (Chapin et al. 1980*b*, Wielgolaski 1986), is still approximately one-half that of temperate grasslands (Chapin and Shaver 1985*a*) even though the arctic growing season is very short.

Primary production in tundra ponds near Barrow is mostly by rooted aquatic plants such as *Carex aquatilis* and *Arctophila fulva*. Alexander et al. (1980) reported several estimates of aboveground production for *Carex* ranging from 89 to 370 gdw•m^{-2}•yr^{-1}, values they characterized as somewhat higher than found for nearby terrestrial production. These authors stated that belowground production in *Carex* in tundra ponds may equal aboveground production. Although production in *Carex* stands in tundra ponds may exceed that occurring in other tundra wetlands, overall pond production depends on the fraction of the pond covered by emergent vegetation. For instance, the ponds studied by Alexander et al. (1980) typically had only 32% coverage by *Carex aquatilis* and only 13% coverage by *Arctophila fulva*. Epipelic algae produced about 10 g $C \cdot m^{-2} \cdot yr^{-1}$, and phytoplankton produced only about 1 g $C \cdot m^{-2} \cdot yr^{-1}$ in these ponds, about 10% the amount of net primary production for rooted aquatic plants adjusted for coverage. Overall, the Barrow ponds were more productive than terrestrial sites because phosphorus was more available and less standing dead material was present to shade photosynthetic tissue (Alexander et al. 1980).

Net primary production supplies the energy on which heterotrophs exist; however, only a portion of the production is consumed by herbivores. Accumulated living plant biomass can be substantial, but in the tundra much biomass is below the ground surface. Near Barrow, belowground biomass (849 $gdw \cdot m^{-2}$) for all plants was more than 4 times greater than aboveground biomass (200 $gdw \cdot m^{-2}$) (P.C. Miller et al. 1980). Some vegetation types had even higher belowground biomasses (e.g., 3119 $gdw \cdot m^{-2}$ for *Carex* [Alexander et al. 1980]). Vertebrate herbivores such as lemmings and caribou feed on the aboveground biomass so that much of the tundra's production is unavailable to these species (Batzli et al. 1980). Plant biomass entering the pool of dead organic matter becomes available to microorganisms and invertebrate detritivores, but these organisms are limited by the arctic environment resulting in net accumulation of organic matter in the tundra (MacLean 1980). Stated in terms of carbon, from 17 to 32 $kg \cdot m^{-2}$ may be present in the top 20 cm of the tundra (Chapin et al. 1980*b*). Nutrients are similarly tied up in accumulated organic matter where low temperature and low oxygen concentration slow their release (Chapin and Shaver 1985*a*). Nevertheless, long-term processes such as the thaw-lake cycle, grazing, and frost action can release stored carbon and nutrients (Chapin et al. 1980*b*).

Nutrient Export: Outflow from wetlands may flush nutrients to downstream communities where they may contribute to food-chain support, but this function is poorly documented for freshwater wetlands, and its overall importance in tidal wetlands has been questioned (Sather and Smith 1984). Some salt marshes export as much as 20 to 45% of net primary production to adjacent estuaries but others export less than 1% (Mitsch and Gosselink 1986:197). Export from tidal freshwater marshes may be most significant in younger, lower marshes subject to vigorous flushing but has rarely been studied in other freshwater wetlands where export is likely dependent on the site-specific degree of flushing (Mitsch and Gosselink 1986:225). Organic material produced in arctic wetlands can be exported to downstream communities by erosion and seasonal flooding. For instance, coastal erosion of peat introduces approximately 110×10^6 kg $C \cdot yr^{-1}$ to the Beaufort Sea while cut-bank erosion and fluvial transport of peat contributes about 570×10^6 kg $C \cdot yr^{-1}$ (Schell and Ziemann 1983). This allochthonous carbon input approximates that of phytoplankton primary production in the nearshore zone of the Beaufort Sea (<10 km offshore). The peat is degraded by microbial activity in the marine environment, but little peat carbon is transferred to higher trophic levels (Schell 1983). Thus, export of carbon to the Beaufort Sea may not be particularly significant to species consumed by humans.

In contrast, transfer of peat carbon to higher trophic levels is pronounced in the freshwater environment where "the aquatic habitats of the tundra represent active sites for peat oxidation and conversion to faunal biomass" (Schell and Ziemann 1983). Active erosion at the margins of large thermokarst lakes places peat into the water column, representing perhaps 26 x 10^6 kg C•yr^{-1} (Schell and Ziemann 1983). Although his techniques were controversial, Schell (1983) demonstrated the ecological significance of this peat carbon by measuring its presence in resident and anadromous fish and in ducks dependent upon freshwater arctic wetlands. The proportion of body carbon derived from peat ranged from less than 4% in late summer to about 32% following overwintering for arctic grayling (*Thymallus arcticus*), ranged up to 52% after overwintering in fresh water for least ciscoes (*Coregonus sardinella*), and was 63% for an oldsquaw duck (*Clangula hyemalis*) sampled after leaving tundra lakes. Schell (1983) summarized the importance of erosional processes in arctic wetlands as follows:

> Freshwater and anadromous arctic fish and oldsquaw ducks, however, rely on the trophic transfer of peat carbon through the critical link of insect larvae and attain partial independence from the seasonal variation in primary production. This "fossil fuel subsidy" is important in an environment where primary production is essentially nil for about 7 months of the year.

Schell's (1983) summary underscores the importance of detrital food chains in arctic ecosystems where 93 to 99% of annual terrestrial primary production becomes dead organic matter (MacLean 1980). This energy source only becomes available to consumers via detritus-based trophic transfer. In aquatic habitats, erosion supplies peat detritus processed by decomposer organisms for insect larvae. Insects so fed are, in turn, eaten by second- and third-level consumers such as fish and birds and provide these consumers a greater and more stable food supply than is available from primary production alone (Schell and Ziemann 1983).

Food-Chain Support: Sather and Smith (1984) state that heterotrophic consumption of nutrients derived from wetlands must be shown to invoke the function of food-chain support. Alaska's Arctic Coastal Plain is largely wetland (Hobbie 1984). These wetlands support both herbivore-based and detritus-based trophic systems (Batzli et al. 1980). Herbivores include caribou (*Rangifer tarandus granti*), voles (*Microtus*), lemmings (*Lemmus, Dicrostonyx*), arctic ground squirrel (*Spermophilus parryii*), ptarmigan (*Lagopus*), geese (*Branta, Chen, Anser*), hares (*Lepus*), and muskox (*Ovibos moschatus*) (Batzli et al. 1980) as well as moose (*Alces alces*) (Coady 1982). Near Barrow and Prudhoe Bay, brown lemming (*L. sibiricus = trimucronatus*) and caribou are, respectively, the major primary consumers among vertebrates (Batzli et al. 1980), but muskox is also important elsewhere on arctic ranges (White et al. 1981). Similarly, the detritus-based food chain for coastal tundra near Barrow includes microorganisms and invertebrates such as nematodes, mites, flies, springtails, and enchytraeid worms, most of which occur in the upper 5 cm of the soil profile (MacLean 1980). A diverse community of insectivorous birds feed on the soil invertebrates, particularly dipterans, consuming up to 35% of the annual production of a single cranefly species (MacLean 1980). Arctic-tundra wetlands clearly perform the function of food-chain support, both through the herbivore-based trophic system from living plant tissues to rodents and ungulates (Batzli et al. 1981) and their predators and through the detritus-based trophic system from dead plant tissue (and other organic matter such as feces) to shorebirds and Lapland longspur (*Calcarius lapponicus*) (MacLean 1980) and their predators.

Summary: Net primary production in arctic-tundra wetlands is limited primarily by the short growing season. Maximum photosynthetic rates of tundra plants are similar to those of comparable growth forms in temperate regions. Organic matter accumulates on the tundra but is released by erosional processes to support aquatic biota during winter when primary production is absent. Herbivore- and detritivore-based food chains support abundant wildlife, particularly during summer. The production and export functions of arctic wetlands are qualitatively similar to those of temperate regions.

Habitat Functions

Wetland habitats result, in part, from the integration of hydrologic, water quality, and production processes, and thus consideration of wetland habitats encompasses previously discussed wetland functions. Habitat for a species or for a community, in its simplest conception, is that portion of the earth on which it can persist (see Appendix A for detailed definitions and discussion of habitat). Habitat may occur in tiny patches scattered over a huge area (e.g., the rotting logs supporting decomposer communities in the boreal forest), in widely spaced, discrete locations (e.g., "black smoker" thermal vents on mid-oceanic ridges supporting chemotrophic communities of bacteria and marine invertebrates), or in a nearly continuous distribution over a large area (e.g., most terrestrial areas of the Northern Hemisphere supporting the wolf prior to modern times). Habitat availability is the ultimate limiting factor on a species' or community's abundance. Wetland habitats are crucial for wetland species and communities, because many species that have evolved in wetland ecosystems have specific requirements for survival, growth, and reproduction that cannot be met by other ecosystems. We provide evidence in subsequent portions of this critique that arctic-tundra wetlands have the same functional relationships to fish and wildlife productivity and abundance as do temperate wetlands.

Senner (1989) concedes "wetlands are crucial to . . . many species of fish and wildlife . . . ." He then attributes the crucial nature of wetlands to their provision of "population-limiting factors that control the productivity and size of [fish and wildlife] populations," a statement that is somewhat ambiguous. Does he mean wetlands contain factors (e.g., resource limitations, predators, etc.) that control animal abundance whereas uplands, by implication, do not possess such factors? This interpretation runs counter to his central thesis that arctic-tundra wetlands do not limit abundances of wetland species. Does he mean wetlands provide resources that are sparse or unavailable in uplands thereby allowing wetland species to become more abundant? This interpretation lends weight to the value of wetlands as fish and wildlife habitat, which is consistent with his position for temperate-latitude wetlands but counter to his position on arctic wetlands. The question of proper interpretation is not easily answered by further reading in *Effects of Petroleum Operations in Alaskan Wetlands*, but its author does argue a direct relationship between wetland area and animal abundance for temperate wetlands while denying any such relationship for arctic-tundra wetlands.

From the standpoint of fish and wildlife resources, the habitat function of wetlands is their preeminent value because fish and wildlife species meet all their needs for existence within their habitats. Many of these species require wetland habitats but others are either not dependent or only partially dependent on wetlands (Adamus and Stockwell 1983, Sather and Smith 1984). For the large segment of North American wildlife that depends on wetland habitats there are few, if any, species that could persist in the absence of wetlands and "no known cases where diminuation [sic] of wetland habitat resulted in a population shift to remaining wetland habitat without adverse impact on the total population" (Adamus and Stockwell 1983). Similarly, most freshwater fishes require shallow water for one life-history function or another (Adamus and Stockwell 1983, Maltby 1986:19-26). Thus, the value we place on wetland habitats reflects the values of the species supported by those habitats. Often these are direct economic benefits. For example, Mitsch and Gosselink (1986:396) state that "About two-thirds of the fish and shellfish species that are harvested commercially are associated with wetlands." Wetland species such as furbearers and waterfowl have direct and indirect economic significance as well (Sather and Smith 1984, Maltby 1986:76-89, Mitsch and Gosselink 1986:394-395). In Alaska, subsistence uses of wetlands by Alaska Natives provide an additional reason to value wetland habitats (see Ellanna and Wheeler 1989). The economic and cultural benefits of wetland habitats are linked to other wetland functions and values. These include hydrologic (e.g., beaver [*Castor canadensis*] dams), water quality (e.g., filter-feeding organisms), and ecological (e.g., nutrient cycling and food-chain support) functions, as well as recreation and heritage values. Since the habitat function of wetlands is exceeded only by the passive recreation and heritage value of wetlands in nationwide extent and probability of occurrence (Adamus and Stockwell 1983), protection of wetland habitats is important.

Recreation and Heritage Functions

Direct and indirect human use of wetlands takes many forms. Recreation is one of these uses; "heritage" value is another. Recreation may be active (e.g., boating, fishing) or passive (e.g., aesthetic enjoyment, open space) (Adamus and Stockwell 1983). Active recreation does not occur in all wetlands, but activities such as fishing and hunting are important wetland uses that often generate more revenues than commercial extraction of fish and wildlife resources (Mitsch and Gosselink 1986:394,397). In general, active recreation does not alter wetland characteristics and therefore does not preclude passive appreciation of wetland vistas and values. Heritage values of wetlands include preservation of rare or endemic species, protection of unique archeological or geological features, and reservation of sites for scientific study (Adamus and Stockwell 1983). The recreation and heritage functions of wetlands may be realized at future dates, even where these uses are not realized at present (Adamus and Stockwell 1983).

Senner (1989) believes that arctic wetlands are much less valuable for recreation than are wetlands elsewhere. His reasons include difficulty of foot travel on the Coastal Plain, insects, lack of landmarks, and the fact that more people visit the Prudhoe Bay Oilfield than the Arctic National Wildlife Refuge (ANWR). He further equates the potential for commercial enterprises such as tour-bus and commercial-aircraft operations with the recreational value of wetlands. While we agree current recreational use of the Coastal Plain is much lower than the use of certain wetlands elsewhere, recreational value is not only measured in commercial potential. Recreational values include the opportunity to experience solitude, wilderness, and adventure and to view wildlife, aspects of recreation not necessarily associated with mass transportation of tourists. Further, these experiences are inversely related to the density of recreational users. Finally, the recreational value of arctic wetlands is, in part, represented by their production of wildlife that supports recreational activity elsewhere. Migratory waterfowl are a good example of a resource used by hunters and nonconsumptive recreationists thousands of miles from the arctic wetlands where the birds are produced (Mitsch and Gosselink 1986:395).

The current pattern of recreation on the North Slope is strongly influenced by the presence of the Dalton Highway, which facilitates bus tours. This should not be taken as evidence that wetland recreation away from the highway is unimportant. Most recreational use of the Arctic Coastal Plain away from the Dalton Highway probably occurs in the ANWR rather than the NPR-A to the west. The ANWR has experienced significantly increased use as a result of national debate and congressional deliberations over potential petroleum development of the refuge's "1002 Area." Visitors to the ANWR typically stay for longer periods than do visitors to Prudhoe Bay where tourists remain for less than 24 hours. Total visitor numbers thus do not adequately reflect refuge use. Visitors to the ANWR accounted for an estimated 1,289 person-use days (PUD) in wetlands of the Arctic Coastal Plain during 1989 (U.S. Fish and Wildl. Serv. ANWR, unpubl. data: letter, Reynolds to Post, 12 March 90). Specifically, river float trips, the largest category of use, contributed 826 guided PUD and 99 unguided PUD to the total, and backpackers (and similar users) added 237 PUD. The remaining wetland use came from sport hunters and unreported (estimated) private activity. We also note that recreational use of some rivers in the ANWR reached a magnitude requiring the refuge to implement controls on commercial operations. Thus, arctic wetlands possess recreational values as well as heritage values (*sensu* Adamus and Stockwell 1983).

THE "VACANT-HOTEL HYPOTHESIS": A MYTH

Habitat loss has occurred and will continue to occur as a consequence of resource development. Senner (1989) postulates that the availability of arctic-wetland habitats (as defined by Senner - see Appendix A for discussion) does not control fish and wildlife abundance because arctic habitats are not fully stocked. He states that, in those situations where an animal population exists in numbers below the carrying capacity (using his definition - see Appendix B for discussion) of its range, which he believes is the case for most or all arctic species, "habitat loss will not affect population size or productivity, until enough reduction in habitat area or quality occurs to lower carrying capacity to the point that it begins to impose an upper limit on the animal population. At that point, habitat becomes a limiting factor on the population." We recognize that animal populations may be depressed by many factors, including human exploitation; however, we view these factors as varying over time whereas habitat loss is essentially permanent. We further believe that most arctic species exist at the carrying capacities (broadly defined - see Appendix B) of their environments. Although he does not state his views in these terms, Senner's hypothesis can be summarized as follows: the North Slope of Alaska is analogous to a large hotel (arctic wetlands) with many unoccupied rooms (habitats) that could accommodate many more guests (organisms) than are currently present. The concept, known as the "Empty-Box Hypothesis" or "Vacant-Hotel Hypothesis" by resource-agency biologists, has been used by the petroleum industry to discount effects of habitat losses associated with oil and gas exploration and development. We refer to the hypothesis in this critique as short-hand notation for conveying the preceding concept.

The significance of habitat loss to fish and wildlife populations is the salient point in discussing the Vacant-Hotel Hypothesis. Should the hypothesis be correct, as Senner contends, resource managers could assign considerably less importance to habitat loss. In fact, *Effects of Petroleum Operations in Alaskan Wetlands* emphasizes the industry position that avoidance and minimization of impacts is sufficient mitigation for loss of North Slope wetlands. However, we contend that the Vacant-Hotel Hypothesis is a myth and that resource managers should place greater emphasis on evaluating habitat impacts of differing development options and on implementing mitigation requirements that offset losses of wetlands in Alaska, since such losses diminish fish and wildlife populations. The following section examines evidence bearing on the hypothesis.

Clarification of the Hypothesis

Control of animal populations is a complex and much-debated subject (McNaughton and Wolf 1973:318) that must be considered in the context of animal-habitat relationships in order to understand the importance of arctic wetlands to fish and wildlife populations. Senner's view overlooks this complexity, apparently assuming all populations are controlled by the same factors, respond to those factors in the same way, have static abundances, occur in habitats with constant carrying capacities, and have no feedback mechanisms relating net reproductive rates to animal densities. We argue such is not the case, concurring with MacArthur and Connell (1966:142) who state, "It is clear that there is no one mechanism which determines the size of populations."

Habitat loss reduces the areas occupied by animal species. If the populations of those species did not decline, their ecological densities (organisms•unit habitat space^{-1}) (Odum 1971:163) would increase. This phenomenon has been observed in the northern spotted owl (*Strix occidentalis caurina*), a species with low reproductive and mortality rates, when subjected to habitat loss in northwest California (Franklin et al. 1990). Franklin et al. (1990) characterize the increased ecological density of these owls following partial habitat loss as "short term" and state that habitat loss and fragmentation is "incompatible with density-dependent mechanisms" of population regulation. Since the Vacant-Hotel Hypothesis holds that animal numbers do not decrease in the long term as arctic habitat is lost, it requires that factors controlling fish and wildlife populations operate independently of ecological density. These factors include those that produce mortality (e.g., predation, disease, weather) and those that influence birth rates (e.g., nutrition, social factors). The hypothesis also requires that competition for resources (e.g., food, cover, and reproductive habitats) not affect fish and wildlife populations, even when those resources are diminished by habitat loss. Thus, the fundamental assumption of the Vacant-Hotel Hypothesis is that density-independent mechanisms control most or all animal populations in the Arctic.

Clarifying Senner's views in terms of density-independent versus density-dependent population control provides the basis for testing his hypothesis. General ecological arguments can be made for or against various limiting factors acting in a density-dependent or density-independent manner. Competition is one such factor. Interspecific competition, the subject of much ecological literature and theory, is extremely difficult to demonstrate in the field (Wiens 1977). Intraspecific competition, however, may be orders of magnitude greater than interactions between species (MacNally 1983). Individuals within populations compete for resources unless resources are superabundant. Because environments vary over many temporal scales and may periodically exert severe stress or resource limitations on populations, resources may be superabundant during the recovery of a population from such an "ecological crunch," and competition may only occur intermittently (Wiens 1977). However, competition should exert density-dependent effects on fish and wildlife populations during periods of resource limitation. Those who espouse the Vacant-Hotel Hypothesis presume that scientists know the precise habitat requirements of arctic species and know the factors controlling their abundance. Both are necessary to unequivocally demonstrate species-specific relationships between animal populations and their habitats. In fact, however, scientists disagree about factors controlling populations, even for well-studied arctic species such as caribou (see reviews by Shideler [1986] and Shideler et al. [1986]). Nevertheless, we review pertinent ecological theory and specific studies of arctic species to suggest that habitat directly or indirectly limits the abundance of most arctic species.

Evidence Against the Hypothesis Based on Population Ecology

The Vacant-Hotel Hypothesis rests on Senner's (1989) assumption that arctic populations of fish and wildlife are controlled by factors that operate independently of animal density. Some population ecologists identify climatic factors as exerting density-independent effects in at least some cases (Odum 1971:196). Adherents of the Climate School of population control regard weather as determining population size; however, this school of thought has primarily been applied to insects (Krebs 1972:271-281), not arctic vertebrates. In addition, different factors may act to control abundance in individual species. For example, small animals in harsh environments might suffer significant mortality from severe weather whereas large animals in similar circumstances might remain unaffected (MacArthur and Connell 1966:131-142). One might successfully argue that a population of small organisms solely controlled by density-independent factors would be insensitive to habitat loss because increased population density engendered by such loss would not differ from increased density resulting from temporary abeyance of a density-independent mortality factor. This argument hinges on two necessary assumptions: no density-dependent factors other than ultimate energy limitations act upon the population, and the density-independent factor (or factors) operates with sufficient regularity to ensure that population density never reaches the limit of available resources. We believe few if any free-ranging vertebrate populations satisfy these assumptions.

In the specific case of a population of small vertebrates temporarily depleted by weather-induced mortality, there is no evidence habitat loss can occur without effect. Severe weather is a limiting factor, which acts to temporarily reduce the carrying capacity (see Appendix B) of the organism's habitat. By the same token, carrying capacity will be higher in years of moderate weather. Not only is it incorrect to say organisms permanently exist below carrying capacity when their population is temporarily depleted by density-independent factors (if such factors actually exist), habitat loss justified by such depletion would prevent the population from rebuilding to its former abundance during years of higher carrying capacity. The cumulative effect of altering supposedly understocked habitats in response to natural fluctuations in animal numbers would be to incrementally decrease peak abundances over time.

Density independence is indicated only when the effect of an ecological force or process on an individual is unrelated to population density (Odum 1971:196). Some population ecologists do not accept the existence of density-independent factors. For instance, Andrewartha and Birch (1954 [in Krebs 1972:277-279]) do not distinguish between density-dependent and density-independent factors because they consider all components of the environment to exert influences related to animal density. If, for example, a large population occupied suboptimal habitat as well as optimal habitat, it might suffer a greater mortality rate from adverse weather than a small population occupying only optimal habitat. Andrewartha (1971:17-19) believes an individual organism's "chance to survive and multiply is determined by its environment" and believes the environment of an organism includes adjacent members of its population. Thus, Andrewartha recognizes that birth rates and death rates are influenced by animal density. In describing populations whose numbers are largely determined by weather, Andrewartha (1971:147-156) states, "the average density that is attained over any period of years depends on the relative rate of increase and decrease during the favorable and unfavorable periods, and the relative duration of the favorable and unfavorable periods." Andrewartha graphs these theoretical relationships for benign and harsh environments. These graphs admit the possibility of a population increasing until all food resources are used up, a condition most likely if favorable periods are long, if unfavorable periods are relatively mild, or if favorable periods are particularly beneficial. Finally, Andrewartha and Birch's (1984:8-13) current theory of environment incorporates the concept that the density of one generation of animals may affect the activity of environmental components on future generations in a positive, neutral (noninteractive), or negative fashion. For example, the effects of overbrowsing by one generation may adversely affect several succeeding generations, a negative interaction. Thus, we find it difficult to reconcile the Vacant-Hotel Hypothesis and its requirement for density independence with Andrewartha and Birch's (1984:3) theory of environment and its axiom that "the environment of an animal consists of everything that might influence its chance to survive and reproduce."

Even if weather were accepted to act in a density-independent fashion on at least some arctic species, the Vacant-Hotel Hypothesis would remain unconfirmed if other factors influenced populations in a density-dependent manner. In fact, large organisms in harsh environments, whose populations are not primarily controlled by weather, are controlled by interactions within the populations, by competing species, or by predators or parasites (MacArthur and Connell 1966:135). Density potentially affects all these population-regulating forces. Nearly all theories of population control have included density-dependent factors (Krebs 1972:269-287, McNaughton and Wolf 1973:193-240, Wilson 1975:82). Such factors, by definition, link population density with natality or mortality rates (or both). Displacement of individual organisms by habitat loss, coupled with the reduced area of habitat, instantaneously increases ecological density. The effects of increased density brought about by habitat loss may differ by species and the dynamics of affected populations. For example, one species might show reduced natality, another might suffer increased mortality, while individuals of yet a third might emigrate to another (potentially less favorable) area; all are population-regulating mechanisms (McNaughton and Wolf 1973:321) that may subsequently reduce local animal density to its original level with consequent reduction of the total population (if emigrants also suffer decreased net reproductive rates).

Predation is a classical example of a density-dependent factor acting on prey populations. Theoretical equations by Lotka and Volterra describe predator-prey cycles in which predator populations track changes in prey populations (Krebs 1972:248-250). Laboratory studies of predator-prey relationships, after some difficulty, established that stable oscillations can occur in experimental systems (Krebs 1972:250-256), and field studies have shown "that in some but not all cases the abundance of predators does influence the abundance of their prey" (Krebs 1972:260). Predators can respond to increased prey density by increasing prey consumption (a functional response) or by increasing predator numbers (a numerical response) (Wilson 1975:85). In either case, prey suffer greater predation as their density increases (McNaughton and Wolf 1973:251). McNaughton and Wolf (1973:276) conclude their review of predator-prey interactions, in part, with the following statement.

> Predator preference is influenced very strongly by energetic foraging efficiency associated with potential prey items. Efficiency is determined by energy spent in foraging and energy uptake. Energy uptake will depend on the amount of energy per prey individual, and the number of prey captured per unit time, clearly a function of the efficiency of predation and prey density.

Since cumulative loss of habitat would increase the ecological density of prey under the assumptions of the Vacant-Hotel Hypothesis (i.e., populations remain constant), it is difficult to believe that predators would not show a density-dependent response to potentially reduced search times and potentially increased efficiency of prey capture.

Competition for resources is another example of a density-dependent factor acting on populations. Resources, as defined by Andrewartha and Birch (1984:13,43-69), are food, water, oxygen, heat, and tokens (e.g., environmental cues or signals such as photoperiod). Food is often the resource proposed as limiting populations. Carnivores may be limited by food more often than herbivores (McNaughton and Wolf 1973:326); however, Caughley (1976 [in Andrewartha and Birch 1984:145-146]) concludes that "Whenever an ungulate population is faced with a standing crop of vegetation in excess of that needed for maintenance and replacement of the animals, an eruption and crash is the inevitable consequence." In contrast, Bergerud (1983) concludes that predation, rather than food, normally controls caribou populations. Whether ungulates are controlled by food or predation, the controlling factor acts in a way influenced by ungulate density (i.e., overgrazing occurs at high densities and the population crashes from starvation or increasing ungulate populations produce a numerical or functional response by predators as previously discussed). Similarly, for carnivore populations limited by food, recruitment may decline as carnivore density increases beyond that supportable by available prey (e.g., survival of wolf [*Canis lupus*] pups declines if summer food availability is inadequate [Packard and Mech 1983]). Food may also limit birds. Lack (1954 [in Krebs 1972:279-281]) believes that shortage of food causes density-dependent juvenile mortality in birds and thus controls their populations. He extends his view of population regulation to most vertebrates, consistent with the preceding carnivore example. Since the Vacant-Hotel Hypothesis requires that most or all arctic populations of fish and wildlife be controlled by factors operating independently of population density, resources in tundra wetlands would have to be superabundant for all species if the hypothesis were correct. Such superabundance appears unlikely for the resource needs of the majority of predator and prey species inhabiting arctic wetlands.

The dynamics of the affected population may also influence its response to habitat loss. For an expanding population, incremental habitat loss may not have an immediate effect, but the ultimate limit on population size (i.e., the potential maximum carrying capacity) will be reduced. This reduction can result both from loss of ecosystem productivity and from loss of space necessary to carry out necessary life-history functions such as nesting, breeding, rearing, overwintering, or simply avoiding predators. In addition, habitat loss can remove crucial, specialized resources necessary to support these life-history functions. The cumulative effect of habitat loss is to reduce potential carrying capacity even when a population is expanding, since such expansion indicates either increasing carrying capacity or a population that has had insufficient time to reach carrying capacity (Edwards and Fowle 1974). Population expansion (e.g., the Central Arctic Caribou Herd) neither provides a rationale for habitat loss nor for its dissection into units that fail to provide critical resources (Harris and Kangas 1988) or space for predator avoidance (Bergerud 1983).

For a stable population, however, increased density resulting from habitat loss may be short-lived as density-dependent factors act to reduce density to its former level. This tendency toward an equilibrium density has been experimentally verified for mollusks in a controlled environment (McNaughton and Wolf 1973:320-321). In natural systems, animal densities also tend toward dynamic, sometimes multiple, equilibria (e.g., ungulates - see Sinclair [1979*a*], Bergerud [1980]). Populations (and thus densities) usually are biologically controlled in ecosystems with high diversity and physically controlled in ecosystems with low diversity (Odum 1971:195-196). Species responsive to carrying capacity (*K*-responsive) stabilize their numbers around the environmental carrying capacity (McNaughton and Wolf 1973:199-201). Species not responsive to carrying capacity continue to increase until checked by depletion of resources, often followed by a decline in numbers (McNaughton and Wolf 1973:201-203). In either case, unusually high densities will sooner or later return to values that can persist under the influence of these biological (e.g., predation, parasitism, and pathogens) and physical (e.g., weather) controls. For example, Errington (1961:34-64) describes factors acting on populations of muskrats (*Ondatra zibethicus*): predation, inhibition of breeding at high densities, harvest, and disease. He states that "strong balancing trends . . . persist irrespective of many year-to-year differences in food and water conditions, differences in birth rates, and differences in other parts of the life equations of the muskrats." Errington (1961:89) further cautions managers not to winter excessive densities of muskrats because such densities risk an outbreak of disease. Sinclair (1979*b*) provides evidence for biotic controls (e.g., disease) holding ruminant populations below limits imposed by forage. Specifically, wildebeest (*Connochaetes taurinus*) and buffalo (*Syncerus caffer*) populations erupted following elimination of the viral disease rinderpest in the Serengeti. These populations increased until they reached a new equilibrium set by dry-season mortality (i.e., by limited forage) demonstrating that rinderpest formerly controlled wildebeest and buffalo numbers below limits imposed by forage. For arctic populations of wildlife subjected to loss of habitat and artificially increased ecological density, the net effect of a return to an equilibrium density, coupled with decreased habitat area, is to reduce overall abundance of the affected population.

In the case where a population is declining, it is difficult to predict the effect of temporarily increased density, but a negative influence is likely. A density increase could accelerate the decline through further depletion of a limiting resource, for instance forage. Since a decline signals decreased carrying capacity (Edwards and Fowle 1974), increased density induced by habitat loss and displacement of individuals reasonably can be assumed to further stress the population. This could be further exacerbated by interspecific competition or immigration of conspecifics to the declining population. Returning to the case of increased density resulting from loss of habitat and displacement, we examine several possibilities. For example, in an ungulate population declining due to a high level of predation, increased prey density may facilitate predation. Bergerud (1983) discussed increased search time for wolves at low caribou density and the possibility that wolves switch to alternate, more abundant prey (e.g., moose) under such conditions. Gasaway et al. (1983) found predation to act in "an inverse density-dependent fashion" so that its effects were more significant in a declining population than in a high population. This is different than, although not necessarily inconsistent with, the preceding point. In either event, since carrying capacity is not constant and is, to an extent, amenable to manipulation (e.g., through harvest management, predator control, habitat improvement, etc.), habitat loss in a declining population would adversely affect, and could potentially prevent, recovery of its former abundance.

Population ecology provides general evidence that most or all factors controlling animal populations act in a way influenced by animal densities, which contradicts the density-independent population control required by the Vacant-Hotel Hypothesis. Nevertheless, we must rule out the possibility that most or all arctic populations of fish and wildlife are controlled in different ways than those occurring elsewhere. Evidence from the ecology of these species can help answer this question.

Evidence Against the Hypothesis Based on Shorebird and Waterfowl Ecology in the Arctic

Senner (1989) asserts, without citation, that "there is no known evidence that arctic wildlife populations are limited by arctic habitat availability." He bases many of his arguments on his perception of animal-habitat relationships and population control in shorebirds and waterfowl. Senner presents two main arguments: the brief arctic summer "imposes limits on the extent to which birds are able to utilize tundra habitats successfully for nesting" and "factors outside of Alaska and the Arctic" control populations of migratory birds. We evaluate his evidence and present the opposing viewpoint in the following discussion.

Length of Breeding Season: Senner believes that weather-influenced variation in the length of the breeding season is "more important than any other [factor] in determining reproductive success." He refers to the lower percentage of young-of-year tundra swans (*Cygnus columbianus*) in Atlantic winter populations breeding in northern Alaska and the Northwest Territories than in Pacific winter populations "produced in the Yukon-Kuskokwim Delta and areas further south" as evidence for his position. Senner continues his discussion by linking "the brevity of the arctic summer" to breeding densities of waterbirds. He states that most North Slope waterbirds occur at their northern limits of distribution and that North Slope habitat is "marginal for many bird species," implying such habitat is expendable. Senner further obscures the relative importance of specific North Slope wetlands by comparing the low breeding density of ducks on the entire Coastal Plain of the NPR-A with those of the somewhat different Yukon-Kuskokwim Delta and the very different Yukon River Flats and neglects the value of arctic wetlands as alternative habitats for waterfowl subjected to drought in the Prairie Region. Finally, Senner offers no evidence that loss of nesting habitat and thus loss of waterfowl production in the Arctic is somehow offset by increased (compensatory) production in more favorable environments, particularly since available habitat and territorial behavior already impose limits on breeding density in optimum environments such as the Yukon-Kuskokwim Delta (Mickelson 1975) (or did prior to the decline of Yukon-Kuskokwim goose populations).

Although several authors have reported smaller broods for the North Slope than for Bristol Bay (Lensink 1973) or the Yukon-Kuskokwim Delta (J. King 1970), this cannot be extended to argue that North Slope habitat is expendable, particularly because it supports an entirely different and discrete population. In fact, J. King (1970) characterizes North Slope tundra swans as important to the eastern (Atlantic) population based on observed cygnet production. Although the following passage from J. King emphasizes the value of North Slope habitat for geese, similar reasoning applies to tundra swans.

> By use of the aircraft we were able to get a more comprehensive picture of the goose populations of the Arctic Slope than have ground-bound observers in the past. Our observations, though scattered over a wide area, when totalled indicated that this area is making a valuable contribution to the continental goose population. The value of such low density habitat may be underrated. Such dispersed production may be of real value in years when the high density production areas fail.

Further, except for several species having long incubation and fledging periods (e.g., tundra swans [Lensink 1973] and loons (*Gavia*) [Johnson and Herter 1989:1-10]), Senner's assertion that length of the breeding season controls reproductive success in waterbirds is totally implausible. In general, ducks and many other migratory species are flexible and adaptive enough to survive adverse weather. For example, even though northern pintails (*Anas acuta*) may occasionally desert nests when subjected to late snow storms, most nest failures are due to predation (Alison 1975, Bellrose 1980:271-273). Similarly, most nest failures experienced by oldsquaws are due to predation (Bellrose 1980:392). This is not surprising since predators have been identified as the most important cause of nest losses for ducks in other regions (e.g., the Prairie Pothole Region [Klett et al. 1988]) as well. Brood size in small Canada geese (*Branta canadensis hutchinsii-parvipes*) can be affected by late snowmelt, but energy reserves of geese arriving on the breeding grounds may primarily control clutch size and incubation success (MacInnes et al. 1974). Variation in the length of the breeding season does not control reproductive success for most waterbirds on the North Slope.

Species whose northern limits of nesting distribution fall on or near the North Slope may exhibit lower density or productivity there than at more central points within their distribution, consistent with the view of Andrewartha (1971:6-10) that distribution and abundance are two aspects of the same phenomenon. Alternatively, the fact that some species reach their distributional limits on the North Slope may simply reflect the geographic distribution of their habitats (i.e., no landmass lies farther north in this portion of the North American Arctic). Simply describing the abundance (density) of an organism cannot address the question of which ecological factors determine its abundance. Derksen et al. (1981) specifically state, in a passage quoted by Senner, that wetlands south and west of the Arctic Coastal Plain are more productive than the Coastal Plain itself, where breeding density of ducks is low. Senner apparently sees no linkage between wetland productivity and duck density, a point we believe Derksen et al. (1981) were making in the quoted passage. Since ecological productivity is lower in the Arctic than in more southerly locations (see "Arctic Wetland Functions" section), we are not surprised that ducks nest at lower densities in the Arctic. In fact, these lower densities are strong evidence that ducks are limited by habitat.

Although the harsh arctic environment may affect waterfowl productivity, some species are well adapted to these conditions and have their central distributions in the Arctic. King eider (*Somateria spectabilis*), oldsquaw, snow goose (*Chen caerulescens*), and brant (*Branta bernicla*), for example, nest in the Canadian High Arctic at much higher latitudes than the North Slope of Alaska (Bellrose 1980:171, 367, 388; Reed et al. 1989). Although the Yukon-Kuskokwim Delta may provide optimum low-arctic habitat for brant (J. King 1970) and formerly produced many of the Pacific Flyway brant (Bellrose 1980:173), colonies there have declined in recent years (King and Derksen 1986, Raveling 1989). Brant production in the Arctic, including the small amount that occurs on Alaska's North Slope, has become more important to the Pacific

Flyway population. Brant nesting in the High Arctic experience a periodically high probability of breeding failure (Reed et al. 1989), a characteristic Senner overemphasizes for southerly North Slope waterfowl. Temporal uncertainty producing nesting failures in some years may be offset by high production in years of favorable conditions. The important point is that even in the High Arctic breeding success of brant is sufficient to maintain a significant breeding population. Thus, an individual recruited to a population from marginal range is no less significant than an individual recruited from optimal range since species abundance is a function of numbers rather than the origins of production, an argument for not considering marginal habitat expendable.

Senner cites the potential breeding density of 2.8 ducks•km^{-2} recorded by aerial survey in 1977 and 1978 for the coastal-plain portion of the NPR-A (R. King 1979 [in Derksen et al. 1981]) but does not discuss the fact that Derksen et al. (1981) recorded potential "breeding densities of 8.9 to 19.2 km^{-2} in 1977 and 9.8 to 11.7 km^{-2} in 1978" by ground surveys in the same area. This is not only a comparison of a generalized wetland province (Coastal Plain) with two specific wetland complexes (both associated with rivers) noted for waterfowl production, but also presents a simplistic, homogeneous view of areas that are latitudinally as far apart as Kansas and northern Minnesota (e.g., North Slope versus Yukon-Kuskokwim Delta) and cover areas as large as West Virginia (e.g., Yukon-Kuskokwim Delta), Maryland (e.g., Yukon Flats), and New Hampshire and Massachusetts (e.g., North Slope). The Yukon-Kuskokwim Delta "is one of the continent's great waterfowl nurseries," and the Yukon Flats is "Alaska's second largest duck factory," together accounting for about one-half of Alaska's duck production (R.H. Smith et al. 1964). Further, the richness of the Yukon-Kuskokwim Delta is dependent upon marine influence (tides range up to 9 feet in the Delta [J. King 1970]) that makes the North Pacific and southern Bering Sea coasts "one of the richest and most-extensive intertidal habitats of the world" (King and Derksen 1986) and is enhanced by nutrient enrichment from the huge Yukon River basin. Comparing several of North America's most productive waterfowl areas with the coastal-plain portion of the NPR-A is thus inappropriate. Senner might more appropriately have used the Colville River Delta, characterized by Meehan and Jennings (1988) as "unique along the Alaskan Beaufort Sea coast," for his comparison because it supports tundra swans, black brant, yellow-billed loons (*Gavia adamsii*), and greater white-fronted geese (*Anser albifrons*) at higher densities than occur in surrounding coastal-plain areas.

It is a mistake to conclude that low nest density on the Coastal Plain renders arctic wetlands unimportant for waterfowl production or population maintenance, particularly because low density over a huge area represents a large number of waterfowl. For example, about 5.4 million waterbirds used the Coastal Plain in the NPR-A alone in 1977 and 4.9 million waterbirds in 1978 (Derksen et al. 1981). Approximately 275,000 ducks (dabblers and divers) were estimated for this area in 1977 and 123,000 ducks in 1978 (R. King 1979). Subsequent comparative analysis of these data using visibility factors (corrections) recommended for ducks by the U.S. Fish and Wildlife Service yielded an estimate of about 423,000 ducks for 1977 as compared to a 1987 estimate of approximately 428,000 ducks (Rod King, Wildl. Biol., U.S. Fish and Wildl. Serv. Migr. Bird Manage., Fairbanks, pers. comm. [file data]). Totals for the entire Alaskan Coastal Plain would be somewhat larger as shown by recent waterbird-survey data. Ducks totaled approximately 622,000, 817,000, 888,000, and 1,010,000 respectively in 1986 through 1989 for the Arctic Coastal Plain of Alaska. During the same period, geese numbered approximately 173,000, 112,000, 112,000, and 169,000; swans numbered approximately 7,000, 5,000, 8,000, and 12,000; and loons were estimated at approximately 29,000, 28,000, 35,000, and 33,000 individuals (R. King 1989: pers. comm. [file data]). For ducks and other waterbirds nesting only in the Arctic, arctic wetlands are crucial regardless of densities elsewhere. Senner's analysis lumps duck density for all species, which obscures the importance of arctic wetlands to individual species. For example, king eiders breed in tundra areas along the Beaufort Sea coast (Meehan 1986*d*, Johnson and Herter 1989:81-82) but do not breed in the Interior (e.g., Yukon Flats) (Gabrielson and Lincoln 1959:221-223). It makes little sense to compare duck densities between areas with different species compositions and habitat requirements.

Drought in the Prairie Region can cause breeding populations of ducks to plummet (A.G. Smith et al. 1964). Northward displacement of ducks to the Arctic occurs during droughts (Hansen and McKnight 1964) when the Arctic Coastal Plain provides a stable environment in terms of water levels (Derksen and Eldridge 1980). Ducks distributed so that they can use both the Prairie Region and the Arctic, as conditions warrant, have apparently evolved a strategy that at least partially compensates for the different environmental uncertainties characteristic of each region. Pintails, for example, have evolved a strategy to take advantage of temporary and spatially unpredictable food resources (Johnson and Grier 1988), expressed as gregarious foraging and high mobility on a continental scale. They are characteristically found in grassland areas with abundant sheetwater and brief richness of invertebrates. When pintails encounter dry conditions in their central-prairie breeding range, they are drawn to northern-tundra regions that provide those same habitat requirements. Although the energetic costs of the pintail's drought-overflight strategy is such that displaced ducks generally do not retain sufficient reserves for a significant reproductive effort in the Arctic, this strategy provides population benefits: the flux of pintails into the Arctic during drought years greatly enhances their survival, without necessitating a major shift in foraging ecology or habitat types, and emigration of nonbreeders from the main prairie breeding grounds reduces competition and depletion of scarce food resources for breeders and broods that remain there (Calverley and Boag 1977). Derksen and Eldridge (1980) reported that in 1977 an estimated 6% of the continental population of pintails summered on the North Slope during a severe drought in the prairies, nearly doubling pintail density at coastal sites over previous years. Only 0.7% of the continental pintail population used the North Slope in 1978 when drought did not occur in the prairies. Since the onset of a major drought cycle in 1980, a growing proportion of the shrinking North American pintail population has been harbored in the

Arctic, surviving to reproduce when conditions improve. In 1988, Alaska summered a record 60% of surveyed pintails (20% is normal) of which over 18% ended up on the North Slope. In the last 4 years (1986-1989), North Slope pintails have comprised 5.0%, 10.2%, 11.0%, and 15.8% of surveyed North American pintails (R. King, pers. comm. [file data]). With the population dropping to its fifth record low in the last 7 years, universal restrictions on hunting, and massive international habitat-restoration programs, the survival value of the Arctic's seasonally-rich wetlands to pintails and their modest production in the far north have grown in significance beyond previous expectations.

From the perspective of human use, as well as from an ecological perspective, production from specific waterfowl populations cannot necessarily be replaced by production occurring in other areas. Waterfowl populations breeding and wintering in specific locations and migrating along specific pathways may be used for subsistence, sport hunting, and nonconsumptive purposes. Those particular users might not have access to other waterfowl populations to supply their needs. Thus, while certain populations may, in fact, nest in uncertain environments of low productivity, neither the population nor its habitat can be considered expendable. Maintaining nesting habitat for waterfowl is important in an uncertain environment in order to maximize waterfowl production in years with favorable weather conditions and to provide an adequate diversity of microhabitats, in which nesting may occur, to ameliorate the effects of suboptimum weather conditions.

<u>Factors Outside Alaska</u>: Senner's second major point is that factors outside Alaska control populations of migratory birds, indirectly using low densities of migratory birds on the North Slope as evidence for his position. Because migrating and wintering shorebirds often are concentrated in small areas vulnerable to disruption by habitat modification outside Alaska, Senner apparently takes the short-term view that such disruptions or catastrophic losses of overwintering birds from disease or pollution are irreversible and thus there is no need to maintain arctic breeding habitat. He does not recognize that production and survival of young birds on the North Slope would be essential for rebuilding affected populations following an episode of disease or pollution. Senner then concludes, without presenting evidence, that the "amount of summer habitat available does not currently appear to control . . . [the] size or productivity" of shorebird populations. His thesis hinges upon sufficient destruction of wetlands in temperate and tropical areas, or mortality from other factors, to render habitat losses in Alaska moot; however, habitat-conservation efforts in countries supporting overwintering shorebirds should not be discounted or rendered ineffective by allowing unnecessary losses of breeding habitat in the Arctic.

Some studies of population control in shorebirds are available. Evans and Pienkowski (1984) review the literature of shorebird population dynamics, drawing heavily on European studies, and conclude that weather, rather than resources, may control shorebird populations in a largely density-independent manner. Baker and Baker (1973) suggest that among adult shorebirds more mortality occurs off the breeding grounds than on the breeding grounds whereas mortality in young of the year is approximately equal on and off the grounds. They view nest failure from starvation or predation of young to be independent of density during the breeding season. These findings are consistent with the Vacant-Hotel Hypothesis, provided weather, starvation, and predation reduce shorebird populations independently of density and frequently enough to prevent occupancy of all available breeding habitat, but neither prove nor disprove the hypothesis. In contrast, evidence from Alaska's North Slope includes Holmes' (1970) conclusion for dunlin (*Calidris alpina*) that territoriality exerts "some control . . . within the breeding population" and his finding that previously excluded birds replaced individuals removed from their territories, indicating fully stocked nesting habitat. MacLean (1980) discusses "striking year-to-year differences in growth rates and survival of wader young" on the North Slope, which "appear to be closely related to weather conditions" during the period when adult insects emerge. For example, Holmes (1966*a*) observed fewer young dunlin and smaller broods in a year of food shortage. Adult insects are the primary food of newly hatched shorebirds, and emergence of adult insects is strongly influenced by mid-summer weather (MacLean 1980). MacLean (1980) states that predation accounts for most egg loss and loss of juveniles in shorebirds as well as the Lapland longspur, a tundra-nesting passerine. Since the number of chicks fledged is a function of number of clutches, clutch size, proportion of eggs hatching, and proportion of chicks fledging (Evans and Pienkowski 1984), factors such as territoriality, weather (either acting directly or affecting the availability of food), and predation cannot be excluded from consideration in the control of the North Slope's shorebird populations. Predation and food shortage are generally accepted as acting in a density-dependent manner, and this could be the case in shorebirds, but conclusive evidence is lacking on this point. For North Slope populations of shorebirds, the Vacant-Hotel Hypothesis can be neither confirmed nor rejected based on species-specific arguments concerning density-independent versus density-dependent population control. It is clear, however, that the blanket assertion that only factors acting outside the Arctic influence shorebird populations is incorrect because it does not consider the relationship between the arctic environment (physical and biotic) and recruitment to shorebird populations.

Migrating and wintering shorebirds are highly vulnerable to habitat loss and pollution events such as oil spills. Although large aggregations of shorebirds occur during migration (Senner and Howe 1984), shorebirds exhibit diverse migration strategies and systems (Morrison 1984). Within species, adults of one or both sexes may migrate southward before their young, and migration timing also differs between species (Holmes and Pitelka 1968, Myers 1981*a*, Morrison 1984). Similarly, one sex may migrate northward in the spring before the opposite sex if early arrival on the breeding ground is advantageous in obtaining breeding sites (Myers 1981*b*). The distribution of migration routes (Morrison 1984) and timing for various shorebird species, and sex and age classes within species, reduces the probability that catastrophe will simultaneously affect all arctic-nesting species or even entire populations of single species during migration. Likewise, shorebird species do not all winter in the same location, which spreads the risk of catastrophic disruption. Meehan (1986*d*) lists lesser golden-plovers (*Pluvialis dominica*) as wintering in South American grasslands and North Slope dunlin as wintering along the Pacific coast of Asia (e.g., the coasts of the Sea of Japan and Yellow Sea [Johnson and Herter 1989:173]). Baird's sandpiper (*Calidris bairdii*) winters in the Andes Mountains in South America (Johnson and Herter 1989:169) after migrating east of the Rocky Mountains and across the Gulf of Mexico (Morrison 1984). "The pectoral sandpiper [*Calidris melanotos*] winters from southern Bolivia, Paraguay, northern Argentina, and Uruguay south to south-central Argentina (Marchant et al. 1986)" (Johnson and Herter 1989:171). Semipalmated sandpipers (*Calidris pusilla*) migrate across North America to the east and west coasts of South America (Morrison 1984). Red phalaropes (*Phalaropus fulicaria*) spend up to 75% of the year at sea as the most pelagic of all shorebirds, often using offshore routes for migration (Burger 1984). From these few examples, and without discounting the importance of winter habitat to shorebird populations, it is clear that North Slope shorebirds are unlikely to simultaneously suffer disaster on their wintering grounds because they winter in different places. Moreover, territoriality in nonbreeding shorebirds spaces individuals of some species on wintering grounds in California and Argentina (Myers et al. 1979), which may further reduce their vulnerability to catastrophic mortality.

Waders maximize lifetime reproductive output by repeated attempts to produce young with "relatively small parental investments" (Evans 1981). This sort of reproductive strategy requires relatively long-lived individuals. In fact, annual survival of adult shorebirds is high. Winter mortality is normally low, even for waders wintering in Europe (Goss-Custard 1980), although severe weather can produce mortality in species wintering at temperate latitudes (Davidson 1981, Evans 1981). Predation can also be a significant source of winter mortality. Raptors took 21% of dunlins, 12% of least sandpipers (*Calidris minutilla*), 8% of western sandpipers (*Calidris mauri*), 13% of sanderlings (*Calidris alba*), and 16% of dowitchers (*Limnodromus*) on a California coastal lagoon (Page and Whitacre 1975). Buchanan et al. (1988) found that merlins (*Falco columbarius*) took dunlins on 22.5% of hunting flights on the Washington coast but did not evaluate the significance of predation on the prey population. In contrast, survival rates of up to 95% have been observed for shorebirds between their departure from California wintering rounds and subsequent return following breeding and fall migration (J.P. Myers, pers. comm. [in Morrison 1984]). This is consistent with the view of Baker and Baker (1973) that the majority of adult mortality occurs off the breeding grounds. Although Goss-Custard (1980) constructed a model showing the importance of small, possibly density-dependent, winter mortality to wader populations, he assumed that territorial behavior during breeding controlled maximum population size. Arctic nesting habitats are fully stocked for at least some territorially breeding shorebird species (Holmes 1966*b*); therefore, incremental losses of wintering habitat with consequently reduced survivorship would not immediately reduce North Slope nest densities because surplus nonterritorial adults would act as a buffer. With further reductions in winter survival, it is possible that decreased nesting populations would be accompanied by increased breeding-territory sizes and greater available food resources per pair with increased survival of young. Again, arctic wetlands would be crucial to production of these young. Thus, despite the importance of habitat loss and mortality factors operating on shorebird populations outside the Arctic, we see no evidence that these factors alone control shorebird populations.

Senner states, *a priori*, that the dispersed pattern of nest distribution for many shorebirds in arctic-tundra habitats means such habitats do not limit populations of these species and incorrectly implies "dispersed" nesting is nesting that does not occupy or otherwise use all available habitat. Low-density, dispersed nesting, in his view, arises from the Vacant-Hotel Hypothesis: a limited number of birds distribute themselves over a surfeit of appropriate habitat because their populations are controlled by winter mortality outside Alaska. In contrast, Watson and Moss (1970) conclude some evidence exists that dominance and spacing behavior limit populations of wild vertebrates and that these behaviors are affected by nutrition. Watson and Moss considered behavioral limitations on breeding populations as ultimately limiting total populations. In the case of shorebirds, Pitelka et al. (1974) explicitly state that "monogamous breeding pairs are dispersed evenly over suitable habitat by territorial systems," and "This implies that the territorial system actively distributes birds over the habitat in relation to resources and that the wide spacing is not simply the result of low population size." These authors discussed dunlin, Baird's sandpiper, and semipalmated sandpiper in northern Alaska and dunlin and western sandpiper in western Alaska as examples of monogamous species with relatively stable breeding densities and territory sizes within specific geographic areas. In Greenland, Meltofte (1985) similarly describes ringed plover (*Charadrius hiaticula*), sanderling, and dunlin as occupying all suitable habitats. Pitelka et al. (1974) believe that 15 of 24 calidridine species exhibit territorial, monogamous breeding systems. Using dunlin as an example, territorial behavior proximately controls breeding density (Holmes 1966*b*), regardless of the potential ultimate role of food in setting territory size, and sets an upper limit on reproductive output because dunlin clutch size is constant (Holmes 1970). Male dunlin removed from territories in experiments at Barrow were immediately replaced by other males, indicating a fully stocked habitat (Holmes 1970). Finally, Troy (1988) reports that nest densities for common avian species in the Prudhoe Bay area, away from oilfield facilities, "were remarkably constant over the 4 years of investigation; no species exhibited statistically significant changes in nest abundance." Unlike nest densities, the observed abundances of these species did fluctuate between years. Troy examined five hypotheses for explaining these differences and concluded that "Changes in abundance of birds appear to be due to the presence or absence of nonbreeding birds, with more birds being present when snow[-] and ice[-]free areas are widespread during early June." The presence of nonbreeding components in shorebird populations potentially is inconsistent with the Vacant-Hotel Hypothesis, if the nonbreeding components are capable of breeding but are prevented from doing so by deficiencies in habitat quantity or quality. Thus, factors outside the Arctic cannot be the sole determinants of shorebird populations.

Although Senner claims that factors outside Alaska control migratory bird populations using shorebirds as his example, waterfowl populations provide contrary evidence. Most (80%) California wetlands were lost prior to 1920. By 1939, only 15% of Central Valley wetlands remained (Frayer et al. 1989). Nearly complete (91%) loss of the Central Valley wetlands of California, which winter 60% of Pacific Flyway waterfowl, had occurred by 1985 (Frayer et al. 1989), and California pintails had declined (J.C. Bartonek, U.S. Fish and Wildl. Serv., waterfowl surv. data summary [1985]). Despite this fact, California maintained large winter populations of mallards (*Anas platyrhynchos*) (0.65 million) and pintails (3.5 million) through the early 1970's (J.C. Bartonek, U.S. Fish and Wildl. Serv., waterfowl surv. data summary [1985]), demonstrating that loss of winter habitat was not the only factor controlling Pacific Flyway waterfowl populations. In contrast, widescale agricultural destruction of breeding habitat in prairie wetlands (e.g., >90% of the basins in Alberta have been affected by agriculture), coupled with drought, precipitated major declines in duck populations. These declines occurred because farmers draining wetlands did not see incremental wetland losses as affecting breeding populations. Since we know that pintails (the most abundant arctic dabbler) maintained healthy populations after substantial loss of wintering habitat but declined after substantial loss of breeding habitat, we infer that breeding-ground conditions are the most important factors controlling pintail populations. Sea ducks, also abundant arctic breeders that predominate on the North Slope, winter in marine waters; the availability of staging and winter habitat is not an issue for these species except when oil spills threaten large expanses of their winter range. Thus, breeding conditions are important determinants of waterfowl populations for arctic-nesting species.

Habitats and Habitat Use in Alaska: Senner does not differentiate between the many different types of wetlands that occur on the North Slope. He does not present any evidence that he examined species-specific habitat requirements or the abundance of appropriate microsites for nesting in reaching his conclusions, despite the fact that several wetland classification systems employing from 8 to 20 classes are commonly used for this area (Bergman et al. 1977, Walker et al. 1980, Meehan 1986*a*). His focus on nesting densities for shorebirds neglects the importance of wetland habitats used for other life-history functions. Senner also does not address species-specific distribution with respect to the Beaufort Sea coast or other geographic components of habitat or discuss philopatry or nest-site fidelity in relation to shorebird use of arctic-wetland habitats.

By lumping North Slope wetlands and not differentiating crude density (organisms•unit total space^{-1}) and ecological density (Odum 1971:163), Senner contrasts the low crude densities of some nesting shorebirds with the large area of summed wetland habitat and infers habitat abundance precludes habitat limitation. Pitelka et al. (1974) describe this view of tundra as a homogeneous habitat as "a popular misconception" when, in fact, tundra is a mosaic of microhabitats with greatly differing prey densities and structural characteristics of significance to shorebirds. For example, shorebirds have species-specific nesting requirements, and stocking of appropriate habitats can only be determined by comparing species-specific nest densities to the availability of their respective nesting habitats. In the Prudhoe Bay area, lesser golden-plovers nest "in dry habitats, either in upland areas or dry microsites of wet areas"; semipalmated sandpipers nest in "moist, low-relief low-centered polygons and in wet strangmoor"; and "Pectoral Sandpipers preferred wet tundra/non-patterned ground, aquatic tundra/non-patterned ground and aquatic tundra/strangmoor during the breeding season" (Meehan 1986*d*). MacLean (1980) describes the distribution of breeding habitats of birds along a mesotopographic gradient near Barrow, demonstrating species-specific differences in habitat requirements. Because arctic-nesting birds are distributed across a mosaic of habitats, any given species may occur at low crude density, depending upon its characteristic ecological density and the amount of appropriate habitat in the area in question. For this reason, it is instructive to examine summed bird densities found in arctic-tundra wetlands. Although Senner cites densities of less than 1 nest•km^{-2} to 21.5 nests•km^{-2} for "waterfowl and shorebirds" on the North Slope, apparently referring to individual species, total shorebird density exceeds 2.5 birds•ha^{-1} (250 birds•km^{-2}) in preferred breeding habitat near Barrow (Myers and Pitelka 1980). Nest densities for 14 species at a study plot in the Kuparuk Oilfield were 67 nests•km^{-2} in 1988 and 66 nests•km^{-2} in 1989. Bird-sighting densities during five surveys on the study plot over the 2 years ranged from 218.4 to 319.4 birds•km^{-2} for all 24 species present and from 99.0 to 176.7 birds•km^{-2} for 10 species of shorebirds alone (U.S. Fish and Wildl. Serv. Northern Alaska Ecol. Serv., unpubl. data: letter Sousa to Kakel, 23 April 90). Troy (1988) reported that bird densities for 36 species on his undisturbed plots averaged 223.9 birds•km^{-2} over 4 years of study near Prudhoe Bay whereas nest densities for 20 species averaged 61.5 nests•km^{-2}. Bird use of tundra wetlands thus is significant when species-specific habitat requirements are taken into account.

Similar evidence of species-specific habitat requirements is available for waterfowl and loons. Bergman et al. (1977) found that Pacific (*Gavia pacifica*) and red-throated (*Gavia stellata*) loons and black brant, king eiders, spectacled eiders (*Somateria fischeri*), and oldsquaws significantly prefer nesting in Deep-*Arctophila* (Class IV) wetlands at Storkersen Point on Alaska's North Slope. Red-throated loons also select Basin-Complex (Class VI) wetlands for nesting while oldsquaws select Shallow-*Carex* (Class II) wetlands and Beaded Streams (Class VII) in addition to Class IV wetlands. King eiders select Shallow-*Arctophila* (Class III) wetlands and Coastal Wetland (Class VIII) for nesting in addition to Class IV wetlands. These preferences are largely confirmed by Derksen et al. (1981). Similarly, in the Colville River Delta, yellow-billed loons occur in highest densities on Deep-Open (Class V) wetlands but use Class IV and VIII wetlands as well (North 1986). The relative abundance of specific wetland types must also be considered. In the Storkersen Point area studied by Bergman et al. (1977), for example, the highly valuable Class IV wetlands make up only 11% of total wetland area and some of the other preferred classes (e.g., III, V, VII, and VIII) are even less abundant. Species-habitat relationships in arctic wetlands therefore must be evaluated based on availability of preferred habitats for each waterbird species.

Habitat requirements for waterbirds change throughout the year. After nesting, for example, "adult sandpipers and their broods move from better drained breeding sites into lowland marshes" in response to food availability (Holmes and Pitelka 1968). Meehan (1986*a*) describes movements of shorebirds (e.g., juvenile dunlin [Holmes 1966*a*]) from breeding areas in tundra habitats to the littoral zone in July and August. Sanderling, ruddy turnstone (*Arenaria interpres*), and red phalarope use littoral habitats almost exclusively after leaving the tundra by early August (Connors et al. 1979). Martin and Moitoret (1981) report a "strikingly obvious" late summer shift of shorebirds to shoreline habitat in the Canning River Delta. A parallel argument can be made for post-breeding waterfowl. Some indication of the importance of arctic-wetland habitats for post-breeding waterfowl is provided by Kiera (1984). Brant arrived in a salt marsh near Prudhoe Bay beginning in mid-August, fed 77% of daylight hours, consumed 283 $\text{gdw}\cdot\text{day}^{-1}$ of vegetation, and exerted a grazing pressure of 373 $\text{goose-days}\cdot\text{ha}^{-1}$. This pressure was believed near the limit set by available forage. Likewise, the Teshekpuk Lake area in the NPR-A provides molting habitat for about one-fifth of the entire black brant population and supports up to 50,000 molting geese of four species (Derksen et al. 1981, King and Derksen 1986). On the coast, oldsquaws molt in large lakes, lagoons, and protected bays (Johnson 1985, Meehan 1986*a*, Johnson and Herter 1989:95-100), and up to 325,000 snow geese stage for fall migration in the ANWR (Garner and Reynolds 1986:141-153). Selection of these habitats by waterfowl indicates they present locally optimal conditions for relevant life-history functions. In addition, waterfowl traditionally use certain sites (e.g., snow goose and brant colonies, waterfowl molting areas, and staging sites), which restricts their use of potentially available habitats. We know little about the specific characteristics of these initially selected areas, but we cannot assume that waterfowl will shift their use to other sites if displaced by development or that alternative areas would provide optimal habitat. Although availability of post-nesting and traditionally used habitats have not been conclusively shown to limit populations, displacement of individuals to suboptimal habitats likely would adversely affect their energy balance and survival.

Species-specific distributional patterns indicate wetlands near the coast of the Beaufort Sea have relatively higher values to some waterfowl and shorebirds than do inland wetlands. For example, Spindler et al. (1984) found that habitat classes did not explain variability in grouped-shorebird and pectoral sandpiper numbers as well as did study-site distances from the coast. These birds use littoral habitats following nesting and thus distribute themselves within an accessible distance from the coast. Martin and Moitoret (1981) found a saline meadow in the Canning River Delta supported a higher concentration and diversity of bird species than upland, lowland, and mosaic habitat plots. Migrating shorebirds and waterfowl were particularly attracted to coastal wetlands. Likewise, Meehan (1986*a*) describes the distribution of selected geese, tundra swans, and loons in relation to physiographic features such as rivers, river deltas, and the Beaufort Sea coast. For example, common eiders (*Somateria mollissima*) are nearly all restricted to barrier islands for nesting along the coast of the Beaufort Sea (Schamel 1974, Johnson and Herter 1989:77-79).

Spectacled eiders are distributed mainly west of the Colville River, with greatest nesting numbers on the Yukon-Kuskokwim Delta, but extend eastward to Demarcation Point (Gabrielson and Lincoln 1959:225-226, Johnson and Herter 1989:87-88). The North American distribution of king eiders is centered in Canada, but their center of abundance in Alaska extends westward to the Colville River (Johnson and Herter 1989:81-82). Waterfowl, particularly ducks, orient toward coastal habitats as shown by surveys in the NPR-A (R. King 1979). Species-specific distribution patterns reflect habitat and ecological requirements that cannot be met elsewhere on the North Slope, demonstrating the folly of lumping species and habitats to conclude that the availability of wetland habitat does not limit shorebird and waterfowl abundance.

Finally, shorebird use of wetland habitats is affected by fidelity to birth sites and previous nest sites. Jehl (1973) found that experienced (i.e., those having previously nested) stilt sandpipers (*Calidris himantopus*) that reunite with their mates return either to nest scrapes occupied the previous year or to sites very near to the old scrapes (e.g., 12, 18, 21, and 76 m distant). Renesting pairs spend less time in pre-nesting behavior and rapidly nest in their old territory, which is advantageous in producing early chicks that can feed during the optimum period before the tundra dries excessively (Jehl 1973). Nearly simultaneous arrival on the old territory appears to account for mate fidelity in stilt sandpipers, and individuals do not nest if a mate fails to return (Jehl 1973). Western sandpipers also show fidelity to former nest sites. For returning males (58%), Holmes (1971) found a mean distance of 38 m between consecutive nest sites, and some individuals reused the same nest cups in consecutive years. Unlike stilt sandpipers, western sandpipers breed even if returning birds are not reunited with previous mates (Holmes 1971). Semipalmated sandpipers also exhibit return rates of 33 to 57% for females and 37 to 57% for males with a few pairs using nestcups from the previous year (Gratto et al. 1985). As in western sandpipers, semipalmated sandpipers that acquire new mates nest successfully although hatching dates can be delayed (Gratto et al. 1985). Oring and Lank (1984) conclude that site tenacity "is greatest in the species and sexes with the greatest competition for territories."

Natal philopatry, the return of breeders to natal nest sites, is less apparent in most shorebird species because young tend to disperse (Oring and Lank 1984). For example, Gratto (1988) showed that only 33% of yearling semipalmated sandpipers breeding on her study area had been banded there as nestlings. Oring and Lank (1984) reported that for spotted sandpipers (*Actitis macularia*) 31 to 40% of breeding females and 17 to 21% of breeding males were locally hatched, but the majority of new breeders in Finnish dunlin were locally hatched. Western sandpipers also showed natal philopatry with 3% of banded nestlings returning to their place of origin (mean distance from hatching location = 156.3 m) to breed (Holmes 1971). Since this figure includes first-year mortality, assumed to be quite high, and the study plots totaled only 15 ha, the actual percentage of breeding western sandpipers of local origin probably was much higher.

Natal philopatry and nest-site fidelity may offer advantages to returning birds. Oring and Lank (1984) suggest these advantages include the following:

> (1) familiarity with environmental factors such as food, cover, and predators; (2) familiarity with conspecifics, including mates, relatives, and others; and (3) enhanced competitive ability stemming directly from increased self-confidence on its home turf (Hinde 1956).

Gratto et al. (1985) felt that return to a familiar area "could increase the probability of [nesting] success." Displacement of shorebirds by habitat loss is therefore likely to influence reproductive output of affected individuals. Although not a test of the Vacant-Hotel Hypothesis, the existence of natal philopatry and adult nest fidelity argues against the notion that displacement of shorebirds has no potential effect on shorebird numbers.

Resource Limitations: Pitelka et al. (1974) describe the evolution of four different social systems in calidridine shorebirds nesting in the Arctic and Subarctic. Dispersed nesting is part of the social system used by 15 of the 24 sandpiper species considered in their paper, and the authors suggest this social system is a conservative adaptation to the arctic environment. These species (e.g., semipalmated sandpiper, Baird's sandpiper, and dunlin) are characterized by strong territoriality, strongly monogamous pair bonds, and relatively constant abundance. In monogamous calidridine species defending large territories, "the defended area provides feeding sites that are free from competition from conspecifics; that is, the territory offers an exclusive food reserve that provides sufficient food for the breeding pair even during periods of food shortage" (Pitelka et al. 1974). The Vacant-Hotel Hypothesis requires that resources be superabundant because significant limitation of resources would violate the assumption of density-independent control of fish and wildlife populations. If resources were superabundant in relation to the density of migratory bird populations, one would not expect to find territorial behavior related to food but might find such behavior related to reproduction. However, if large amounts of vacant habitat were present, monogamous species with balanced sex ratios would have little need to incur the energetic costs of territorial maintenance. Territorial behavior limits population density, often in response to varying levels of resources such as food, particularly in those species maintaining territories for only short periods (Patterson 1980). Such limitation is not consistent with the Vacant-Hotel Hypothesis.

In addition to the monogamous system in which species follow a "conservative" reproductive strategy, non-monogamous species such as the pectoral sandpiper follow an "opportunistic" reproductive strategy. Opportunistic species, unlike conservative species, exhibit great fluctuations in distribution and density in response to local food abundance. Nonmonogamous species "occupy small territories packed into the more productive lowland marshy habitat, balancing the risk of breeding failure in the event of adverse weather against the probability of a very successful breeding effort if conditions remain favorable" (Pitelka et al. 1974). Not only can the evolution of both a conservative and an opportunistic strategy among shorebirds be interpreted as circumstantial evidence of resource competition (but see Wiens 1977, MacNally 1983), but the direct relationship between food abundance and reproductive success in opportunistic species underscores the importance of resources to shorebird production. Myers (1981*a*) offers a different interpretation of this evidence. He hypothesizes that sandpiper social systems evolved as an adaptation to differing migration distances for sandpiper species: long-distance migrants depart the breeding grounds earlier leading to development of single-parent care. Myers does not exclude a role for resource competition on the breeding grounds in determining calidridine social systems because the hypothesis of Pitelka et al. (1974) is not inconsistent with his own. Thus, evolutionary arguments related to sandpiper social systems do not provide conclusive tests of the Vacant-Hotel Hypothesis based on currently available data.

Several studies have shown that food is a limiting aspect of avian habitat in the Arctic. For example, Holmes (1970) found that dunlin occurred at much higher breeding densities in the Yukon Delta than near Barrow and concluded greater food abundance and availability in the Yukon Delta accounted for the different densities. This is consistent with the inverse relationships between prey density and feeding-territory size in birds developed by Schoener (1968). Likewise, Pitelka et al. (1974) state that "sandpipers are almost exclusively dependent upon tundra arthropods, mainly insects" while on the tundra, that arctic insect diversity is low and thus vulnerable to large variations in abundance, and that spatial distribution of food influences the dispersion and density of these birds. Similarly, Seastedt and MacLean (1979) found an inverse relationship between the size of Lapland longspur breeding territories and indices of resource densities for various habitats. Longspurs, like shorebirds, are insectivorous members of the detritus-based trophic system of arctic-tundra wetlands (MacLean 1980). Starvation of longspur nestlings occurs, particularly in years of bad weather, but predation is the major cause of mortality (MacLean 1980).

Waterfowl and loons also provide examples of territoriality functioning to allocate limited food resources, demonstrating that their arctic-wetland habitats are fully occupied (i.e., populations are at their environmental carrying capacity). For instance, the oldsquaw, the most abundant breeding duck on the North Slope, is strongly territorial (Alison 1975) and dependent upon invertebrate foods in tundra ponds and lakes (Taylor 1986). Drakes defend breeding territories that remain fixed in locality from year to year, even when defended by different individuals, which limits breeding density (Alison 1975). Alison (1975) describes female oldsquaws as nesting within range of their mate's vocalizations but not necessarily within their mate's territory. He believes the fixed number of adjacent territories and the vocalization constraint limit the potential number of nests in a particular colony and thus the potential for local depletion of food. In addition, a female feeds on her mate's territory even when her nest is located in a different drake's territory, distributing prey consumption prior to brood hatching. Likewise, tundra swans are highly territorial and defend areas of up to 1 to 2 km^2. Hawkins (1986) describes functional defense of scarce food resources early in the nesting season, foods for the pair and brood throughout the entire breeding season (June through August), and the significance of secure foods close to the nest. Red-throated, Pacific, and yellow-billed loons are territorial as well, particularly the latter two species. Bergman and Derksen (1977) discuss niche partitioning between Pacific and red-throated loons, noting the strong territoriality of Pacific loons and their dependence on pond invertebrates within those territories. For yellow-billed loons, which are highly territorial and exhibit interspecific aggression toward other loons, Sjölander and Ågren (1976), describe complete dependence on the breeding lake for feeding broods from limited sources of small freshwater fish and some plants near Alaktak (129 km SE of Barrow). North (1986) supports these observations and describes restrictive habitat-use patterns, competition, and foods of yellow-billed loons on the Colville River Delta. Red-throated loons frequently leave their territories to feed in the nearshore Beaufort Sea and to gather food for their young (Bergman and Derksen 1977); therefore, territoriality in this species is not likely to be related to food resources although distribution is closely linked to availability of nearby fish resources (Derksen et al. 1981). Nevertheless, a dispersed nesting pattern that apportions all or nearly all available resources through territoriality strongly implies the nesting population is limited by habitat availability.

Resource partitioning between sex and age classes can be viewed as evidence of resource limitations for shorebirds in arctic-tundra wetlands, although other interpretations are possible (see Myers 1981*a*). Holmes (1966*a*) found that adult dunlin prefer tipulid larvae in early and late summer, with weaker selection of chironomid larvae in midsummer, whereas young dunlin feed entirely on small, adult insects, mainly chironomid flies. He concluded adult and young dunlin select different foods and habitats in midsummer to reduce intraspecific competition at a time when food supplies are most variable. Holmes (1966*a*) observed other evidence of dunlin experiencing food shortage. In a year (1963) when prey availability in upland habitats was low in mid-summer, adult dunlin moved to the coast or prematurely started their southward migration. Remaining adults returned to tundra habitats in late summer as tipulid larvae became more abundant there. Likewise, Holmes and Pitelka (1968) postulated that interspecific competition for food might explain habitat preference, food preference, and timing of migration for dunlin, pectoral sandpiper, semipalmated sandpiper, and Baird's sandpiper. Although their diets broadly overlap, adult sandpipers show greatest species separation (based on diet) in late June "when insect diversity is maximal"; young sandpipers show greatest dietary separation in early August "when insect supply is declining rapidly and most young are completing growth." The adults of three species (semipalmated, pectoral, and Baird's sandpipers) migrate before their young and before adult dunlin. Holmes and Pitelka (1968) believed this early migration reduced both intraspecific and interspecific competition for food. Further reduction occurred through "partial habitat separation" between the two largest species (dunlin and pectoral sandpiper) and the two smallest species (Baird's and semipalmated sandpipers), "partial separation by modal size of prey," and "some habitat separation of young from remaining adults in the latter part of summer." Two of the species (dunlin and pectoral sandpiper) exhibited different strategies for coping with variable food supplies as reflected by different social systems.

Finally, studies of waterbird energetics potentially could shed light on the presence or absence of resource limitations in arctic-tundra wetlands. Energetic demands on waterbird populations are extremely critical on the nesting grounds; energy is needed for breeding, molting, and conditioning for fall migration. Canvasback ducks (*Aythya valisineria*), for example, have been shown to <u>gain</u> weight during fall migration, with time spent at migration stopover points related to fat reserves (i.e., birds with low fat reserves remain longer than heavier birds) (Serie and Sharp 1989). Juvenile shorebirds need large energy inputs for growth and to develop sufficient reserves for migration. Adults also need to make up any energy deficits associated with nesting activity. For example, semipalmated sandpipers exhibited generally negative energy budgets calculated over the summer season near Barrow (Ashkenazie and Safriel 1979). Stilt sandpipers do not gain weight prior to initiation of fall migration, and the females show continual weight loss during the summer (Jehl 1973). Hawkins (1986) cites literature describing selective grazing by geese "on protein-rich, newly emerging shoots and roots on spring staging areas" and describes similar behavior for a female (prelaying) tundra swan that grazed 10%•day^{-1}. She believes this behavior potentially is a "strategy to obtain protein for a clutch." Similarly, Taylor (1986) cites literature showing that breeding females of several species of duck "fed more intensively than their mates." Negative energy budgets do not prove that resource limitations exist, only that energy demands exceed energy intake. Nevertheless, it is difficult to reconcile the existence of negative energy budgets in nesting and post-nesting birds with the superabundance of resources required by the Vacant-Hotel Hypothesis. The availability of post-breeding feeding and rearing habitats and associated food resources potentially limits shorebird populations, even if it could be shown that nesting habitats were not fully stocked. Detailed energetics studies are needed to answer this question.

<u>Summary</u>: Shorebirds, waterfowl, and loons provide many examples of the relationships between arctic wetlands and animal populations. The Arctic Coastal Plain is a mosaic of habitats that meet the needs of these migratory species for reproduction, brood rearing, molting, and staging for the flights to wintering areas. The arctic summer is sufficiently long to allow successful rearing of waterbird broods. Although mortality of chicks can occur in particularly severe weather, which reduces food supplies such as emerging insects, predation of eggs and chicks is a major factor limiting reproductive output. Arctic-tundra wetlands also provide alternative habitat for waterfowl displaced by drought in the Praire Region.

Factors outside Alaska can influence waterbird populations; however, there is no evidence that factors acting within Alaska can be ignored since the rate of population increase is the difference between the rates of births and deaths. Winter mortality is only half the equation. In fact, shorebirds have low mortality rates and winter in widely distributed areas of Asia, the Pacific, and the Americas, lessening the probability of catastrophic losses in multiple species.

In the Arctic, nest densities of many waterbirds are relatively constant from year to year. Many shorebirds return to the same nesting territories, and some even to the same nest cup, perhaps gaining advantage from rapid and efficient nesting on familiar ground. Habitat preferences of waterbirds change during the summer to take advantage of food resources and to use optimum locations for molting and staging for migration, thus belying the view of tundra as a homogeneous expanse.

The role of resources such as food in controlling waterbird populations is uncertain, but adverse weather can affect the abundance and timing of emergence of insects upon which shorebirds feed. Social behavior that includes territoriality and resource partitioning between sex and age classes may be driven by factors related to migration distance in shorebirds, but these factors do not exclude a role for resource limitation in the evolution of such behavior. Generally negative energy balances in some nesting and post-nesting birds is not an indication of superabundant food resources.

From the standpoint of the Vacant-Hotel Hypothesis, the evidence from shorebirds and waterfowl is at best inconclusive. There is no evidence that habitat for nesting, brood rearing, molting, or staging is available in surplus in tundra wetlands when examined in terms of species-specific habitat selection and social behavior. Neither is there evidence that most North American waterbird populations are solely or even predominantly controlled by winter mortality or the length of the arctic summer. Intrinsic spacing mechanisms, number of clutches, clutch size, proportion of eggs hatching, and proportion of chicks fledging all influence recruitment to bird populations and all act during summer. The majority of the evidence indicates that migratory birds in the Arctic respond to their environment in the same way that birds do elsewhere, which does not support the Vacant-Hotel Hypothesis.

Evidence Against the Hypothesis Based on Avian Predators

Senner (1989) does not discuss avian species other than waterbirds. Avian predators, however, are closely linked to their prey base, which in the Arctic is closely linked to wetland habitats. Avian predators found in the Arctic include the snowy owl (*Nyctea scandiaca*), short-eared owl (*Asio flammeus*), pomarine jaeger (*Stercorarius pomarinus*), parasitic jaeger (*Stercorarius parasiticus*), long-tailed jaeger (*Stercorarius longicaudus*), peregrine falcon (*Falco peregrinus*), gyrfalcon (*Falco rusticolus*), and glaucous gull (*Larus hyperboreus*) (Pitelka et al. 1955, Kuyt 1980, Burnham and Mattox 1984, Barry and Barry 1990). On the coastal plains of northern Asia and North America, the pomarine jaeger potentially is the primary predator of lemmings (Pitelka et al. 1955), and the three jaeger species in aggregate are the most important avian predators found in northern Alaska (Maher 1974). Snowy owls are relatively common on the North Slope (Johnson and Herter 1989:223) but their abundance at a given location is highly variable (Pitelka et al. 1955, Wiklund and Stigh 1986). Short-eared owls occasionally breed at Barrow (Pitelka et al. 1955, Custer and Pitelka 1987) but are fairly common breeders only in "the southeastern portion of the Beaufort Sea area" (Johnson and Herter 1989:225-226). Peregrine falcons are associated with river systems on the North Slope, in particular the Colville and Sagavanirktok (Ambrose et al. 1988), and thus have restricted local distributions. Gyrfalcons generally occur inland rather than on the Arctic Coastal Plain; most of the North Slope population is associated with the Colville River (Johnson and Herter 1989:131). Nevertheless, these falcons, like peregrines, are widely distributed in the Arctic, occurring in West Greenland (Burnham and Mattox 1984), northern mainland Canada (Kuyt 1980), western Alaska (Swartz et al. 1984 [in Mindell et al. 1987]), and the Canadian High Arctic (Muir and Bird 1984). Glaucous gulls nest both colonially and as solitary pairs in the Beaufort Sea Region (Barry and Barry 1990) and prey on young birds and small mammals (Pitelka et al. 1955, DeKorte and Wattel 1988, Barry and Barry 1990). Most arctic-nesting avian predators are migratory, but gyrfalcons and snowy owls winter in the Beaufort Sea area of northern Alaska and Canada (Johnson and Herter 1989:131-134,223-225).

The Vacant-Hotel Hypothesis requires that habitat availability not limit animal populations in the Arctic. Resources such as food or nesting sites must be superabundant and competition for resources must be low under the hypothesis. Studies of avian predators provide evidence that the availability of resources strongly influences their breeding density (e.g., Village 1982). These resources are found within the habitats of avian predators, underscoring the importance of habitat availability. For the Vacant-Hotel Hypothesis to be correct, population control in arctic-nesting avian predators would have to be fundamentally different than in similar birds elsewhere.

Food Resources: Newton (1980) reviewed the role of food in limiting bird numbers and concluded that breeding density and reproductive output of predaceous birds are higher when prey is plentiful than when prey is scarce. He stated that avian predators feeding on the most cyclic prey experience the largest fluctuations in density and breeding rate, those feeding on prey of intermediate cyclicity occur at relatively stable densities but exhibit large fluctuations in breeding rate, and those feeding on prey species of constant density occur at stable densities with stable breeding rates. Schoener (1968) provided indirect evidence for the relationship between bird numbers and food supplies by showing that carnivorous birds have larger territories than omnivorous birds, which in turn have larger territories than herbivorous birds. Territory sizes in birds also correlate with body weights, evidence that breeding density is related to food requirements (Schoener 1968). This relationship is seen among raptors where large species breed at low densities because they take larger prey, which occur at lower densities than smaller prey (Newton 1980).

On Alaska's North Slope, the relationship between prey abundance and the breeding density of predators has been studied in detail. In particular, the density of brown lemmings varies by three or more orders of magnitude near Barrow (Batzli et al. 1980). During times of peak lemming abundance avian predators respond by increasing their breeding density but may not breed at all during prey declines (Pitelka et al. 1955, Maher 1974, Custer and Pitelka 1987). For example, pomarine jaegers failed to breed at Barrow in 1951, 1954, 1957, and 1958 during periods when lemming densities were very low (<2.5 ha^{-1} in the latter 3 years) (Pitelka et al. 1955, Maher 1974). Snowy owls also did not breed in 1951 or 1956 at this location (Pitelka et al. 1955). Conversely, during periods of lemming abundance such as 1949, 1952, and 1953, snowy owls nested in territories of 5.2 to 10.4 km^{2}•pair^{-1}, and pomarine jaegers reached mean densities of 6.9 pairs•km^{-2} in 1953 (Pitelka et al. 1955). Maher (1974) reported similar densities for nesting pomarines in 1956 and 1960. He concluded that the variation in breeding densities of pomarine jaegers (0.05 to 7.3 pairs•km^{-2}) near Barrow was directly related to the lemming population found by arriving jaegers in the spring.

These close relationships between reproduction and food availability provide circumstantial evidence (*sensu* Newton 1980) that food limits pomarine jaegers and snowy owls. Gross (1947) related snowy owl reproduction to the prey base. Pitelka et al. (1955) felt that food shortage for snowy owls was almost inevitable during midsummer because lemming populations decline while multiple predators are exploiting this prey. Clutch size in snowy owls at Barrow averaged seven eggs during lemming highs; feeding five or six young would require several dozen lemmings each day (Pitelka et al. 1955). However, production of young snowy owls in peak rodent years in northern Sweden averaged only 2.18 ± 0.32 nest^{-1} in 1978 and 1.25 ± 0.48 nest^{-1} in 1982 (Wiklund and Stigh 1986), perhaps indicating food limitation between hatching and fledging in this species. Likewise, Maher (1974) found that food shortage was a major mortality factor for pomarine jaeger chicks at Pitt Point in 1957 and near Barrow in 1956. In 1971 near Barrow, chick mortality was 65.9% by 25 days of age, and about half of the dead chicks were found in their nests following an abrupt decline in lemming numbers over the summer (Custer and Pitelka 1987). Within pomarine populations, differences in food supply cause wide variations in growth rates of young (Maher 1974).

Ovsyanikov and Menushina (1986) reported that wintering snowy owls on Wrangel Island systematically attacked arctic foxes (*Alopex lagopus*) to pirate their prey during a time when lemmings were abundant but inaccessible to the owls under deep snow. These authors believed this method of obtaining food permitted owls to winter on the island. Snowy owls may need 400 g•day^{-1} of food at -40°C, which can't be met if lemming abundance is low (or lemmings are unavailable), triggering southward movement to areas of greater food availability (Fitzgerald 1981). Lein and Webber (1979) found that prey density and availability appeared to drive habitat selection by wintering snowy owls in Alberta. These owls primarily fed on deer mice (*Peromyscus maniculatus*) and meadow voles (*Microtus pennsylvanicus*) (Boxall and Lein 1982). Snowy owl movements are influenced by food availability, with some birds wintering in the Arctic when lemmings are common (Pitelka et al. 1955, Ovsyanikov and Menushina 1986) but many regularly moving southward, primarily to the Great Plains, to winter (Kerlinger and Lein 1986). Periodically, significant numbers of birds also appear in areas east and west of the Great Plains (Bent 1938: 369-370, Kerlinger and Lein 1986, Smith and Ellis 1989), which has been attributed to irruptions in owl populations (Gross 1947, Kerlinger and Lein 1986) and to declines in lemming abundance in the Arctic (Bent 1938:370, Gross 1947). The role of food in limiting winter populations of snowy owls is uncertain but substantial winter mortality from lack of food occurs in the Duluth-Superior area (D. Evans, pers. comm. [in Smith and Ellis 1989]).

Short-eared owls also exhibit close relationships between prey availability and breeding density. These owls can achieve breeding densities in the Arctic that are comparable to those found at lower latitudes (Pitelka et al. 1955), perhaps because they are nomadic and respond functionally and numerically to microtine abundance found during "searching migrations" (Clark 1975, Korpimäki 1985). Fennoscandian populations fluctuate with microtine prey populations without time lags (Korpimäki 1985), although irregular densities may occur during rodent peaks (Andersson 1981). Similar fluctuations in owl and rodent populations occur in South Scotland (Village 1987) and in the McConnell River area of Keewatin in North America (MacInnes, pers. comm. [in Clark 1975]). Short-eared owls nesting on more southerly Welsh heather moor with stable populations of diverse vertebrate prey exhibit a stable breeding population, illustrating the versatile response of short-eared owls to differing prey densities and stabilities (Roberts and Bowman 1986). Near Barrow, short-eared owls bred in 1953 (Pitelka et al. 1955) and 1971 (Custer and Pitelka 1987), both years of lemming abundance (Pitelka 1973). Breeding density in 1953 averaged 1.2 to 1.5 pairs•km^{-2}, with a maximum density of 2.7 pairs•km^{-2} and a mean clutch size of 6.3 $nest^{-1}$ (Pitelka et al. 1955). Clutch size and number of young produced in short-eared owls tends to correlate with prey abundance (Korpimäki 1985, Village 1987). Since young short-eared owls in captivity consume up to 14 lemmings•day^{-1}•owl^{-1} with a mean of 7 lemmings•day^{-1}•owl^{-1} during the period of maximum growth (Pitelka et al. 1955), fledgling production demands significant amounts of food. Lockie (1955 [in Clark 1975]) suggests that females may be forced off nests if males fail to bring sufficient food, again illustrating the role of food in determining nesting success of short-eared owls. Finally, the relationship between prey abundance and owl densities continues throughout the year because short-eared owls tend to overwinter where fall vole populations are high (Clark 1975). For example, Baker and Brooks (1981) observed that large numbers of short-eared owls overwintered at the Toronto airport when vole numbers were high, but few owls were present at low vole numbers. Short-eared owls hunt by the energetically expensive method of quartering over the ground at low elevation and therefore require relatively high prey availability, such as might occur in snow-free areas (Sonerud 1986).

Parasitic jaegers nest between the Brooks Range and the arctic coast, primarily prey on birds or on birds and microtine rodents when breeding, and may breed opportunistically in areas of overlap with pomarine and long-tailed jaegers in years when these jaegers fail to breed (Pitelka et al. 1955, Maher 1974). The parasitic jaeger occasionally breeds at Barrow with five pairs nesting between 1951 and 1960; at Kaolak River on the western North Slope, breeding density over 3 years of observation was 0.1 pair•km $^{-2}$ (Maher 1974). Nonbreeding parasitic jaegers forage on the arctic coast and nearby tundra, sometimes occurring in mixed flocks with the other jaeger species (Maher 1974). Colonial nesting of parasitic jaegers has been observed in northeastern Norway where pairs can forage at sea (Andersson and Götmark 1980). Long-tailed jaegers nest from the Brooks Range to the southern portion of the Arctic Coastal Plain but rarely nest on the coast (Maher 1974). In northern Sweden, long-tailed jaegers do not breed during lows in the rodent population, but most or all pairs nest in years of rodent abundance, reaching densities of 0.63 pair•km $^{-2}$ (Andersson 1976, 1981). Failure to nest has also been noted in Northeast Greenland during a year of long snow cover and few lemmings (DeKorte and Wattel 1988). The importance of food resources to long-tailed jaeger populations is illustrated by Andersson's (1976, 1981) finding that egg volume, clutch size, natality rate, production of fledglings, chick growth rate, and adult weight are greater in good rodent years than in poor years. He also found that chick mortality decreased and the proportion of young breeders probably increased in good rodent years. Over two rodent cycles, about 75% of chick production occurred during rodent peaks and mean chick production was 0.5 fledglings•pair $^{-1}$•yr $^{-1}$. Andersson (1976) concluded that the availability of rodents and other food, coupled with a maximum clutch size of two, probably limited populations of long-tailed jaegers in northern Sweden.

Glaucous gulls are opportunistic feeders (Barry and Barry 1990) that prey upon lemmings (Pitelka et al. 1955, DeKorte and Wattel 1988) or scavenge lemming remains left by pomarine jaegers and snowy owls (Pitelka et al. 1955). Near Barrow, glaucous gulls reached densities of 1.9 to 3.9 km $^{-2}$ in 1953, a year of lemming abundance, but were generally absent from the tundra in 1951 and 1952, times of low lemming abundance. These gulls were more numerous than jaegers in May 1953 and were important lemming predators until displaced by the primary lemming predators (e.g., jaegers) in June (Pitelka et al. 1955). Although glaucous gulls appear to benefit from the abundance of lemmings, the studies cited here do not show that food availability limits gull populations.

Gyrfalcon populations fluctuate on Alaska's Colville River (Mindell et al. 1987) and near Canada's Thelon River where nest-site occupancy varied from 100% to 33% between 1961 and 1969 (Kuyt 1980). Population fluctuations in gyrfalcons have been correlated with prey abundance. In Alaska, Barichello (1983) found that breeding failure and poor hatching success, including clutch abandonment, correlate with low ptarmigan density. Breeding populations of gyrfalcons in West Greenland also fluctuate with prey abundance, and no young were produced at 14 coastal sites in 1974 when ptarmigan and hares were very low (Burnham and Mattox 1984). Ptarmigan are the major prey of gyrfalcons in western Alaska (Roseneau 1972 [in Walker 1977]), where little other prey is available in winter (Walker 1977), and in central Norway (Langvatn 1977). Barichello (1983) also reported that ptarmigan formed the bulk of the gyrfalcon diet in late winter and early spring in Alaska. Ptarmigan and ground squirrels are frequently taken on the Colville River (Mindell et al. 1987), but on Ellesmere Island in the High Arctic, gyrfalcons primarily ate arctic hare (*Lepus arcticus*), and no ptarmigan were observed (Muir and Bird 1984). Hare and ptarmigan make up most of the gyrfalcon diet in West Greenland (Burnham and Mattox 1984). The importance of food availability to the reproductive success of gyrfalcons is illustrated by Cade's (1960 [in Langvatn 1977]) estimate that approximately 200 ptarmigan are necessary to raise gyrfalcon young over a 120-day period. Langvatn (1977) also estimates that 180 to 200 prey items of ptarmigan size are necessary during the nesting season, based on prey remains found at gyrfalcon nests.

Newton and Mearns (1988) characterize breeding populations of peregrine falcons as extremely stable in the absence of anthropogenic influences such as pesticide pollution, probably due to relatively constant food supplies and a fixed number of potential nest sites that "naturally limit breeding densities." However, the density of breeding pairs varies considerably between regions, again probably due to the availability of food and nest sites (Newton 1988), and breeding densities can vary within a given region if food supplies are highly variable (Court et al. 1988). Burnham and Mattox (1984) believe that prey abundance determines nest location in West Greenland where unoccupied cliffs are available. These authors found that prey density near occupied eyries averaged 2.1 individuals•ha^{-1} whereas prey densities near abandoned eyries were <0.4 individuals•ha^{-1}. Since mean prey density near occupied sites in West Greenland is 5 times lower than typical for Alaska and since gyrfalcons and peregrines do not nest on the same cliffs in Greenland, unlike Alaska, Burnham and Mattox (1984) conclude that indirectly food is the greatest factor limiting peregrine density in West Greenland.

Newton (1988) discusses the relationship between cliff availability and prey availability. He states that large, high cliffs allow more efficient hunting, but if food availability is high, smaller cliffs may be used for nesting. Peregrine abundance has been shown to decline when prey bases become smaller (Newton 1988). For example, grazing in western Scotland and Ireland reduced prey abundance and peregrines declined, but in other areas peregrine breeding densities increased when rock doves (*Columbia livia*) became abundant (Ratcliffe 1988). Although food may not limit the nonbreeding component of peregrine populations (Newton 1988), a potential breeding site is only usable if surrounded by habitat supporting appropriate prey (Hunt 1988). Ratcliffe (1988) states that human-induced changes in habitat structure and food supply have had more effect on peregrines than has direct mortality from shooting, egg collecting, or consumption. Kiff (1988) provides evidence that habitat loss, in particular loss of wetlands, is the most important ultimate control on peregrine populations. Habitat loss or alteration that renders potential breeding locations unsuitable by reducing prey abundance or destroying nest sites limits potential breeding populations of peregrines by reducing the pool of "serviceable breeding locations" (*sensu* Hunt 1988). Although some sites are unoccupied in a given year even in a healthy population (Burnham and Mattox 1984), Calef and Heard (1979) found a reoccupancy rate of at least 54%, and perhaps as high as 91%, at Wager Bay in northern Canada. Since peregrine falcons are still recovering their former abundance on Alaska's North Slope (Ambrose et al. 1988), loss of peregrine habitat cannot be assumed to be benign without understanding the site-specific reasons why some eyries are not occupied in a given year.

Other Resources: Food is only one of the resources that might limit populations of avian predators in the Arctic. Nest sites are a resource that may affect breeding density and thus potential reproductive output of predaceous birds. In West Greenland, peregrines nest primarily on cliffs of 27 m to >117 m in height (Burnham and Mattox 1984), unlike the situation in northern Canada where cut banks or low sandy mounds may also be used (Hickey and Anderson 1969 [in Burnham and Mattox 1984]). Nest sites near Canada's Thelon River usually are on south- or west-facing cliffs (Kuyt 1980); southward orientation is also the case in West Greenland (Burnham and Mattox 1984). In some locations, gyrfalcons and peregrines do not nest on the same cliffs (Kuyt 1980, Burnham and Mattox 1984), whereas in other locations the two species tolerate each other's presence (White and Cade 1971 [in Burnham and Mattox 1984]). Gyrfalcons nest before peregrines and can displace them from nesting cliffs where prey density is insufficient to support both species (Burnham and Mattox 1984). In other cases, the distribution of nesting pairs appears limited primarily by the availability of suitable nesting sites rather than prey availability (Kuyt 1980). Thus, serviceable breeding locations for peregrine falcons are constrained by a number of factors, some of which involve interactions with other species and food supply, as well as physical characteristics of potential nest sites (e.g., in interior and arctic Alaska, cliffs are largely limited to river valleys [Mindell et al. 1987]).

Gyrfalcons also have specific nesting requirements that may influence their distribution. As with peregrine falcons, food availability may influence the suitability of gyrfalcon nesting sites. Gyrfalcon nests are concentrated in valleys where willow ptarmigan are common in northern Yukon (Platt 1976 [in Kuyt 1980]). Cliffs are often used for gyrfalcon nesting, as are rocky outcrops and river bluffs (Johnson and Herter 1989:131). Gyrfalcons share the preference of peregrines for south- or west-facing cliffs (Kuyt 1980) but often use stick nests built by ravens (*Corvus corax*) (Burnham and Mattox 1984), including tree nests in timberline habitats in Canada (Kuyt 1980). Raven nests are not reusable by gyrfalcons in consecutive years because young gyrfalcons tear the nests apart (Burnham and Mattox 1984). This source of nests may be less dependable than cliff nests, consistent with the observation of Burnham and Mattox (1984) that sites where gyrfalcons are not dependent on ravens are used more frequently than cliffs lacking permanent eyrie locations. Gyrfalcon nest sites may be characterized by steep cliffs and overhanging shelter (Cade 1960 [in Kuyt 1980], Burnham and Mattox 1984) in some areas, but this is not always the case (Platt 1976 [in Kuyt 1980]). In many cases the same sites may be used by both peregrines and gyrfalcons in different years (Beebe 1977 [in Calef and Heard 1979], Calef and Heard 1979, Burnham and Mattox 1984, Mindell et al. 1987).

Snowy owl nest sites are less specialized than those of falcons. Snowy owls nest on the ground, usually on hummocks or other dry sites providing a perch for surveillance of surrounding terrain (Johnson and Herter 1989:224). In northern Sweden, these owls nest mainly on hillocks, but some use the surface of large boulders (Wiklund and Stigh 1986). Short-eared owls are ground nesters (Johnson and Herter 1989:227). Roberts and Bowman (1986) observed their nests on steep heather slopes and in tussocky bogs between clumps of vegetation. It is unlikely that the availability of nest sites *per se* limit populations of snowy or short-eared owls. Sonerud (1986) concludes that nest-site availability is less important than prey availability "as determined by hunting habit and hunting mode" in Fennoscandian owls, including the short-eared.

Pomarine jaegers prefer *Carex* marsh for nesting, long-tailed jaegers prefer tussock-heath, and parasitic jaegers nest in both habitats (Maher 1974). Pomarines are ground nesters on elevated mounds within wet areas; parasitic and long-tailed jaegers use similar mounds or rises within their preferred nesting habitats (Johnson and Herter 1989:186-192). Glaucous gulls also nest on the ground, often on barrier islands, but colonial nesting can occur on cliffs as well (Johnson and Herter 1989:201). As with owls, it is unlikely that the availability of nest sites limits jaeger or gull populations because their nesting requirements are relatively nonspecific.

The availability of nest sites may limit species such as the peregrine falcon and the gyrfalcon that have very specific requirements for nesting. Such limitation has been shown for another falcon, the Eurasian kestrel (*Falco tinnunculus*) (Newton 1980). Geological forces determine the distribution and abundance of suitable nesting ledges or bluffs, which are only serviceable breeding locations if sufficient prey are located nearby. Interactions with other species further limit nest-site availability for cliff-nesting raptors. Maximum potential reproductive output for these species may be determined by the number of nest sites that can accommodate breeding pairs at a given prey density. In contrast, ground-nesting arctic owls, jaegers, and the glaucous gull may not experience limitations imposed by the availability of nest sites; rather, they may be limited by social factors and prey density.

Territoriality: Territorial behavior of breeding individuals can limit the number of breeding pairs, which must also limit the total population (Watson and Moss 1970, Patterson 1980) by setting maximum potential reproductive output. Many examples of territorial behavior being influenced by the level of available resources are present in the literature (e.g., see review by Newton [1980]). For practical purposes, however, the presence of spacing behavior means that displaced territorial individuals cannot simply go elsewhere to breed with the same probability of success, particularly if surplus nonterritorial individuals are already present on the breeding grounds, regardless the role of nutrition in territorial behavior.

Most avian predators breeding in arctic wetlands are territorial. Pomarine jaegers increased during a lemming high at Barrow in 1956 until they occupied all available habitat as well as some habitat that was obviously marginal (Maher 1974). Although lemmings can reach densities of more than 220 ha^{-1} (Batzli 1980), a high proportion of excess pomarine jaegers (about 25% of total population) may be present early in the breeding season (Maher 1974). Excess birds drift along the coast as territories are established by breeders (Maher 1974). Pomarines are strongly territorial throughout the nest cycle, with mean territory size varying from as little as 6 to 8 ha during the lemming peak of 1953 (Pitelka et al. 1955) to as much as 68 ha during low prey density at Barrow (Maher 1974). At low prey densities, pomarine jaegers may not be completely territorial and may forage off their territories during late-season food shortages (Maher 1974). Shortage of prey and chick starvation in 1956 caused pomarines to cease territorial defense (Maher 1974), perhaps illustrating the relationship between territoriality and food availability.

Long-tailed and parasitic jaegers are territorial breeders in many situations, although parasitics may nest colonially in some locations (Andersson and Götmark 1980). Nonbreeding, nonterritorial individuals occur in all three jaeger species (Maher 1974). Reported territory sizes for solitary pairs of parasitic jaegers are 40 to 120 ha near Barrow (Maher 1974) and 95 ha in Northeast Norway (Andersson and Götmark 1980). Parasitic jaegers sometimes forage off territory and in relatively undefended portions of their territories (Maher 1974), but colonial pairs forage at sea far from their nests (Andersson and Götmark 1980). Long-tailed jaegers show similar variability in territorial defense and foraging location. For example, males may forage off territory and at sea in Northeast Greenland (DeKorte and Wattel 1988) and actively defend only core areas of their territories on Alaska's North Slope (Maher 1974). Conversely, territories of ≥ 1 km^2 are strongly defended by long-tailed jaegers and regularly distributed in northern Sweden, and the jaegers obtain much of their food within their territories. Long-tailed jaegers also exhibit strong site tenacity, returning to the same territory in subsequent years even when food supplies are insufficient to support breeding (Maher 1974; Andersson 1976, 1981). Territorial behavior does not persist in years when rodent populations are low, and the long-tailed jaegers leave the breeding grounds after about 1 month (Andersson 1981). During such years, mixed flocks of nonbreeding jaegers may forage on the coast and nearby tundra, and food competition may account for the early departure of jaegers from the Arctic (Maher 1974).

Jaegers are interspecifically territorial, and pomarines defend their territories against gulls, short-eared owls, snowy owls, loons, and arctic foxes, as well as other jaegers (Maher 1974). Superficial examination of the density of a single species without consideration of interspecific territoriality might lead one to erroneously conclude that available habitat was not fully occupied by that species. In fact, one species may well be excluded from a particular area by the presence of individuals of another species. Maher (1974) states that "selection for interspecific territoriality should not occur until the degree of [food] overlap between two species is great enough that it becomes advantageous." Long-tailed and pomarine jaegers have the greatest dietary overlap of the jaeger species and also have the greatest degree of geographic separation, with the pomarine being the dominant competitor where sympatric with the long-tailed jaeger (Maher 1974). Pomarines may also exclude parasitic jaegers during high lemming years (Pitelka et al. 1955). Maher (1974) states, "Several aspects of territories among jaegers suggest that they are adapted primarily to insure that nesting pairs have enough food for the breeding season." He believes this is especially true for long-tailed and pomarine jaegers.

Snowy owls are also territorial breeders with males forming territories and displaying frequently early in the season (Wiklund and Stigh 1986). Significant numbers of surplus, nonbreeding individuals have been documented in North Slope populations of snowy owls (Pitelka et al. 1955). Near Barrow, territory size was 5 to 10 km^2 in 1952 and 1953, but more nonbreeders were present in 1953 (Pitelka et al. 1955). Mean territory sizes in Sweden in three study areas were 2.41 ± 0.36, 1.82 ± 0.54, and 2.86 ± 0.57 km^2 in 1978, a period of rodent abundance, and 6.53 ± 0.71 km^2 in one study area in 1982, another rodent high (Wiklund and Stigh 1986). Snowy owls defend their territories against arctic foxes (Litvin et al. 1985) but are harassed by pomarine jaegers (Pitelka et al. 1955). Pitelka et al. (1955) believe that local concentrations of nonbreeding snowy owls may be influenced by large numbers of territorial jaegers. Territoriality has been observed in female snowy owls during winter (Boxall 1979 [in Kerlinger and Lein 1986]). In fact, female social dominance, potentially mediated by territoriality, appears to explain the winter distribution of snowy owls wherein female adults winter farthest north and immature males winter farthest south (Kerlinger and Lein 1986). Boxall and Lein (1982) believe that sexual dimorphism potentially reduces winter food competition in snowy owls because females take larger prey species in southern Alberta whereas males specialize in deer mice. Social behavior, including territoriality, and physical characteristics of snowy owls appear to be adaptations to limited food supplies, at least in part.

Short-eared owl territories varied from 42 to 112 ha, and territory size was negatively correlated with vole abundance in South Scotland (Village 1987). Territory size can increase as prey declines (Lockie 1955 [in Newton 1980]). Clark (1975) observed that the limits of breeding territories were rarely violated. These territories averaged 73.9 ha in Manitoba during a year with larger food supplies and a single territory was 121.4 ha in a year with smaller food supplies. Short-eared owls observed by Clark usually hunted within their breeding territories but occasionally went outside territorial limits; territorial aggression decreased over the breeding season. Clark states that territorial behavior is an important density-dependent mechanism for regulating short-eared owl populations, operating on both winter and breeding ranges.

Peregrine falcons are territorial breeders (Newton 1988). A pool of nonbreeders presumably exists in peregrine falcon populations (Newton 1988), and the presence of nonbreeding young peregrines in Alaska can be inferred from the ages of recaptured breeding females banded as nestlings (Ambrose and Riddle 1988). In optimum nesting habitat at Wager Bay and the Melville Peninsula in northern Canada, mean internest distances were 8.0 km (range: 3.2-19.3 km) and 9.2 km (range: 4.8-12.9 km), respectively (Calef and Heard 1979). Mean internest distances of 4.8 km to 6.4 km were reported for various portions of the British Isles before pesticide-induced declines (Ratcliffe 1972 [in Burnham and Mattox 1984]), and a distance of 7.7 km was reported for West Greenland in 1972 and 1973 (Burnham and Mattox 1984). Gyrfalcons are also territorial breeders (Peter Bente, Wildl. Biol., U.S. Fish and Wildl. Serv. Endangered Species, Fairbanks, pers. comm.); internest distances in West Greenland average 10.4 km at inland sites (Burnham and Mattox 1984). Mindell et al. (1987) state that gyrfalcons and rough-legged hawks (*Buteo lagopus*) nest within 1 to 2 km of each other on the Colville River but do not provide internest distances for gyrfalcon pairs. Internest distances of several km are reasonable for North Slope rivers such as the Colville, varying with visual separation of adjacent pairs, but nests typically are separated by 16 to 20 km in the Alaska Range (P. Bente, pers. comm.). Interspecific interactions, food supply, and nest sites influence spacing of these falcons, as previously discussed, but their breeding densities are also limited by territoriality.

Summary: The role of food in limiting the abundance of avian predators in arctic-tundra wetlands is clear; most species show strong relationships between breeding density, reproductive output, and prey availability. These relationships do not conclusively prove that food limits the numbers of avian predators in arctic wetlands, absent controlled experiments that manipulate food availability (Newton 1980), but they provide strong circumstantial evidence that this is the case. In addition, the availability of suitable nesting sites further limits the breeding density and local distribution of cliff-nesting raptors in the Arctic. Finally, most avian predators breeding in the wetlands of Alaska's North Slope exhibit territorial behavior that spaces breeding pairs in suitable habitat. Based on the available evidence, the densities of avian predators using arctic wetlands appear to be limited by prey density, availability of nest sites, or territorial behavior with the presence of surplus, potentially breeding, individuals. These mechanisms are not consistent with the requirements of the Vacant-Hotel Hypothesis for superabundant resources, excess habitat, and density-independent population control.

Evidence Against the Hypothesis Based on Mammals

Senner (1989) selected four large mammalian species for discussion: caribou, muskox (*Ovibos moschatus*), polar bear (*Ursus maritimus*), and wolf. He acknowledges that none of these species is uniquely associated with wetlands, but all range across them during portions of the year. He then claims wetlands, as defined for regulatory purposes, are irrelevant to these species. By selectively limiting his discussion to two ungulates and two large carnivores, one of which barely uses North Slope terrestrial habitats and then only in winter, Senner presents a skewed picture of mammalian relationships to arctic wetlands. Other large mammals and many small mammals are more strongly associated with arctic-wetland habitats than the species he selected. For example, moose occur on the North Slope, chiefly in riparian corridors, north to the Beaufort Sea coast (Manville and Young 1965, Coady 1982). Garner and Reynolds (1986:270-288) cite literature describing the largest North Slope population of moose as occurring in the Colville drainage, with other concentrations along the Canning and Kongakut drainages. Although moose are not an issue in the currently producing oilfields on the North Slope, potential petroleum development in the ANWR and the Colville River drainage could affect this species. Likewise, Senner does not discuss the brown bear (*Ursus arctos*), a major predator in arctic ecosystems, which may use wetlands during a portion of the year. Among the small mammals, he does not discuss the voles and lemmings, major components of the arctic food web associated with wetland habitats. For example, the tundra vole (*Microtus oeconomus*) as a herbivore may "affect productivity of [the] tundra ecosystem," and habitat effects of tundra voles have been noted during population irruptions (Johnson and Johnson 1982). Hobbie (1980*b*) cited literature stating that the brown lemming is "by far the dominant consumer at Barrow," completely cutting all standing plants at peak lemming abundance. Similarly, Senner does not discuss arctic or red foxes (*Vulpes vulpes*), weasels (*Mustela*), or the wolverine (*Gulo gulo*). Although we question his selection of species to discuss, selective use of pertinent literature, and conclusions, space limitations preclude greatly expanding Senner's scope. Nevertheless, we discuss moose, brown bear, and lemmings as arctic species showing definite relationships to wetlands and evaluate points raised by Senner for caribou, muskox, polar bear, and wolf. These discussions are presented by species as was done by Senner.

Lemmings: Two species of lemming occur on the North Slope: brown lemming and Greenland collared lemming (*Dicrostonyx groenlandicus*) (Manville and Young 1965). "The brown lemming . . . is the dominant herbivore" of coastal tundra near Barrow (Batzli et al. 1980). Collared lemmings prefer drier sites, a relatively scarce habitat in the Barrow area, and thus collared lemmings are generally less common in this area than are brown lemmings (Pitelka 1973). In other portions of the North Slope, collared lemmings may be more abundant than brown lemmings (Batzli et al. 1980). Lemmings exhibit cyclic peaks of abundance every 3 to 4 years (Pitelka et al. 1955) ranging from a low of 0.02 ha^{-1} to a high of 225 ha^{-1} near Barrow (Batzli et al. 1980). During population highs lemmings heavily graze green stems of monocotyledons, completely devastating their food supply during the winter preceding the peak (Batzli 1981). The lemmings continue to consume new growth during the summer, which reduces standing vegetation sufficiently to expose the lemmings to predation (Pitelka 1973). Standing crop of monocotyledons may be reduced by 50% from summer grazing (Batzli 1981).

Schultz (1974) hypothesized (based on experimental results at Barrow) that heavy grazing by lemmings at population highs increased active-layer depth, tied up calcium and phosphorus in undecomposed organic matter, and reduced levels of these nutrients below that required for lemming reproduction. Gradually increasing nutrient concentrations in forage over several subsequent years would eventually create conditions (e.g., cover, forage quality) conducive to another lemming population high, thus, in part, accounting for their cyclicity. Schultz's hypothesis that nutrient cycling controls lemming cycles is only partially accepted because its predictions concerning increased depth of thaw, increased rooting depth, and decreased plant production from lemming grazing are not supported by more recent studies (Batzli et al. 1980). Batzli et al. (1980) conclude that the nutrient-recovery hypothesis should be modified but accept that the effects of forage quality (nutrient content) as well as quantity must be considered in relation to rodent populations. Batzli (1981) discusses other hypotheses of population control in microtine rodents such as selection for different genetic types at high and low rodent populations and the effects of winter conditions and weasel predation, but no single factor appears to explain cycles in microtine rodents in general and lemmings in particular (Collier et al. 1975, Batzli 1981, Lidicker 1988). For example, Lidicker (1988) believes that as many as eight intrinsic and extrinsic factors are required to explain cycles in the California vole (*Microtus californicus*). What is certain is that populations of microtine rodents affect their habitats, which in turn influence rodent populations.

Batzli et al. (1980) state, "Lemming populations often increase up to a limit imposed by their food supply and begin to decline when there is not enough food to meet energy demands." Factors other than food, for instance heavy predation by snowy owls and pomarine jaegers, reduce lemming populations during the growing season (Pitelka et al. 1955, Pitelka 1973). Predation is not believed to "stop population growth at high microtine densities" (Lidicker 1988) but may be important "during and after the decline phase in cyclic populations of small mammals" (Andersson and Erlinge 1977). Predator-prey systems with few alternative prey species, with predators that specialize in single prey species, and with predators that show a delayed numerical response to increased prey density may exhibit cyclicity (Erlinge et al. 1983). In the case of lemmings in the North American Arctic, avian predators truncate population highs and resident mammalian predators active in the subnivean environment (e.g., weasels) drive populations to low levels (Andersson and Erlinge 1977). Pitelka (1973) believes that the combined action of predators may reset the clock for lemming cycles but also specifically recognizes the role of other factors such as food and cover in the process. The relationships between prey density, food supply, cover, and predation are illustrated by the previously discussed observation of Pitelka (1973) that heavy grazing reduces cover and facilitates predation. Baker and Brooks (1982) verify that cover strongly affects avian predation on microtine rodents.

Most of the evidence concerning population control in lemmings contradicts the Vacant-Hotel Hypothesis. Brown lemmings appear to minimize foraging time, perhaps to reduce risk of predation, and consequently do not accumulate large fat reserves in the wild (Peterson and Batzli 1984). Since Peterson and Batzli (1984) estimated minimum survival time until starvation as 8.6 ± 2.3 hours, lemmings require readily available food at all times. Food availability may be limited in late winter, however, because calculated energy requirements of a moderately dense lemming population indicate that "suitable forage would be completely utilized before snowmelt (Batzli 1975a)," and lemming carcasses collected around snowmelt have levels of body fat indicative of starvation (Batzli et al. 1980). Lemming reproduction, especially in winter, is also a function of forage quality as shown by fertilization experiments conducted by Schultz (1974). Weather influences snow cover, snowpack characteristics, breakup flooding, and thermal conditions experienced by lemmings (Batzli et al. 1980). These factors also determine differential mortality and reproduction of lemmings in various subnivean and unflooded snowmelt habitats in a largely density-dependent manner (e.g., better thermal conditions in polygon troughs with deeper snow cover [Batzli et al. 1980]). Density-dependent mortality and reproduction in lemmings, acting through food availability and predation, is not consistent with the Vacant-Hotel Hypothesis.

Habitat-induced limitations on lemmings ultimately are reflected as limitations on avian and mammalian predators through reduced prey bases (Hobbie 1980*b*) (see "Avian Predators"). Hobbie (1980*b*) cites research relating abundances of least weasel (*Mustela nivalis*), ermine (*Mustela erminea*), and arctic fox to highs in the lemming population cycle. Cyclicity in predator populations, driven by cyclicity in lemming populations, may affect other components of the tundra community. Predator species that numerically or functionally respond to high lemming numbers face starvation when lemmings subsequently crash unless the predators can feed on alternative prey. For example, prey-switching behavior by avian and mammalian predators appears to explain the 3-year cyclicity in breeding production of brant and several species of shorebirds correlating with lemming cycles on Siberia's Taimyr Peninsula (Summers 1986, Summers and Underhill 1987). Although the lemming may easily be overlooked as insignificant, its relationship to its habitat as a major herbivore can propagate throughout the tundra community, affecting species that may not otherwise show obvious limitation by density-dependent factors. Thus, cumulative habitat losses limit species at higher trophic levels as well as primary consumers, and the Vacant-Hotel Hypothesis fails for small mammalian predators (and for avian predators) using arctic-wetland habitats.

<u>Moose</u>: Among ungulates occurring on Alaska's North Slope, moose exhibit density-dependent changes in natality in response to their nutritional status. When food is limiting, as can occur at high moose density, fewer yearling moose breed and fewer adults produce twin calves than is the case when food is abundant (Coady 1982). In the boreal forest, fire can produce superabundant food supplies for moose; conversely, harsh winters over most of the area occupied by moose can greatly reduce moose movements and available

browse. The ability of moose to adjust natality in response to resource availability probably evolved as an adaptation to their rapidly fluctuating environment (Peek and Eastman 1983). In the absence of increased mortality rates, cumulative habitat loss would displace individual moose, increase intraspecific competition for food, produce nutritional stress in potentially reproductive females, and decrease natality rates in the same way as do declining range conditions and harsh winters.

Moose also exhibit density-dependent mortality, usually as a result of malnutrition. As previously discussed, deep snow can impede moose movement and cover low-growing food items (Coady 1982). Weakened or relatively immobile animals may be predisposed to predation as well (Peek and Eastman 1983). Calves are susceptible to differential mortality under such conditions because they "have less fat and protein available for catabolism than do adults and are therefore less able to maintain themselves during periods of low-quality forage intake" (Coady 1982). Although winter mortality can occur at either high or low moose densities, competition for forage generally would be greatest under the former condition, making malnutrition and starvation more likely.

In addition to mortality induced by harsh winters, density-dependent mortality in moose also occurs following population irruptions and has occurred both in the presence and absence of predators (Coady 1982). Over-browsing has been observed in some, but not all, population crashes following irruptions (Peek and Eastman 1983). These facts led Peek and Eastman (1983) to "hypothesize that as populations approach levels where competition for food becomes intensive, or where succession advances to where the forage base deteriorates, causing intraspecific competition, moose populations begin to decline in productivity and become more vulnerable to a complex of mortality factors." Such mortality factors include disease, hunting, and predation (Coady 1982). Predation by wolves (Gasaway et al. 1983) and grizzly bears (Larsen et al. 1989) may be particularly important in this regard since dramatic irruptions of moose are relatively infrequent in ecosystems not heavily influenced by man (e.g., through elimination of predators or through excessive harvest of moose) (Coady 1982). By temporarily increasing moose density, cumulative habitat loss and displacement of individual animals would increase intraspecific competition for forage. Malnutrition and increased susceptibility to predation could then reduce the moose population.

Riparian-willow habitats are by definition wetlands, and moose on the North Slope are almost entirely dependent upon these high-value habitats. Density-dependent population control in moose using limited riparian habitats on the North Slope is not consistent with the Vacant-Hotel Hypothesis, which requires density-independent control and superabundant resources.

<u>Caribou</u>: Senner selectively uses references to support one view of caribou population control but neglects extensive literature supporting other views. For example, he cites articles by Bergerud (1971, 1974, 1980) and Bergerud et al. (1984) proposing that predation and hunting currently limit the size and productivity of

continental caribou populations. However, even here Senner is selective. Bergerud et al. (1984) have also stated that habitat, as an ultimate limit on caribou numbers, provides caribou the space to avoid predators, and many others believe that habitat is the primary limitation. For example, Shideler et al. (1986) present a thorough discussion of the three prevailing views of *Rangifer* population dynamics: the "forage" theory, the "predation" theory, and the "dispersal" theory. Habitat is at the heart of the forage theory but also plays a role in the predation theory and some formulations of the dispersal theory. Caribou nutrition is a function of forage quality and quantity, and forage is a component of caribou habitat. Nutrition, in turn, influences caribou "body size, pregnancy rates, age at initial conception, and calf survival" (Shideler et al. 1986). White et al. (1981) cite literature indicating that the intake of digestible organic matter by grazing herbivores is limited by forage availability when total biomass (presumably aboveground biomass since that is the grazed component) is less than 200 to 220 gdw•m^{-2} (roughly the value measured at Barrow [P.C. Miller et al. 1980]) or an available green biomass of 50 g•m^{-2}. The latter value appeared low to these authors, based on reindeer (*R.t. tarandus*)-grazing experiments at Prudhoe Bay. Available green biomass at Prudhoe Bay is expected to exceed 50 g•m^{-2} only in "July and early August in *Carex-Eriophorum* meadows" (Batzli et al. 1980). Thus, although about 80% of tundra net primary production is not consumed by herbivores (MacLean 1980), we cannot conclude that food supply for those herbivores is unlimited. Available green biomass of vascular plants must exceed approximately 25 to 35 g•m^{-2} just to maintain body weight in non-lactating and lactating reindeer (and presumably caribou), much less gain weight (White et al. 1981) and achieve peak condition. Since these factors directly influence population dynamics, caribou habitat is central to the forage theory. Loss of high-quality habitat, or access to such habitat, through development activities would be reflected in reduced reproductive potential of caribou.

Although not mentioned by Senner, the predation theory specifically recognizes that different mechanisms may control caribou populations in different regions (Shideler et al. 1986). Bergerud (1983) believes arctic caribou herds solely occupying tundra habitat are frequently controlled by food availability as influenced by snow and ice (e.g., Peary caribou [*R.t. pearyi*] as discussed by Bergerud [1978]) and believes meningeal worm (*Parelaphostrongylus tenuis*) infections caused the decline of herds that once occupied the Lake State-Acadian forests. It is in boreal and subalpine forests that Bergerud proposes predation as the mechanism controlling caribou populations. Stocking levels are commonly 0.4 to 0.8 caribou•km^{-2} for herds subject to predation (Bergerud 1980). However, even in these habitats, Bergerud et al. (1984) state, "We must not permit the dissection of caribou populations into small discrete units so that they lose their ultimate adaptation -- mobility, to seek space to cope with an ever-changing extrinsic environment." Specifically, caribou require about 2.6 km^{2}•animal^{-1} "in order that contacts with predators be sufficiently limited that recruitment can equal natural mortality" (Bergerud 1980).

Bergerud (1983) describes (but does not support) the dispersal theory that caribou have an intrinsic spacing mechanism, which presumably would lead to emigration whenever caribou density exceeded some critical value. Skoog (1966:326-328,357) set this value at 2 to 4 caribou•km^{-2}. Since most boreal caribou populations with normal wolf predation exist at densities averaging 0.4 caribou•km^{-2} (Bergerud 1983), the intrinsic spacing hypothesis rarely can be tested and has few proponents. One criticism is that caribou normally aggregate at high densities, which makes the concept of a threshold density for social intolerance difficult to accept (Miller 1982). Nevertheless, should the intrinsic-spacing theory operate under appropriate conditions (e.g., absence of predation [Bergerud 1980]), marginal habitat would be occupied by caribou in response to increased density in optimal habitat. Recruitment of caribou in marginal habitat would be less (by definition) than in optimal habitat. Cumulative habitat loss and displacement of caribou (including restriction of caribou movements) increase local caribou density, which could trigger emigration and a subsequent decline in overall abundance as marginal range is occupied.

In the specific case of the Prudhoe Bay area of Alaska's North Slope, contrary to Senner's assertion that wetland habitats are irrelevant to large mammals, caribou intensively use two categories of such habitat: "the sedge meadows comprising the calving concentration areas on the coastal plain, and coastal beaches, promontories, and river deltas that are used intensively as mosquito relief areas" (Shideler 1986). No single explanation for selection of coastal sedge meadows for calving by the Central Arctic Herd has been shown, but low predator densities and proximity to insect-relief habitat may be factors (Shideler 1986). Forage availability may also be a factor (Dr. Susan Cargill Bishop, Wildl. Biol., Alaska Dep. of Fish and Game, Fairbanks, pers. comm.). These factors are components of habitat and plausibly influence caribou population dynamics. Low predator densities would enhance calf survival, proximity to insect-relief habitat would reduce energy expenditures, and better forage would contribute to maintenance of favorable energy balances. Loss of appropriate calving and insect-relief habitat, or access to such habitat, would adversely affect the caribou population's potential for growth. Cameron and Whitten (1979, 1980) have shown that calving caribou and maternal pairs occur with lower frequency within the Prudhoe Bay oilfields than in other portions of the region, evidence that some caribou avoid developed areas. Likewise, White and Trudell (1980) present data indicating that caribou populations in arctic Alaska may be at or near carrying capacity in terms of forage availability. Recent data on recruitment and body composition in the Central Arctic Herd and Porcupine Herd also tend to support forage limitation (S. Bishop, pers. comm.). The Central Arctic Herd has grown in past years; however, there is little evidence that habitat does not limit its long-term potential abundance.

Debate over population control in caribou likely will continue for years to come. Currently the George River Herd of Canada's Quebec-Labrador Peninsula is one of the world's largest (Williams and Heard [in Couturier et al. 1990]) but has been decreasing in size since 1984 (Couturier et al. 1990). Courturier et al.

(1990) believe that a combination of factors may account for the herd's decline. These factors include "decline of the physical condition of females, habitat deterioration on the current calving grounds (former summer range), increase in energy expenditures related to more extensive movements, delayed birth dates, increase in density within their range and especially on calving grounds, increase in wolf populations, and exceptionally high snow accumulation during the 1980-81 winter." Clearly, population control in caribou is complex and may well include aspects of habitat such as space for predator avoidance and forage quality and quantity. The effect of predation, in those herds where it predominates, may be density-dependent. Thus, population control in caribou does not appear consistent with the requirements of the Vacant-Hotel Hypothesis for density-independent population control and superabundant resources.

Muskox: Senner states that muskoxen "are not really limited by any factor at present" and presents the case that periodically severe winter weather may ultimately "impose the greatest [limiting] effect, provided hunting is regulated to allow continuing population growth," implying habitat is less important to muskoxen than is weather. Even though the total North Slope muskox population is increasing, the preceding statements cannot be sustained. North Slope muskox populations are derived from introductions that occurred in 1969 at Barter Island and in 1970 at Kavik River (Jingfors and Klein 1982). By 1979, the ratio of calves to reproductive-age cows was 0.89 (Jingfors and Klein 1982), and population growth on the ANWR was approximately exponential through 1985 (Garner and Reynolds 1986:250-279). The rate of muskox population growth is affected by mortality; mortality, although light, has been documented from controlled hunting and predation (Garner and Reynolds 1986:250-279). Although weather causes mortality in some muskox populations by creating ice and crusted or deep snow that reduces forage availability (Gunn 1982), Garner and Reynolds (1986:250-279) reported only four known muskox mortalities ascribed to old age or malnutrition on the ANWR between 1982 and 1985. Three of these animals were 16 to 19 years old and probably died of old age. Severe winter weather apparently has not played an important role in reducing muskox numbers in the ANWR during recent years.

Muskox and caribou, among other species, may emigrate in response to increased density. Reynolds (1989) reported dispersal of muskoxen after their peak abundance (within the refuge) was reached in 1986. The ANWR population has now stabilized (or slightly declined) at about 400 animals. Emigration eastward to Canada and westward to Game Management Unit 26B (roughly the area between the Canning and Itkillik rivers), coupled with a slight decline in productivity, appears responsible for the stabilized ANWR population. Pat Reynolds (Ecol., U.S. Fish and Wildl. Serv., ANWR, Fairbanks, pers. comm.) hypothesizes that social (i.e., density-dependent) factors may play a role in emigration of muskoxen. In this particular population, the emigrants are colonizing unoccupied habitat vacated by historic extirpation of the muskox from Alaska and thus are unlikely to suffer increased mortality or decreased natality. Emigrants from a population that had already occupied all optimal habitat probably could not achieve the density existing in the source population, being limited by suboptimal habitat (see Andrewartha [1971] for discussion of animal distribution and abundance).

Growth rates of muskox populations in ANWR may have been influenced by local availability of suitable habitat, as well (Garner and Reynolds 1986:250-279). Muskoxen on the Canadian mainland feed heavily on willows during summer, especially *Salix alaxensis*, a species associated with riparian areas (Tener 1965, Gunn 1982). Similarly, during summer, muskoxen in the ANWR select riparian willows as well as low shrub/forb vegetation associated with river and stream valleys (Robus 1984, O'Brien 1988). About 95% of muskox observations occurred along rivers and creeks during this period as well as during the rut and fall season (Garner and Reynolds 1986:250-279). Snow depth is an important determinant of muskox distribution (Gunn 1982). In severe winters, muskoxen in the ANWR often are found on slopes and tops of hills and mountains, areas of decreased snow cover; greatest use of these areas occurs during pre-calving (Garner and Reynolds 1986:250-279). In mild winters, muskoxen remain in the riparian corridors (P. Reynolds 1989: pers. comm.). Thus, muskoxen have specific habitat requirements (see O'Brien 1988) and certain arctic wetlands are necessary components of muskox habitat. North Slope riparian corridors, although not currently fully stocked by muskoxen, are high-value muskox habitat.

The availability of high-value muskox habitats ultimately may limit muskox populations through the effects of nutrition on reproduction. Hauer et al. (1989) have shown a direct relationship between body mass and female reproduction in muskox. Young, maternally raised females must exceed a body mass of 180 kg during the rutting period to achieve sexual maturity. The age of first reproduction, an important determinant of population growth rate, is thus linked to nutrition. Likewise, lactating multiparous females experimentally reduced to body masses less than 185 kg during rut failed to conceive. The conception rate of adult females also is an important determinant of population growth rate linked to nutrition. Malnutrition may occur more frequently in females since males maintain year-round dominance and may compete more successfully for available forage (White et al. 1981). Weather-induced mortality or reduced reproduction act through nutrition, a density-dependent mechanism of population control. Resources thus are not superabundant for muskoxen during winter, and preferred summer habitats have limited distributions (O'Brien 1988) as well. Since the nutritional needs of muskoxen are met by their habitat, the availability of such habitat controls muskox numbers and production in a manner inconsistent with the Vacant-Hotel Hypothesis.

Polar Bear: Senner correctly states that the "fate of breeding-age females and their cubs" is an important factor in determining polar bear populations. He then dismisses the importance of onshore den availability because most Beaufort Sea maternity dens occur on sea ice rather than on land (Amstrup et al. 1986). Although the polar bear, largely a marine species, is a poor choice for discussion in relation to arctic-wetland habitats on the North Slope, onshore maternity dens in drifted snow do occur (Lentfer 1982), and the topographic relief provided by riparian areas generates snowdrifts suitable for denning. Amstrup (1986) reported that "of 27 known or suspected dens located by radiotelemetry . . . 21 or 78% were on the pack ice." This left six dens (22%) on land or coastal fast ice. Amstrup has conducted further polar bear research in the Beaufort Sea Region. Out of 81 radiocollared females, 61 (75%) denned in pack ice, 4 (5%) denned on land-fast ice, and 16 (20%) denned on land between October 1981 and May 1988. In winter of 1988-1989, eight radiocollared bears denned on land and eight on the pack ice (Steven C. Amstrup, Wildl. Biol., U.S. Fish and Wild. Serv. Office of Fish and Wildl. Res., Anchorage, pers. comm. [unpublished data]). Thus, approximately 25% of polar bear denning in the Beaufort Sea population occurs on land or fast ice adjacent to land.

One fact concerning the importance of land dens has become clear: dens on land contribute significantly to recruitment in the Beaufort Sea population of polar bears. Land dens produce a mean of 1.27 cubs•den^{-1} while dens on sea ice produce a mean of only 0.69 cubs•den^{-1}, a statistically highly significant difference; thus, of known polar bear dens, the 23% occurring on land account for 37% of cub production (S.C. Amstrup 1989: pers. comm. [unpublished data]). This production is important because Amstrup et al. (1986) show that at current mortality rates for female bears, the number surviving to breeding age (6 yr) and entering the breeding population each year is approximately equal to the annual loss of breeding females in the Beaufort Sea population. Disruption of denning uniquely affects breeding-age females and cubs at a time when this component of the population is stressed by unregulated U.S. harvest. Amstrup et al. (1986) conclude that "the Beaufort Sea population can sustain little if any increase in mortalities of females" and express concern that "pipelines and roadways may prevent female polar bears from moving to and from inland denning areas. This may force them to den in less desirable locations." These authors also emphasized the importance of cumulative stresses on polar bear populations and that "hydrocarbon exploration and development have allowed unprecedented increases in human numbers in coastal areas of the Beaufort Sea, and habitat is changing at an accelerating rate." While on-going research has not yet answered the question of whether the availability of denning habitat limits polar bear populations (S.C. Amstrup 1989: pers. comm.), neither is there evidence that Senner's position -- "onshore den site availability is not thought to limit [polar bear] productivity" -- is correct.

<u>Wolf</u>: Senner's choice of the wolf as a carnivore representative of arctic wetlands suffers from the difficulty that this species may have had the widest distribution (e.g., most of the Northern Hemisphere) of any post-Pleistocene, wild land animal (Paradiso and Nowak 1982). Clearly, wolves are very adaptable predators. Nevertheless, Senner's statement that "habitat-related factors are not considered to limit wolf populations, except where changed conditions have reduced the prey base or eliminated denning sites," citing Paradiso and Nowak (1982), requires examination. Paradiso and Nowak, in fact, specifically relate extirpation of certain Eurasian wolf populations to "human persecution and habitat modification." Further,

these authors state that wolf populations are potentially threatened by economic developments and that "the most critical of these operations is oil and gas exploration, which is penetrating even the most remote parts of the arctic." We agree with Paradiso and Nowak that "such activities seldom directly affect wolves . . . [but] ungulate herds, on which wolves depend, could be disrupted and movements hindered."

Another aspect of habitat modification and development that potentially affects wolves is the density of roads. Mech et al. (1988), working in Minnesota, verified Thiel's (1985 [in Mech et al. 1988]) finding that wolves occupying habitats in temperate regions generally do not occur where road densities exceed 0.58 $\mathrm{km{\bullet}km^{-2}}$. They state that road densities above the threshold level allow human access to wolves, facilitating harvest and accidental deaths of wolves. Mech et al. also emphasize that their results might not apply to areas with different patterns of human occupancy or to roads with restricted access. The North Slope oilfields clearly are such a case at this time. Nevertheless, road density in the Prudhoe Bay Field was about 0.82 $\mathrm{km{\bullet}km^{-2}}$ by 1983 and the rate of road development in the Kuparuk Field was similar to the historic rate for Prudhoe (Walker et al. 1986). This road density is nearly equal to that (0.83 $\mathrm{km{\bullet}km^{-2}}$) at which Mech et al. found primary wolf range devoid of wolves. Although perhaps not a problem under existing conditions on Alaska's North Slope, the road network might adversely affect wolves under conditions of unrestricted public access or increased human population at some future time.

Disruption and hindrance of movements have been demonstrated for the Central Arctic Caribou Herd (Cameron et al. 1983 [in Shideler 1986], Lawhead and Curatolo 1984 [in Shideler 1986], Smith and Cameron 1985*a,b*). Shideler (1986) reviews evidence that North Slope petroleum development has displaced cow/calf pairs of the Central Arctic Herd, has hindered the herd's coastal insect-relief movements, and has created barriers that render portions of their range essentially inaccessible. While the herd has grown in the absence of high predation rates, further disruption could affect wolf numbers. Unexploited wolf populations appear to be regulated by the interaction of social factors and nutrition (Packard and Mech 1983), but disease may occasionally be important (Mech 1970:311-314, Carbyn 1982). In addition, recruitment of wolves to the population is sensitive to wolf density as shown by large differences in the percentage of pups between natural and exploited wolf populations (Mech 1970:59-67). Packard and Mech (1983) "consider the primary mechanism of population to be pack territoriality. It regulates the number of breeding units in an area, according to food resources. A primary non-social regulating factor is summer food availability, influencing pup survival." Thus, wolves show density-dependent responses to their environment, in particular to food resources. Such responses are not consistent with the Vacant-Hotel Hypothesis.

Brown Bear: Senner does not discuss the brown bear, which ranges across the North American Low Arctic (Craighead and Mitchell 1982), northern Europe, and Siberia (Nowak and Paradiso 1983:970). This is a surprising omission in light of the grizzly's (*U.a. horribilis*) role as a consumer in tundra ecosystems and in light of its use of wetland habitats for foraging (Hechtel 1985, Phillips 1986). Brown bears occur at greater density in the mountains and foothills of the Brooks Range than on the Arctic Coastal Plain (Curatolo and Moore 1975, Reynolds 1980). "Brown bears occurring north of the Brooks Range are at the northern extent of the species range. These populations are characterized as having low reproductive potential, short periods of food availability, large individual home ranges, and habitats that provide little protective cover (Reynolds et al. 1976, Reynolds 1979)" (Garner and Reynold 1986:307). Reynolds (1980) estimated that bear density on the coastal-plain portion of the NPRA was 1 bear•780 km $^{-2}$ based on several North Slope bear studies. However, Nagy et al. (1983) found a fall bear density of 1 bear•255 to 262 km $^{-2}$ on the Tuktoyaktuk Peninsula on Canada's Beaufort Sea coast. Although coastal habitats may not provide optimum conditions for brown bears in the Arctic in the absence of the rich fisheries resources (e.g., Pacific salmon [*Oncorhynchus*]) found in other coastal regions, bears using the Arctic Coastal Plain must depend on the wetlands that dominate this landscape for sustenance.

The digestive system of the brown bear is not efficient for assimilating the plant material that makes up a variable portion of its diet, which implies that rich, high-protein food resources are important (Craighead and Mitchell 1982, Schoen 1990). Nagy et al. (1983) recorded large weight losses (0.22 kg•day $^{-1}$ over 239 days for adult males and over 238 days for adult females) and gains (0.29 kg•day $^{-1}$ over 111 days for adult males and 0.42 kg•day $^{-1}$ over 111 days for adult females) for bears near the Beaufort Sea, illustrating the importance of nutrition to bears in the Arctic. Food controls the reproductive potential of brown bears by influencing age of first reproduction, litter size, and breeding interval of females in a density-independent manner (Bunnell and Tait 1981). Reynolds (1980) attributes the high density of bears (1 bear•42 km $^{-2}$) estimated for his Utukok River study area to the availability of caribou, since the Western Arctic Herd calves nearby. Mean litter size in this population is 2.03, somewhat higher than for other North Slope populations (e.g., 1.8 west of the Canning River [Curatolo and Moore 1975]) for a reproductive rate of 0.503 cub•female $^{-1}$yr $^{-1}$. Reynolds (1980) states that "Caribou may be a particularly important segment of the grizzly bears' diet because they are available during a time when those portions of vegetation upon which bears feed are of poor nutritive quality."

Studies by Hechtel (1985) and Phillips (1986) demonstrate that brown bears feed on the roots of *Hedysarum alpinum* and *Oxytropis borealis* in the spring, as well as feed on caribou to the extent that it is available; graze on green vegetation such as *Equisetum arvense*, *Boykinia richardsonii*, and grasses and sedges in the summer; and eat berries, arctic ground squirrels, and roots in the fall. Nagy et al. (1983) found similar food habits for brown bears using Richards Island and the Tuktoyaktuk Peninsula in the Mackenzie River Delta, Northwest Territories. Reindeer and *H. alpinum* were important spring foods; *Equisetum* spp. and sedges were important in summer; and arctic ground squirrels, monocots, *H. alpinum*, forbs, and berries were important fall foods. *H. alpinum*, *O. borealis*, and arctic ground squirrels occur in riparian communities, as well as nonfloodplain sites (Hechtel 1985); herbaceous tundra used for grazing occupies wet lowland sites (Phillips 1986); and berries occur in string bogs as well as drier sites (Hechtel 1985). Brown bears selected shrub tundra, herbaceous tundra, and tall shrubland, all wetland (including riparian) habitats, at various times of the year in the ANWR (Phillips 1986). To the west of the ANWR, brown bears using only mountain or river valley habitats most frequently were observed in river valleys during spring and used both habitats with approximately equal frequency in the fall (Curatolo and Moore 1975). Curatolo and Moore (1975) believed that bears searched river valleys for winter-killed moose or fresh vegetation in spring and for berries in the fall. Nagy et al. (1983) observed bear trails in spring on "lakes, deltas and channels, revealing where bears had dug into numerous muskrat push-ups" on the Tuktoyaktuk Peninsula. Wetland habitats thus are important foraging locations for bears in the foothills of the Brooks Range and on the Tuktoyaktuk Peninsula.

An increasing amount of research on bear-habitat relationships has been conducted in recent years (Schoen 1990). The brown bear "has been able to survive in North America only where spacious habitat has insulated it from excessive human-caused mortality" (Craighead and Mitchell 1982). Although such habitat exists in the Arctic, human activities and land uses, particularly those that fragment bear habitat, must be considered by resource managers (Reynolds 1980, Schoen 1990) because brown bears cannot adapt to large-scale habitat modification and human habitation (Reynolds 1980, Craighead and Mitchell 1982). Cumulative displacement of bears through loss of habitat or merely by contact with humans (Phillips 1986) conceivably could increase mortality rates. Population sinks -- areas where bears "are removed from the ecosystem after coming in contact with humans" -- may develop in areas of human settlement or other development activities (Schoen 1990). Brown bears require extensive freedom of movement to reach necessary resources (Craighead and Mitchell 1982); therefore, fragmentation of landscapes used by brown bears may lead to their extirpation (see island biogeography theory [MacArthur and Wilson 1967] and its application to wildlife conservation in old-growth forests [Harris 1984] as examples). Schoen (1990) views multiple-use management of brown bear range as having an uncertain outcome for bear conservation.

Although most contemporary mortality of brown bears results from hunting, in unexploited populations adult males may regulate bear abundance in a density-dependent manner by "killing or evicting younger males" (Bunnell and Tait 1981). Most bear mortalities in Reynolds' (1980) study appeared to be caused by adult males. At least one component of population regulation in brown bears - mortality - is density dependent. Although food may not limit female reproductive rates in a density-dependent manner, cumulative habitat loss reduces total food supply for female bears, and the inverse relationship between latitude and reproductive rates (Bunnell and Tait 1981) indicates that food in the Arctic is not superabundant for bears. Factors that limit the abundance and distribution of prey species such as caribou may also affect the nutritional state of individual bears with consequent effects on reproduction. In aggregate, these considerations do not support the Vacant-Hotel Hypothesis.

Summary: Mammalian herbivores using arctic-tundra wetlands are ultimately limited by forage, although predation and other factors also affect their abundance. Mammalian predators in turn are ultimately limited by prey density but are also influenced by social behavior. Limitations imposed on herbivores by the quality and quantity of their habitats are reflected in predator populations, which affect prey populations. Evidence from arctic mammals indicates a complex system of biotic interactions that does not support the assumptions of density-independent controls over populations and superabundant resources inherent in the Vacant-Hotel Hypothesis.

HABITAT-BASED RESOURCE MANAGEMENT: A RATIONAL ALTERNATIVE TO MEASURING POPULATION-LEVEL IMPACTS

Senner (1989) states that the oil and gas industry currently avoids high-value wetlands and minimizes project impacts on fish and wildlife habitats by carefully designing and locating oilfield facilities. He believes these actions sufficiently mitigate wetland losses based on his assertion that habitat availability does not limit animal populations in arctic-tundra wetlands. Senner therefore concludes that regulatory agencies should not require further mitigation until the cumulative impacts of wetlands fills demonstrably reduce fish and wildlife populations on Alaska's North Slope. These views raise the fundamental issue of how resource managers should address the impacts of development on fish and wildife populations. One approach, inherent in the concept of mitigation, is to compensate for, or otherwise offset, developmental impacts through habitat management. The alternative approach, favored by the oil and gas industry, is to monitor populations of fish and wildlife and to apply offsetting mitigation only after a decline attributable to the development activity has been conclusively demonstrated by resource agencies. The relative merits of these management systems should be considered in the debate over wetlands policies as applied to arctic-tundra wetlands.

Population-Based Management

Leopold (1933:139) offers the census of wildlife populations as the first step in managing land for wildlife production. Wildlife management uses population measurement and analysis to address three general problems: conserving small or declining populations, harvesting populations for sustained yields, and controlling populations that are too dense (Caughley 1977:168). Managers attempt to influence birth and mortality rates of fish and game species to meet management objectives, usually sustainable harvests for sport, commercial, personal, and subsistence use. These actions usually are directed at a small number of species used for human consumption. The manager often focuses on short-term changes in populations occurring in fixed areas of habitat. In the long-term, those habitats may be manipulated to increase their carrying capacity as part of the management strategy, but the amount of habitat is viewed as constant. Why, then, should population-based management of developmental impacts on wetlands be inappropriate? Traditional uses of population measurement, including such things as composition counts and mortality studies, deal with dynamic and potentially reversible factors that acutely affect substantial numbers of individuals within a population over a relatively short period. Harvest, predation, and lethal disease in theory can be rapidly evaluated by counting carcasses. Similarly, births in principle can be directly counted. These gross events of fecundity or mortality usually add or subtract population increments measurable with relatively modest efforts.

In contrast, incremental wetland loss acts chronically and diffusely to reduce the total area of habitat available, not only to fish and game species used for human consumption but to all components of the biological community (see discussion of cumulative impacts in Meehan and Webber [1986]). Individuals experience displacement, altered patterns of movement, disturbance from the activities occurring on wetland fills, potentially increased competition for resources, and loss of community production. These effects are for practical purposes permanent, but they accumulate slowly. Incremental habitat loss rarely produces instantaneous mortality or large-scale reproductive failure, assuming critical habitats were avoided during fill placement. Rather, subtle changes in age-specific fecundity and mortality rates are likely to occur, but such changes may be difficult to detect in response to small losses of habitat. In the limit, as habitat goes to zero, the population supported by the habitat also goes to zero. Thus, resource managers eventually detect the effects of cumulative habitat loss at the population level. Since habitat lost to development is often permanently removed from production, detection of population-level effects must be extremely sensitive in order to prevent irreparable losses to fish and wildlife populations. Factors affecting this sensitivity include the species monitored, the precision of population estimates, and the certainty with which changes in species abundance can be assigned to specific causes. These factors severely constrain the practicality of population-based mangement of development impacts.

Burden of Proof: Some government agencies are statutorily charged with monitoring the status of certain fish and wildlife populations. For instance, the U.S. Fish and Wildlife Service has such responsibilities for migratory nongame birds. Although agencies do monitor populations for purposes of conservation and management, population-based management of wetland fills would shift the burden of proof for habitat protection from the private to the public sector. This shift would be accompanied by a huge economic burden on the public, which would continue indefinitely or until wildlife populations declined sufficiently to demonstrate habitat loss as the cause. Should government be unable to respond to greatly expanded research needs to study populations of all wetland species, resource-management decisions would be based on expediency rather than biology, and many unmonitored but ecologically important species might decline from habitat loss. Responsibility for mitigating past habitat losses might then fall on the public as well, completing the transformation of industry savings to public expenses. Realistically, population-based management of wetlands is beyond government's current or conceivable fiscal capability, reinforcing the argument against this approach. Second, cumulative habitat loss is not easily reversed once a population decline has been detected and shown to be caused by such loss. It is very likely that the resultant population decline would persist for a long time on the scale relevant to human user groups and ecological functions. These losses would exacerbate depression of animal abundance from other causes.

Population Estimation: Sampling ecological densities of fish and wildlife will not reveal the direct effects of habitat loss on their populations but may reveal the local effects of disturbance and other secondary impacts. For example, Meehan (1986*b*) modeled cumulative habitat loss for six species of shorebirds in the Prudhoe Bay Oilfield and estimated that 5,206 fewer birds were present than had existed under natural conditions, a 9% reduction. The estimated loss resulted from the direct effects of gravel fill as well as secondary impacts from habitat alteration adjacent to the fills. In addition, estimated grouped shorebird density in "undisturbed" habitat within the developed area was 13% less than in control areas outside the oilfield. Thus, overall density of the six species of shorebirds in the oilfield was an estimated 22% less than in the control area. Troy (1988) did not find that overall bird density was lower in undisturbed oilfield habitats away from roads than in control areas but stated that much more intensive study would be necessary to rigorously show this point. Meehan (1986*b*) stated that "the actual fates of birds displaced by development activities are difficult if not impossible to determine directly." This leaves the question of whether or not the ecological density of these species increased outside the oilfield.

The direct effect of habitat loss, in principle, is a decline in crude density unless crowding commensurately increases ecological density in remaining species-specific habitat, which is unlikely in the long term for species existing at their environmental carrying capacities. Assuming that ecological density remains constant for small, incremental habitat losses, a fractional change in crude density is unlikely to be statistically significant if measured over a reasonably large area. Since crude density is a function of ecological density and habitat area, resource managers would have to determine causes for all changes in ecological density to explain changes in crude density. Monitoring animal densities even then would not provide all the information necessary for population-based management of developmental impacts because it is not possible to know with certainty whether or not changes in crude density are reflected at the population level.

Likewise, chronic effects of wetland fills on wildlife populations may not be apparent, or may be only subtly apparent, in measurements of birth and death rates if the affected species maintains its ecological density on a slowly diminishing habitat base. A single wetland fill removes only a tiny increment of habitat for a widely distributed, abundant species; only a tiny, assuredly unmeasurable, temporary increase in death rate or decline in birth rate is necessary to adjust the species' ecological density to its environmental carrying capacity. For a threatened species such as the arctic peregrine falcon (*F.p. tundrius*) with a small regional population and relatively limited nesting distribution, habitat loss might produce an effect (e.g., failure to occupy an otherwise suitable breeding territory) measurable at the population level (Hunt 1988, Ratcliffe 1988), but such losses are not likely to be permitted under existing management strategies. This suggests that, for the majority of species, sampling population parameters such as birth and death rates will yield little information on the cumulative impacts of habitat loss. Complete censuses or precise population estimates, conducted repeatedly over long periods of time, might be the only way to detect eventual population declines caused by a diminishing habitat base.

Few populations are easy to enumerate with certainty and many can be determined only approximately even with large expenditures of money and effort. The ability to enumerate an animal population is dependent upon the size of the organism and its habitat, abundance, mobility, pattern of distribution, and to some extent its trophic level. Naturally, large organisms are easier to see than small organisms. For example, a muskox is visible from a light aircraft whereas a lemming is not. An animal's habitat strongly influences its visibility to a human observer conducting a census. Arctic ciscoes (*Corregonus autumnalis*) are not readily seen in the aquatic environment, but wolverines can be seen on snow-covered tundra. Animals functioning at high trophic levels (e.g., peregrine falcon) tend to have less energy potentially available to them than do herbivores and thus the former have smaller populations that may be more difficult to locate but are potentially more amenable to counting. Finally, animals such as caribou or spawning Dolly Varden char (*Salvelinus malma*) that seasonally congregate in discrete locations can be censused more easily than animals with wide-spread distributions such as passerine birds. Nevertheless, complete censuses are not possible for most animal populations. Population estimation through scientific sampling is then necessary. Population estimation is subject to error, which inherently limits any attempt to statistically link habitat loss to a population decline. In general, the error of the estimate can only be reduced by increasing sample sizes, implementing more sophisticated sampling designs (e.g., stratification), and replicating samples, all steps that increase costs.

Obtaining a complete census or a precise population estimate is only a prelude to interpretation of the population data. A central problem with population-based management is assigning a cause or causes to population change because populations respond to a variety of biotic and abiotic factors and are rarely, if ever, constant (MacArthur and Connell 1966:132). The cyclicity of wildlife populations in boreal regions is well known (Pruitt 1978:51-52). For example, the brown lemming exhibits periodic swings in abundance that change its density by several orders of magnitude (Batzli 1981). Caribou change in abundance over much longer periods (Skoog 1968:318-328). Other species exhibit year-to-year variation. The abundance of pintail ducks in the Arctic may change by as much as 123% between years (Derksen and Eldridge 1980; R. King, pers. comm. [file data]) and some shorebirds may fluctuate by even greater amounts (Pitelka et al. 1974; Thomas C. Rothe, Waterfowl Coord., Alaska Dep. of Fish and Game, Anchorage, pers. comm.). These natural population fluctuations combined with errors of population estimation further reduce the statistical probability of detecting the effects of habitat loss on populations until the losses are dramatic and perhaps irreversible. The probability of detecting these effects could only be improved by species-specific studies of predation, nutrition, reproduction, disease, weather, and perhaps other factors. Funding for such studies is unlikely; therefore, large population declines would be necessary to demonstrate the effects of habitat loss. Great public expense has been required to restore or otherwise focus on species such as the Aleutian Canada goose (*B. c. leucopareia*), wood duck (*Aix sponsa*), black duck (*Anas rubripes*), whooping crane (*Grus americana*), and piping plover (*Charadrius melodus*) that declined from the effects of habitat loss, introduced predators, and other factors. Allowing large declines in arctic species as tests of impacts of development would unjustifiably risk animal populations.

Indicator Species: Resource-management agencies would bear the costs of managing developmental impacts by monitoring fish and wildlife populations. Economics would limit such monitoring to at most several "indicator species." Although several federal agencies use indicator species to evaluate habitat quality and population trends for other species or for entire communities, Landres et al. (1988) have criticized such use. These authors conclude that indicators should not be used in cases where direct measurement of resources or habitat components is feasible. Nonetheless, if population-based management of development impacts in arctic wetlands became necessary, conflicting criteria would constrain the choice of indicator species. Indicator species must be susceptible to census or precise population estimation, must represent and be specifically linked to the ecological communities subject to habitat loss, and probably should include species of particular socioeconomic or aesthetic significance. Even careful selection of indicator species would not preclude damage to other species whose habitat requirements did not closely overlap those of the indicators (Landres et al. 1988). Worse, it would be difficult to detect such effects until they had become pronounced and perhaps irreversible. Thus, selecting appropriate species for monitoring the effects of habitat loss would be neither easy nor without ecological risk.

On Alaska's North Slope, indicator species would have to represent both the herbivore-based and the detritus-based trophic systems. Rodents and ungulates are the major herbivores (Batzli et al. 1981), although geese, ptarmigan, and hares are also present (Batzli et al. 1980). Of the herbivores, ungulates are perhaps easiest to census and have direct significance because they are harvested for human consumption. Caribou are widely distributed on the North Slope (Hemming 1971:5-19) but select specific forage plants within specific communities (White et al. 1981), possibly complicating their use as indicators. Also, caribou might not respond quickly to localized habitat losses because of their mobility, irruptive population dynamics (Skoog 1968:318-328, Bergerud 1978), and periodic shifts of range (Skoog 1968:312-317). Muskox and moose are more sedentary than caribou, select primarily riparian areas (Coady 1982, Gunn 1982, Robus 1984), and are present in relatively low numbers (Coady 1982, Garner and Reynolds 1986:250-288). Muskox and moose might quickly respond to loss of riparian habitat but would not be good indicator species for other wetland communities. Among the remaining herbivores, geese similarly select a limited number of wetland communities (Bergman et al. 1977, Derksen et al. 1981), although their relatively large size and seasonal molting and staging might make them reasonable to enumerate. Nevertheless, human harvest, occurring in an international as well as domestic context and perhaps not precisely measurable, would impede detecting the effects of habitat loss on geese, consistent with the arguments of Landres et al. (1988) against use of migratory species as indicators.

Shorebirds, unlike geese, are insectivorous members of the detritus-based trophic system (MacLean 1980). These species are widely distributed in arctic wetlands, but their small size and tremendous abundance would make precise estimation of their populations difficult. Avian and terrestrial predators might be considered as indicator species for the detritus-based as well as the herbivore-based trophic system. Certainly, the threatened arctic peregrine falcon has great aesthetic significance, depends on wetland prey, has a relatively stable breeding population under natural conditions, and is already censused on a fairly regular basis (Ambrose et al. 1988). Peregrine distribution is limited primarily to major river corridors, however, and loss of important wetlands within peregrine nesting territories is not likely to be allowed. The snowy owl and jaegers are more widely distributed but their breeding densities fluctuate in response to cyclic fluctuations in their prey populations (Pitelka et al. 1955, Maher 1974). The arctic fox exhibits similar cycles (Fitzgerald 1981). Such variation in predator and prey numbers would greatly complicate any attempt to show that loss of wetlands had reduced populations of avian and terrestrial predators.

Based on the preceding discussion, we do not see any good candidates for indicator species to monitor the effects of habitat loss on wildlife populations in arctic wetlands. Resource managers would have great difficulty selecting indicators meeting the previously outlined criteria, estimating populations, and interpreting multivariate causes of population change.

Carrying Capacity: Senner's view that wetland habitat can be destroyed until populations of fish and wildlife demonstrably decline from loss of habitat suffers from many inherent flaws. One such flaw is his belief that the carrying capacity of arctic wetlands (apparently defined as that set by forage) greatly exceeds the number of animals currently found there. However, the ecological definition of carrying capacity advanced by Edwards and Fowle (1974) (see Appendix B for discussion) includes predation, disease, weather, nutrition, reproduction, and other factors controlling a population, consistent with the original usage of Leopold (1933) and more recent usage by Bergerud (1983). For a stable resident population, Edwards and Fowle (1974) regard the minimum number of animals present over a specified time period, often 1 year, as a measure of carrying capacity. Even nonresident arctic species such as dunlin establish breeding territories occupying all suitable habitat (Pitelka et al. 1974). At least for the nesting period, breeding dunlin exist at the carrying capacity of their environment. Since arctic wetlands have resident species, some of which are not harvested by humans, by the reasoning of Edwards and Fowle (1974) these species generally are at carrying capacity.

Factors setting carrying capacities control ecological densities, and total populations are the integrated ecological densities of available habitats. As wetland habitats are lost, total populations of animals existing at the carrying capacities of their environment must decline. Displaced individuals temporarily increase ecological density, which in most situations cannot persist because the carrying capacity of a habitat generally is not increased by increasing the number of animals using the habitat. Game stocking and "putand-take" fisheries demonstrate this point. Industry argues that ecological densities simply increase as wetlands are lost. This view completely disregards the mechanisms controlling fish and wildlife densities, is certainly incorrect for resident species with stable populations, and may well be incorrect for most migratory species.

Managing wetland impacts on fish and wildlife by monitoring their populations can be summarized as requiring resource managers to expend great effort and expense researching indirect effects of development activities while failing to regulate direct causes such as loss of habitat. As previously discussed, very large declines in fish and wildlife populations might occur before the cause could be assigned with certainty to the effects of habitat loss. Fish and wildlife populations would then be permanently capped at the level where the effects of habitat loss were demonstrated because in practical terms the losses would be largely irreversible. The futility of monitoring populations to demonstrate development impacts is amply illustrated by fisheries studies associated the Endicott Project on Alaska's North Slope. Years of data collection, involving expenditures of approximately $12 million, have yielded little conclusive information on fish populations in the unbounded nearshore Beaufort Sea environment. On the other hand, extensive habitat alteration (e.g., altered temperature and salinity of water masses) detrimental to anadromous fish using nearshore waters has been documented to result from the project's causeway to offshore drilling islands (Dr. Alvin G. Ott, Reg. Supervisor, Alaska Dep. of Fish and Game, Fairbanks, pers. comm.). We conclude that population-based management of petroleum development in Alaska's wetlands would be neither cost effective nor practical and would fail to properly protect fish and wildlife resources.

Habitat-Based Management

Senner (1989) faults habitat-based management, particularly as applied to the Arctic, placing considerable emphasis on what he considers to be the "traditional" wildlife-management perspective - wildlife populations. To bolster his position, Senner cites Leopold (1933). And yet, even in the formative years of wildlife management as a discipline, Leopold (1933:4-5) listed reservation of game lands (i.e., habitat preservation) after restriction of hunting and application of predator control in the sequence of "controls" that he felt constituted the historical development of game management. Leopold then stated, "North America has reached the stage where controls of the fifth class [control of food, cover, special factors, and disease] are becoming necessary. The present game conservation movement is groping toward the realization of this fact." Food and cover are, of course, components of habitat. Leopold (1933:253-323) devoted several chapters to management of food and cover to increase game production, an implicit recognition of the importance of high-value habitats to game species. Today, nearly 60 years later, cumulative loss of fish and wildlife habitat has made habitat management more important than ever. Habitat management, one of Leopold's (1933:4) stated underpinnings of game management, retains its fundamental position.

Wetland management based on habitat protection is a rational, cost-effective alternative to population-based management of developmental impacts. Habitat-based management is rational because it is based on ecological principles, deals directly with the immediate environmental impact of gravel fills, is quantifiable, and does not subject fish and wildlife populations to undue risk. Habitat-based management is cost effective because industry can map wetland covertypes in areas of proposed development, allowing resource managers to evaluate potential habitat losses and to require mitigation without need for widespread population monitoring.

If fully applied, mitigation, defined in federal regulations (40 CFR 1508.20) pursuant to the National Environmental Policy Act (NEPA), would remove much of the risk of necessary wetland development to fish and wildlife populations by ensuring that substantial degradation of arctic wetlands did not occur. Although Senner states that the petroleum industry is willing to avoid high-value wetlands and minimize impacts to other wetlands, individual permit applications sometimes do not reflect this philosophy (pers. obs.), and fish and wildlife agencies have primarily worked to achieve avoidance and minimization. "Rectification," "reduction," and "compensation," the remaining steps of the NEPA mititgation sequence, will become much more important if a national policy of "no net loss" of wetlands is applied to Alaska. These mitigation steps will be needed to maintain wetland functions such as providing fish and wildlife habitats.

High-Value Habitats: Habitat is the place where an organism is found, including both biotic and abiotic factors (Smith 1966:13, Odum 1971:234). Predator density, prey density, climate, and other factors that act upon an organism are part of its habitat because they determine whether the organism can persist in a given location. Habitat value represents the degree to which a given location approaches the optimum habitat for a population or for specific life-history functions of a population. In general, the distribution of a population within its habitat at a given time is a measure of habitat value. Loss of certain portions of a species' habitat may affect the species more immediately and more severely than loss of other portions of its habitat. For example, on Alaska's North Slope fish overwinter in a limited amount of deepwater habitat and spring-fed areas, some caribou herds repeatedly use the same calving grounds, and some waterfowl species congregate in huge groups to molt and feed. These areas are high-value habitats where large numbers of animals carry out important life-history functions. Loss of high-value habitats could have immediate adverse consequences for the populations that they support. Habitat-based management is predicated on identification and protection of high-value habitats so that necessary development can be directed into those areas having less value for fish and wildlife. Nevertheless, in order to maintain fish and wildlife populations, these necessary habitat losses must also be mitigated.

Ecosystem Functions: Senner believes that individual populations are not fully occupying their habitats and are consequently unaffected by habitat loss, but a similar assertion cannot be applied to a community.

A biotic community is "any assemblage of populations of living organisms in a prescribed area or habitat" (Krebs 1972:379), and communities are the biotic components of ecosystems (McNaughton and Wolf 1973:5-6). Gravel fill in arctic wetlands covers areas of vegetation, including emergent aquatic plants, or covers waterbodies supporting phytoplankton and epipelic algae, eliminating their primary production. This diminishes the area of the natural ecosystem, substituting areas of extremely low productivity, and may otherwise alter ecosystem character. Primary production is a major wetland function that contributes to nutrient and carbon export, food-chain support, and fish and wildlife habitat (Adamus and Stockwell 1983, Sather and Smith 1984). Reduced primary production means less energy is available to support secondary production by consumer organisms within biotic communities.

Similarly, nutrients necessary for primary production cycle from reservoirs such as organic material (Chapin et al. 1980*b*) that become unavailable if covered by fill. Fill-induced alteration of wetland character is very likely to affect nutrient-cycling mechanisms (Sather and Smith 1984) and produce secondary effects, such as blocking sheet flow and causing thaw subsidence at the toes of fill embankments, that also influence wetland functions, for example by altering shorebird habitat (Meehan 1986*b*). Depletion of both energy and nutrients may reduce the number, and perhaps the diversity, of organisms in affected communities. Thus, it is highly improbable that elimination or alteration of community habitat does not also eliminate or reduce component populations and diminish ecosystem functions. Resource managers can maintain ecosystem functions by managing habitats affected by development.

Costs of Habitat Management: Those who profit from siting development in wetlands would largely bear the costs of habitat management by incorporating required mitigation features in project design and construction. Resource managers would be responsible for identifying the wetland functions and values affected by proposed projects, for determining appropriate mitigation to maintain affected functions and values, and for ensuring that necessary mitigation procedures are properly and successfully executed by the developer. Overall regulatory costs for implementing habitat-based management would be far smaller than attempting to monitor populations of fish and wildlife species potentially affected by wetland losses.

Implementation of Mitigation Procedures: Although Senner states that revegetation of gravel fills has no benefit to wildlife (even where active grazing by geese or caribou is noted), that removal of fill may cause thermokarst topography, and that agencies and industry approach conversion of flooded gravel mines to fish and wildlife habitat with caution, the newly implemented Memorandum of Agreement between the EPA and the U. S. Army Corps of Engineers concerning Section 404 permitting under the federal Clean Water Act generally requires application of the NEPA mitigation sequence to maintain overall wetland functions and acreage. Governmental agencies can manage habitats to maintain ecosystem functions by identifying and requiring replacement of significant functions impaired by necessary development.

Determining wetland functions is a difficult task. Mitsch and Gosselink (1986:406-414) reviewed several methods of wetland evaluation, but these methods would need calibration for specific regions of Alaska. Nevertheless, in situations where wetland fills will remove specific covertypes from production, it is sometimes a relatively simple task to identify their general fish and wildlife values from past studies of habitat use by specific species (e.g., waterbirds [Bergman et al. 1977, Derksen et al. 1981]). Even where such values are not known, compensation might be obtained by designing wetland restoration, enhancement, or creation projects to yield similar habitats to those lost. It seems likely that wetland functions other than habitat might coincidentally be restored or created as additional benefits of mitigating habitat losses.

Arctic-wetland rehabilitation is currently under study in the Kuparuk Oilfield with emphasis on providing "a diverse assemblage of habitats that will be useful to fish, caribou, waterfowl, and shorebirds" (Jorgenson 1989). As a result of these studies, Jorgenson (1989) has proposed the following rehabilitation strategies:

> (1) habitat enhancement for fish in flooded mine sites; (2) restoration of wetlands in littoral zones of flooded mine pits for fish and shorebirds; (3) restoration of wetlands in shallow ponds on overburden stockpiles for shorebirds and waterfowl; (4) restoration of original tundra on miscellaneous, less severely modified land; (5) revegetation of thick gravel fill with grass and/or forb cultivars to compensate for lost habitat; and (6) selected removal of gravel to help restore original vegetation and surface drainage patterns in critical areas.

Partial or complete fill removal (strategy #6 above) from abandoned sites may be an excellent mechanism to compensate for new fills in arctic wetlands. Not only would removed fill reduce the need for newly mined gravel, but Jorgenson (1989) has shown that revegetation is enhanced when fill thickness is reduced. He also noted "the highest rates of natural colonization on gravel pads have been those that have undergone thermokarst and polygonization," conditions enhanced by substantial or complete fill removal.

From an ecological perspective, revegetation changes barren gravel to an area supporting primary production. Even thermokarst is not necessarily a bad thing when compared to a barren gravel fill. Thaw and slumping can create wetland habitat suitable for some avian species (McKendrick 1986, Troy 1985) and contribute peat carbon to the production of aquatic systems (Schell 1983, Schell and Ziemann 1983). Naturally, rehabilitation programs involving fill removal should be carefully conducted to consider thermal effects. Removal of all or a substantial portion of gravel fill from abandoned sites increases the probability that adequate soil moisture will be present to promote revegetation. Studies of sites disturbed by petroleum exploration in the NPR-A showed that "plant colonization has been most rapid on the sites where soil moisture was elevated by the disturbance, such as around the edges of impoundments and thermokarst pools" and that revegetation initiates "chemical and biological influences to promote soil development and improve habitat for plant colonization" (McKendrick 1986). Colonization by native species, in turn, initiates a process of ecological succession that eventually produces a well-developed plant community on the disturbed site. Such a community restores at least some of the ecological values lost when the fill was originally placed. McKendrick (1986) reported geese and shorebirds used thermokarst pools, geese and caribou grazed revegetated areas, ground squirrels burrowed in dry embankments, and predators appeared as small mammal numbers increased at rehabilitated sites. He also noted revegetated sites grazed by geese were colonized by *Arctophila fulva*, perhaps because the geese transferred propagules to the sites. The Alaska Department of Fish and Game is also enthusiastic about its program to encourage industry to rehabilitate gravel mines as fish habitat based upon departmental research and fish-transplantation efforts (Hemming et al. 1989). Industry consultants have incorporated this approach in their recommended rehabilitation strategies (Jorgenson 1989). Off-site mitigation offers challenges; however, rehabilitation of disturbed sites benefits fish and wildlife through at least partial restoration of ecosystem functions.

Creation or restoration of wetlands is not a simple task, but positive habitat value can be obtained even from out-of-kind compensation or partial restoration as compared to sterile gravel pads. Resource managers can require mitigation of development impacts before or during project construction. Industry can incorporate mitigation features in project designs. On Alaska's North Slope, industry can mitigate wetland losses by rehabilitating abandoned fills, removing temporary fills at completion of use, enhancing low-value habitats to increase their productivity, restoring wetlands elsewhere in the region, or creating new wetlands. This approach markedly contrasts with monitoring fish and wildlife populations for signs of impact and applying full mitigation only after large losses of habitat have occurred.

Summary

Managing the impacts of development on arctic-tundra wetlands by monitoring fish and wildlife populations is not practical for reasons of cost, lack of appropriate indicator species, difficulty of estimating populations, and difficulty of statistically separating multivariate causes of population fluctuation. Population-based management shifts the burden of proof for showing these impacts from industry - where the burden should lie - to governmental agencies and hence the public. This approach exposes fish and wildlife populations to unjustifiable risks, given the difficulties of detecting and demonstrating the effects of cumulative habitat losses, since such losses are for practical purposes permanent. Permanent habitat losses effectively cap maximum fish and wildlife populations at the level where the effects of the losses are finally demonstrated.

In contrast, mitigating the impacts of wetland losses on fish and wildlife populations by managing habitats places the responsibility for offsetting project impacts on those who benefit from development (e.g., industry) rather than on the public. This is a rational approach for managing the impacts of development because it is dynamic and maintains overall wetland functions and the productivity of wetland habitats as development occurs. Habitat-based management also is cost effective because it deals with the measurable, direct impacts of development rather than indirect effects that can be measured only with great difficulty and expense, if measured at all. Habitat management based on sound scientific assessments of wetland functions and values is the only realistic approach for implementing the "no net loss" policies for wetlands being developed by state and federal governments.

LITERATURE CITED

Adamus, P.R. 1983. A method for wetland functional assessment: Vol. II. FHWA assessment method. U.S. Dep. Transport. Rep. No. FHWA-IP-82-84. 124 pp. + appendix.

________, and L.T. Stockwell. 1983. A method for wetland functional assessment: Vol. I. Critical review and evaluation concepts. U.S. Dep. Transport. Rep. No. FHWA-IP-82-23. 162 pp. + appendices.

Alexander, V., D.W. Stanley, R.J. Daley, and C.P. McRoy. 1980. Primary producers. Pages 179-250 *in* J.E. Hobbie, ed. Limnology of tundra ponds, Barrow, Alaska. Academic Press.

Alison, R.M. 1975. Breeding biology and behavior of the oldsquaw (*Clangula hyemalis L.*). Ornithol. Monogr. No. 18, Am. Ornithol. Union. 52 pp.

Ambrose, R.E., and K.E. Riddle. 1988. Population dispersal, turnover, and migration of Alaska peregrines. Pages 677-684 *in* T.J. Cade, J.H. Enderson, C.G. Thelander, and C.M. White, eds. Peregrine falcon populations: their management and recovery. The Peregrine Fund, Inc., Boise, ID.

_______, R.J. Ritchie, C.M. White, P.F. Schempf, T. Swem, and R. Dittrick. 1988. Changes in the status of peregrine falcon populations in Alaska. Pages 73-82 *in* T.J. Cade, J.H. Enderson, C.G. Thelander, and C.M. White, eds. Peregrine falcon populations; their management and recovery. The Peregrine Fund, Inc., Boise, ID.

Amstrup, S.C. 1986. Research on polar bears in Alaska, 1983-1985. Pages 85-108 *in* Polar bears. Proc. of the Ninth Working Meeting of the IUCN/SSC Polar Bear Specialist Group, Edmonton, Canada. 9-11 August 1985.

_______, I. Stirling, and J.W. Lentfer. 1986. Past and present status of polar bears in Alaska. Wildl. Soc. Bull. 14(3):241-254.

Andersson, M. 1976. Population ecology of the long-tailed skua (*Stercorarius longicaudus* Vieill.). J. Anim. Ecol. 45(2): 537-559.

_______. 1981. Reproductive tactics of the long-tailed skua *Stercorarius longicaudus*. Oikos 37(3): 287-294.

_______, and S. Erlinge. 1977. Influence of predation on rodent populations. Oikos 29(3): 591-597.

_______, and F. Götmark. 1980. Social organization and foraging ecology in the arctic skua *Stercorarius parasiticus*: a test of the food defendability hypothesis. Oikos 35(1): 63-71.

Andrewartha, H.G. 1971. Introduction to the study of animal populations, Second ed. Univ. Chicago Press. Chicago and London. 283 pp.

_______, and L.C. Birch. 1984. The ecological web: more on the distribution and abundance of animals. Univ. Chicago Press, Chicago and London. 506 pp.

*Ashkenazie, S., and U.N. Safriel. 1979. Time-energy budget of the Semipalmated Sandpiper, *Calidris pusilla*, at Barrow, Alaska. Ecology 60:783-799.

Baker, J.A., and R.J. Brooks. 1981. Raptor and vole populations at an airport. J. Wildl. Manage. 45(2): 390-396.

_______, and _______. 1982. Impact of raptor predation on a declining vole population. J. Mammal. 63(2): 297-300.

Baker, M.C., and A.E.M. Baker. 1973. Niche relationships among six species of shorebirds on their wintering and breeding ranges. Ecol. Monogr. 43: 193-212.

Barry, S.J., and T.W. Barry. 1990. Food habits of glaucous gulls in the Beaufort Sea. Arctic 43(1): 43-49.

Barichello, N. 1983. Productivity of gyrfalcons (*Falco rusticolus*) as a response to changes in the ptarmigan (*Lagopus* spp.) abundance over a five year period [abstract only]. Proc. Alaska Sci. Conf. 34:65.

Barsdate, R.J., M.C. Miller, V. Alexander, J.R. Vestal, and J.E. Hobbie. 1980. Oil spill effects. Pages 388-406 *in* J.E. Hobbie, ed. Limnology of tundra ponds, Barrow, Alaska. Academic Press.

Batzli, G.O. 1981. Populations and energetics of small mammals in the tundra ecosystem. Pages 377-396 *in* L.C. Bliss, O.W. Heal, and J.J. Moore, eds. Tundra ecosystems: a comparative analysis. Cambridge Univ. Press, Cambridge.

________, R.G. White, and F.L. Bunnell. 1981. Herbivory: a strategy of tundra consumers. Pages 359-375 *in* L.C. Bliss, O.W. Heal, and J.J. Moore, eds. Tundra ecosystems: a comparative analysis. Cambridge Univ. Press, Cambridge.

________, _______, S.F. MacLean, Jr., F.A. Pitelka, and B.D. Collier. 1980. The herbivore-based trophic system. Pages 335-410 *in* J.Brown, P.C. Miller, L.L. Tieszen, and F.L. Bunnell, eds. An arctic ecosystem: the coastal tundra at Barrow, Alaska. Dowden, Hutchinson & Ross, Inc., Stroudsburg, PA.

Bay, R.R. 1969. Runoff from small peat watersheds. J. Hydrol. 9(1):90-102.

Bellrose, F.C. 1980. Ducks, geese and swans of North America, Third ed. A Wildl. Manage. Inst. Book sponsored jointly with the Illinois Nat. History Surv. Stackpole Books, Harrisburg, PA. 540 pp.

*Benson, C., R. Timmer, B. Holmgren, G. Weller, and S. Parrish. 1975. Observations of seasonal snow cover and radiation climate at Prudhoe Bay, Alaska during 1972. Pages 13-52 *in* J. Brown, ed. Ecological investigations of the Tundra Biome in the Prudhoe Bay Region, Alaska. Biol. Pap. Univ. Alaska, Spec. Rep. No. 2.

Bent, A.C. 1938. Life histories of North American birds of prey. Part Two. Smithsonian Inst. U.S. Natl. Mus. Bull. 170. [Reprinted in 1961 by Dover Publications, Inc. New York. 482 pp.]

Bergerud, A.T. 1971. The population dynamics of Newfoundland caribou. Wildl. Monogr. No. 25. 55 pp.

_______. 1974. Decline of caribou in North America following settlement. J. Wildl. Manage. 38(4): 757-770.

_______. 1978. Caribou. Pages 82-101 *in* J.L. Schmidt and D.L. Gilbert, eds. Big game of North America: ecology and management. Wildl. Manage. Inst. Book, Stackpole Books, Harrisburg, PA.

_______. 1980. A review of the population dynamics of caribou and wild reindeer in North America. Pages 556-581 *in* E. Reimers, E. Gaare, and S. Skjenneberg, eds. Proc. 2nd Int. Reindeer/Caribou Symp., Roros, Norway, 1979. Direktoratet for vilt og ferskvannsfisk, Trondheim.

_______. 1983. The natural population control of caribou. Pages 14-61 *in* F.L. Bunnell, D.S. Eastman, and J.M. Peek, eds. Symposium on natural regulation of wildlife populations. Proc. Northwest Sect. The Wildl. Soc. For., Wildl. and Range Exp. Stn. Univ. Idaho, Moscow.

_______, R.D. Jakimchuk, and D.R. Carruthers. 1984. The buffalo of the north: caribou (*Rangifer tarandus*) and human developments. Arctic 37(1): 7-22.

*Bergman, R.D., and D.V. Derksen. 1977. Observations on arctic and red-throated loons at Storkersen Point, Alaska. Arctic 30: 41-51.

_______, R.L. Howard, K.F. Abraham, and M.W. Weller. 1977. Water birds and their wetland resources in relation to oil development at Storkersen Point, Alaska. U.S. Fish and Wildl. Serv. Resour. Publ. 129. Washington, DC. 38 pp.

Bliss, L.C. 1981. North American and Scandinavian tundras and polar deserts. Pages 8-24 *in* L.C. Bliss, O.W. Heal, and J.J. Moore, eds. Tundra ecosystems: a comparative analysis. Cambridge Univ. Press, Cambridge.

Boxall, P.C., and M.R. Lein. 1982. Feeding ecology of snowy owls (*Nyctea scandiaca*) wintering in southern Alberta. Arctic 35(1): 282-290.

*Brown, J., and R. Berg, eds. 1980. Environmental engineering investigations along the Yukon River to Prudhoe Bay Haul Road, Alaska. U.S. Army Cold Regions Res. Eng. Lab. Spec. Rep. 80-19. 187 pp.

Buchanan, J.B., C.T. Shick, L.A. Brennan, and S.G. Herman. 1988. Merlin predation on wintering dunlins: hunting success and dunlin escape tactics. Wilson Bull. 100(1): 108-118.

Buckman, H.O., and N.C. Brady. 1969. The nature and properties of soils, Seventh ed. The Macmillan Co./Collier-Macmillan Limited, London. 653 pp.

Bunnell, F.L., O.K. Miller, P.W. Flanagan, and R.E. Benoit. 1980. The microflora: composition, biomass, and environmental relations. Pages 255-290 *in* J. Brown, P.C. Miller, L.L. Tieszen, and F.L. Bunnell, eds. An arctic ecosystem: the coastal tundra at Barrow, Alaska. Dowden, Hutchinson & Ross, Inc., Stroudsburg, PA.

_______, and D.E.N. Tait. 1981. Population dynamics of bears - implications. Pages 75-98 *in* C.W. Fowler and T.D. Smith, eds. Dynamics of large mammal populations. John Wiley & Sons, New York.

Burger, J. 1984. Shorebirds as marine animals. Pages 17-81 *in* J. Burger and B.L. Olla, eds. Shorebirds: breeding behavior and populations. Plenum Press, New York and London.

Burnham, W.A., and W.G. Mattox. 1984. Biology of the peregrine and gyrfalcon in Greenland. Meddelelser om Gronland, Biosci. 14.

Butler, M., M.C. Miller, and S. Mozley. 1980. Macrobenthos. Pages 297-339 *in* J.E. Hobbie, ed. Limnology of tundra ponds, Barrow, Alaska. Academic Press.

Calef, G.W., and D.C. Heard. 1979. Reproductive success of peregrine falcons and other raptors at Wager Bay and Melville Peninsula Northwest Territories. Auk 96(4): 662-674.

Calverley, B.K., and D.A. Boag. 1977. Reproductive potential in parkland- and arctic-nesting populations of mallards and pintails (Anatidae). Can. J. Zool. 55:1242-1251.

**Cameron, R.D., and K.R. Whitten. 1979. Distribution and movements of caribou in relation to the Kuparuk Development Area. First interim rep., Alaska Dep. Fish and Game, Fairbanks. 32 pp.

**_______, and _______. 1980. Influence of the Trans-Alaska Pipeline corridor on the local distribution of caribou. Pages 475-484 *in* E. Reimers, E. Gaare, and S. Skjenneberg, eds. Proc. 2nd Int. Reindeer/Caribou Symp., Roros, Norway, 1979. Direktoratet for vilt og ferskvannsfisk, Trondheim.

Carbyn, L.N. 1982. Incidence of disease and its potential role in the population dynamics of wolves in Riding Mountain National Park, Manitoba. Pages 106-116 *in* F.H. Harrington and P.C. Paquet, eds. Wolves of the world: perspectives of behavior, ecology, and conservation. Noyes Publ., Park Ridge, NJ.

Carter, L.D., J.A. Heginbottom, and M. Woo. 1987. Arctic lowlands. Pages 583-628 *in* W.L. Graf, ed. Geomorphic systems of North America: Boulder, Colorado, Geol. Soc. of Am., Centennial Spec. Vol. 2.

Caughley, G. 1977. Analysis of vertebrate populations. John Wiley & Sons, London. 234 pp.

Chapin, F.S., III. 1980. The mineral nutrition of wild plants. Ann. Rev. Ecol. Syst. 11:233-260.

________, P.C. Miller, W.D. Billings, and P.I. Coyne. 1980*b*. Carbon and nutrient budgets and their control in coastal tundra. Pages 458-482 *in* J. Brown, P.C. Miller, L.L. Tieszen, and F.L. Bunnell, eds. An arctic ecosystem: the coastal tundra at Barrow, Alaska. Dowden, Hutchinson & Ross, Inc., Stroudsburg, PA.

________, and G.R. Shaver. 1985*a*. Arctic. Pages 16-40 *in* B.F. Chabot and H.A. Mooney, eds. Physiological ecology of North American plant communities. Chapman and Hall, New York and London.

________, and ______. 1985*b*. Individualistic growth response of tundra plant species to environmental manipulations in the field. Ecology 66(2):564-576.

________, L.L. Tieszen, M.C. Lewis, P.C. Miller, and B.H. McCown. 1980*a*. Control of tundra plant allocation patterns and growth. Pages 140-185 *in* J.Brown, P.C. Miller, L.L. Tieszen, and F.L. Bunnell, eds. An arctic ecosystem: the coastal tundra at Barrow, Alaska. Dowden, Hutchinson & Ross, Inc., Stroudsburg, PA.

Clark, R.J. 1975. A field study of the short-eared owl, *Asio flammeus* (Pontoppidan), in North America. Wildl. Monog. No. 47. 67 pp.

Coady, J.W. 1982. Moose. Pages 902-922 *in* J.A. Chapman and G.A. Feldhamer, eds. Wild mammals of North America: biology, management, and economics. Johns Hopkins Univ. Press, Baltimore and London.

Collier, B.D., N.C. Stenseth, S. Barkley, and R. Osborn. 1975. A simulation model of energy acquisition and utilization by the brown lemming *Lemmus trimucronatus* at Barrow, Alaska. Oikos 26(3): 276-294.

Connors, P.G., J.P. Myers, and F.A. Pitelka. 1979. Seasonal habitat use by arctic Alaskan shorebirds. Stud. in Avian Biol. 2:101-111.

Court, G.S., D.M. Bradley, C.C. Yates, and D.A. Boag. 1988. The population biology of peregrine falcons in the Keewatin District of the Northwest Territories, Canada. Pages 729-739 *in* T.J. Cade, J.H. Enderson, C.G. Thelander, and C.M. White, eds. Peregrine falcon populations: their management and recovery. The Peregrine Fund, Inc., Boise, ID.

Couturier, S., J. Brunelle, D. Vandal, and G. St-Martin. 1990. Changes in the population dynamics of the George River caribou herd, 1976-87. Arctic 43(1): 9-20.

Craighead, J.J., and J.A. Mitchell. 1982. Grizzly bear. Pages 515-556 *in* J.A. Chapman and G.A. Feldhamer, eds. Wild mammals of North America: biology, management, and economics. Johns Hopkins Univ. Press, Baltimore and London.

Crawford, C.S., and J.R. Gosz. 1986. Dynamics of desert resources and ecosystem processes. Pages 63-87 *in* N. Polunin, ed. Ecosystem theory and application. John Wiley & Sons, New York.

Curatolo, J.A., and G.D. Moore. 1975. Home range and population dynamics of grizzly bear (*Ursus arctos* L.) in the eastern Brooks Range, Alaska. 77 pp. *in* R.D. Jakimchuk, ed. Studies of large mammals along the proposed Mackenzie Valley gas pipeline route from Alaska to British Columbia. Arct. Gas Biol. Rep. Ser. Vol. 32.

Custer, T.W., and F.A. Pitelka. 1987. Nesting by pomarine jaegers near Barrow, Alaska, 1971. J. Field Ornithol. 58(2): 225-230.

Dahl, E. 1986. Zonation in arctic and alpine tundra and fellfield ecobiomes. Pages 35-62 *in* N. Polunin, ed. Ecosystem theory and application. John Wiley & Sons, New York.

Davidson, N.C. 1981. Survival of shorebirds (Charadrii) during severe weather: the role of nutritional reserves. Pages 231-249 *in* N.V. Jones and W.J. Wolff, eds. Feeding and survival strategies of estuarine organisms. Plenum Press, New York and London.

DeKorte, J., and J. Wattel. 1988. Food and breeding success of the long-tailed skua at Scoresby Sund, Northeast Greenland. Ardea 76(1): 27-41.

Derksen, D.V., and W.D. Eldridge. 1980. Drought-displacement of pintails to the Arctic Coastal Plain, Alaska. J. Wildl. Manage. 44:224-229.

_______, T.C. Rothe, and W.D. Eldridge. 1981. Use of wetland habitats by birds in the National Petroleum Reserve - Alaska. U.S. Fish and Wildl. Serv. Resour. Publ. 141. Washington, DC. 27 pp.

_______, M.W. Weller, and W.D. Eldridge. 1979. Distributional ecology of geese molting near Teshekpuk Lake, National Petroleum Reserve-Alaska. Pages 189-207 *in* R.L. Jarvis and J.C. Bartonek, eds. Management and biology of Pacific Flyway geese: a symposium. OSU Book Stores, Inc., Corvallis, OR.

Dingman, S.L., R.G. Barry, G.Weller, C. Benson, E.F. LeDrew, and C.W. Goodwin. 1980. Climate, snow cover, microclimate, and hydrology. Pages 30-65 *in* J. Brown, P.C. Miller, L.L. Tieszen, and F.L. Bunnell, eds. An arctic ecosystem: the coastal tundra at Barrow, Alaska. Dowden, Hutchinson & Ross, Inc., Stroudsburg, PA.

_______, and F.R. Koutz. 1974. Relations among vegetation, permafrost, and potential insolation in central Alaska. Arct. and Alp. Res. 6(1):37-42.

Edwards, R.Y., and C.D. Fowle. 1974. The concept of carrying capacity (1955). Pages 353-360 *in* J.A. Bailey, W. Elder, and T.D. McKinney, eds. Readings in wildlife conservation. The Wildl. Soc., Washington, DC. [Reprinted from: Trans. North Am. Wildl. Conf. 20:589-602.]

Ellanna, L.J., and P.C. Wheeler. 1989. Wetlands and subsistence-based economies in Alaska, U.S.A. Arct. and Alp. Res. 21(4):329-340.

Erlinge, S., G. Göransson, L. Hansson, G. Högstedt, O. Liberg, J.N. Nilsson, T. Nilsson, T. von Schantz, and M. Sylven. 1983. Predation as a regulating factor on small rodent populations in southern Sweden. Oikos 40(1): 36-52.

Errington, P.L. 1961. Muskrats and marsh management. [A Wildl. Manage. Inst. Publ.] Univ. Nebraska Press, Lincoln. 183 pp.

Evans, P.R. 1981. Migration and dispersal of shorebirds as a survival strategy. Pages 275-290 *in* N.V. Jones and W.J. Wolff, eds. Feeding and survival strategies of estuarine organisms. Plenum Press, New York and London.

_______, and M.W. Pienkowski. 1984. Population dynamics of shorebirds. Pages 83-123 *in* J. Burger and B.L. Olla, eds. Shorebirds: breeding behavior and populations. Plenum Press, New York.

Everett, K.R., V.D. Vassiljevskaya, J. Brown, and B.D. Walker. 1981. Tundra and analogous soils. Pages 139-179 *in* L.C. Bliss, O.W. Heal, and J.J. Moore, eds. Tundra ecosystems: a comparative analysis. Cambridge Univ. Press, Cambridge.

Fitzgerald, B.M. 1981. Predatory birds and mammals. Pages 485-508 *in* L.C. Bliss, O.W. Heal, and J.J. Moore, eds. Tundra ecosystems: a comparative analysis. Cambridge Univ. Press, Cambridge.

Flanagan, P.W., and F.L. Bunnell. 1980. Microflora activities and decomposition. Pages 291-334 *in* J. Brown, P.C. Miller, L.L. Tieszen, and F.L. Bunnell, eds. An arctic ecosystem: the coastal tundra at Barrow, Alaska. Dowden, Hutchinson & Ross, Inc., Stroudsburg, PA.

Ford, J., and B.L. Bedford. 1987. The hydrology of Alaskan wetlands, U.S.A.: a review. Arct. and Alp. Res. 19(3):209-229.

Franklin, A.B., J.P. Ward, R.J. Gutierrez, and G.J. Gould, Jr. 1990. Density of northern spotted owls in Northwest California. J. Wildl. Manage. 54(1): 1-10

Frayer, W.E., D.D. Peters, and H.R. Pywell. 1989. Wetlands of the California Central Valley: status and trends - 1939 to mid-1980's. U.S. Fish and Wildl. Serv., Portland, OR. 28 pp.

Gabrielson, I.N., and F.C. Lincoln. 1959. The birds of Alaska. The Stackpole Company, Harrisburg, PA and Wildl. Manage. Inst., Washington, DC. 922 pp.

Garner, G.W., and P.E. Reynolds, eds. 1986. Arctic National Wildlife Refuge Coastal Plain resource assessment. Final report, baseline study of the fish, wildlife, and their habitats. U.S. Fish and Wildl. Serv., Anchorage, AK. 695 pp.

Gasaway, W.C., R.O. Stephenson, J.L. Davis, P.E.K. Shepard, and O.E. Burris. 1983. Interrelationships of wolves, prey, and man in interior Alaska. Wildl. Monogr. 84:1-50.

Gersper, P.L., V. Alexander, S.A. Barkley, R.J. Barsdate, and P.S. Flint. 1980. The soils and their nutrients. Pages 219-254 *in* J. Brown, P.C. Miller, L.L. Tieszen, and F.L. Bunnell, eds. An arctic ecosystem: the coastal tundra at Barrow, Alaska. Dowden, Hutchinson & Ross, Inc., Stroudsburg, PA.

Goss-Custard, J.D. 1980. Competition for food and interference among waders. Ardea 68: 31-52.

Gratto, C.L. 1988. Natal philopatry, site tenacity, and age of first breeding of the semipalmated sandpiper. Wilson Bull. 100(4): 660-663.

_______, R.I.G. Morrison, and F. Cooke. 1985. Philopatry, site tenacity, and mate fidelity in the semipalmated sandpiper. Auk 102: 16-24.

Gross, A.O. 1947. Cyclic invasions of the snowy owl and the migration of 1945-1946. Auk 64: 584-601.

Gunn, A. 1982. Muskox. Pages 1021-1035 *in* J.A. Chapman and G.A. Feldhamer, eds. Wild mammals of North America: biology, management, and economics. Johns Hopkins Univ. Press, Baltimore and London.

Hansen, H.A., and D.E. McKnight. 1964. Emigration of drought-displaced ducks to the Arctic. Trans. North Am. Wildl. Nat. Resour. Conf. 29:119-127.

Harris, L.D. 1984. The fragmented forest: island biogeography theory and the preservation of biotic diversity. Univ. Chicago Press, Chicago and London. 211 pp.

_______, and P. Kangas. 1988. Reconsideration of the habitat concept. Trans. North Am. Wildl. Nat. Resour. Conf. 53:137-143.

Hauer, W.A., R.G. White, and K.L. Parker. 1989. Pubertal body mass in the muskox and a role for body mass in the control of annual reproduction. Poster Presentation. 69th Ann. Meet., Am. Soc. Mammal. Abstracts. Univ. Alaska, Fairbanks.

Hawkins, L.L. 1986. Tundra swan (*Cygnus columbianus columbianus*) breeding behavior. M.S. Thesis. Univ. Minnesota. 145 pp.

Hechtel, J.L. 1985. Activity and food habits of barren-ground grizzly bears in arctic Alaska. M.S. Thesis. Univ. Montana, Missoula. 74 pp.

Hemming, C.R., P.K. Weber, and J.F. Winters. 1989. Limnological and fisheries investigations of flooded North Slope gravel mine sites, 1988. Alaska Dep. Fish and Game Habitat Div. Tech. Rep. No. 89-1. 60 pp.

Hobbie, J.E. 1980*a*. Major findings. Pages 1-18 *in* J.E. Hobbie, ed. Limnology of tundra ponds, Barrow, Alaska. Academic Press.

_______. 1980*b*. Introduction and site description. Pages 19-50 *in* J.E. Hobbie, ed. Limnology of tundra ponds, Barrow, Alaska. Academic Press.

________. 1984. The ecology of tundra ponds of the Arctic Coastal Plain: a community profile. U.S. Fish and Wildl. Serv. FWS/OBS-83/25. 52 pp.

*Hok, J.R. 1969. A reconnaissance of tractor trails and related phenomena on the North Slope of Alaska. U.S. Dep. Inter. Bur. Land Manage. 66 pp.

Holmes, R.T. 1966*a*. Feeding ecology of the redbacked sandpiper (*Calidris alpina*) in arctic Alaska. Ecology. 47:32-45.

_______. 1966*b*. Breeding ecology and annual cycle adaptations of the red-backed sandpiper (*Calidris alpina*) in northern Alaska. Condor 68: 3-46.

_______. 1970. Differences in population density, territoriality, and food supply of dunlin on arctic and subarctic tundra. Pages 303-317 *in* A. Watson, ed. Animal populations in relation to their food resources. Symp. British Ecol. Soc. 10:303-319.

_______. 1971. Density, habitat, and the mating system of the western sandpiper (*Calidris mauri*). Oecologia 7: 191-208.

_______, and F.A. Pitelka. 1968. Food overlap among coexisting sandpipers on northern Alaska tundra. System. Ecol. 17:305-318.

Hunt, W.G. 1988. The natural regulation of peregrine falcon populations. Pages 667-676 *in* T.J. Cade, J.H. Enderson, C.G. Thelander, and C.M. White, eds. Peregrine falcon populations: their management and recovery. The Peregrine Fund, Inc., Boise, ID.

Jehl, J.R., Jr. 1973. Breeding biology and systematic relationships of the stilt sandpiper. Wilson Bull. 85(2): 114-147.

Jingfors, K.T., and D.R. Klein. 1982. Productivity in recently established muskox populations in Alaska. J. Wildl. Manage. 46(4): 1092-1096.

Johnson, D.H., and J.W. Grier. 1988. Determinants of breeding distributions of ducks. Wildl. Monogr. No. 100. 37 pp.

Johnson, M.L., and S. Johnson. 1982. Voles. Pages 326-354 *in* J.A. Chapman and G.A. Feldhamer, eds. Wild mammals of North America: biology, management, and economics. Johns Hopkins Univ. Press, Baltimore and London.

Johnson, S.R. 1985. Adaptations of the long-tailed duck (*Clangula hyemalis*) during the period of molt in arctic Alaska. Proc. Int. Ornithol. Congr. 18: 530-540.

_______, and D.R. Herter. 1989. The birds of the Beaufort Sea. BP Exploration (Alaska) Inc., Anchorage. 372 pp.

Jorgenson, M.T. 1989. An overview of rehabilitation research in the Kuparuk Oilfield. Prepared for ARCO Alaska, Inc. and Kuparuk River Unit by Alaska Biol. Res., Inc., Fairbanks, AK. 64 pp.

Kadlec, J.A. 1987. Nutrient dynamics in wetlands. Pages 393-419 *in* K.R. Reddy and W.H. Smith, eds. Aquatic plants for water treatment and resource recovery. Magnolia Publ. Inc.

Kadlec, R.H., and J.A. Kadlec. 1978. Wetlands water quality. Pages 436-456 *in* P.E. Greeson, J.R. Clark, and J.E. Clark, eds. Wetland functions and values: the state of our understanding. Proc. Natl. Symp. on Wetlands. Am. Wat. Resour. Assoc.

Kalff, J. 1968. Some physical and chemical characteristics of arctic fresh waters in Alaska and northwestern Canada. J. Fish. Res. Bd. Can. 25(12):2575-2587.

Kane, D.L., S.R. Bredthauer, and J. Stein. 1981. Subarctic snowmelt runoff generation. Pages 591-601 *in* Proc. Special. Conf. on The Northern Community: A Search for a Quality Environment, ASCE, Seattle, WA.

_______, and R.F. Carlson. 1973. Hydrology of central arctic river basins of Alaska. Inst. of Water Resourc. Rep. No. IWR-41. Univ. Alaska, Fairbanks. 50 pp.

_______, and L.D. Hinzman. 1988. Permafrost hydrology of a small arctic watershed. Pages 590-595 *in* Proc. of V Int. Conf. on Permafrost, Tapir Publ., Trondheim, Norway.

Keith, L.B., and L.A. Windberg. 1978. A demographic analysis of the snowshoe hare cycle. Wildl. Monogr. 58:1-70.

Kerlinger, P., and M.R. Lein. 1986. Differences in winter range among age-sex classes of snowy owls (*Nyctea scandiaca*) in North America. Ornis Scandinavica 17(1): 1-7.

Kiera, E.F.W. 1984. Feeding ecology of black brant on the North Slope of Alaska. Pages 40-48 *in* D.N. Nettleship, G.A. Sanger, and P.F. Springer, eds. Marine birds: their feeding ecology and commercial fisheries relationships. Proc. Pacific Seabird Group Symp., Seattle, WA, 6-8 January, 1982. Can. Wildl. Serv. Spec. Publ.

Kiff, L.F. 1988. Changes in the status of the peregrine in North America: an overview. Pages 123-139 *in* T.J. Cade, J.H. Enderson, C.G. Thelander, and C.M. White, eds. Peregrine falcon populations: their management and recovery. The Peregrine Fund, Inc., Boise, ID.

King, J.G. 1970. The swans and geese of Alaska's Arctic Slope. Wildfowl 21:11-17.

_______, and D.V. Derksen. 1986. Alaska goose populations: past, present and future. Trans. North Am. Wildl. Nat. Resour. Conf. 51:464-479.

King, R. 1979. Results of aerial surveys of migratory birds on NPR-A in 1977 and 1978. Pages 187-226 *in* P.C. Lent, ed. Studies of selected wildlife and fish and their use of habitats on and adjacent to the National Petroleum Reserve in Alaska 1977-1978. Vol. 1. U.S. Dep. Inter., Nat. Petroleum Reserve in Alaska, 105(c) Land Use Study, Anchorage, Alaska.

Klett, A.T., T.L. Shaffer, and D.H. Johnson. 1988. Duck nest success in the Prairie Pothole Region. J. Wildl. Manage. 52(3): 431-440.

Korpimäki, E. 1985. Rapid tracking of microtine populations by their avian predators: possible evidence for stabilizing predation. Oikos 45(2): 281-284.

Krebs, C.J. 1972. Ecology: the experimental analysis of distribution and abundance. Harper & Row, New York. 694 pp.

Kuyt, E. 1980. Distribution and breeding biology of raptors in the Thelon River area, Northwest Territories, 1957-1969. Can. Field-Nat. 94(2): 121-130.

Landres, P.B., J. Verner, and J.W. Thomas. 1988. Ecological uses of vertebrate indicator species: a critique. Conserv. Biol. 2(4): 316-328.

Langvatn, R. 1977. Characteristics and relative occurrence of remnants of prey found at nesting places of gyrfalcon *Falco rusticolus*. Ornis Scandinavica 8(2): 113-125.

Larsen, D.G., D.A. Gauthier, and R.L. Markel. 1989. Causes and rate of moose mortality in the southwest Yukon. J. Wildl. Manage. 53(3):548-557.

Larson, J.S., P.R. Adamus, and E.J. Clairain, Jr. 1988. Functional assessment of freshwater wetlands: a manual and training outline. Prepared for the Inter. Union for the Conserv. of Nature and Nat. Res. and funded by the Worldwide Fund for Nat. 78 pp.

Lawson, D.E. 1986. Response of permafrost terrain to disturbance: a synthesis of observations from northern Alaska, USA. Arct. and Alp. Res. 18:1-17.

*______, J. Brown, K.R. Everett, A.W. Johnson, V. Komarkova, B.M. Murray, D.F. Murray, and P.J. Webber. 1978. Tundra disturbances and recovery following the 1949 exploratory drilling, Fish Creek, northern Alaska. U.S. Army Cold Reg. Res. Eng. Lab. Rep. 78-28. Hanover, NH. 81 pp.

Lein, M.R., and G.A. Webber. 1979. Habitat selection by wintering snowy owls (*Nyctea scandiaca*). Can. Field-Nat. 93: 176-178.

Lensink, C.J. 1973. Population structure and productivity of whistling swans on the Yukon Delta, Alaska. Wildfowl 24:21-25.

Lentfer, J.W. 1982. Polar bear. Pages 557-566 *in* J.A. Chapman and G.A. Feldhamer, eds. Wild mammals of North America: biology, management, and economics. Johns Hopkins Univ. Press, Baltimore and London.

Leopold, A. 1933. Game management. Charles Scribner's Sons, New York. 481 pp.

Lidicker, W.Z., Jr. 1988. Solving the enigma of microtine "cycles." J. Mammal. 69(2):225-235.

Litvin, K.E., A.I. Pulyaev, and E.V. Syroechkovsky. 1985. Colonies of the snow goose (*Anser caerulescens*), brent goose (*Branta bernicla*) and eider (*Somateria mollissima*) near the snowy owl (*Nyctea scandiaca*) nests on Wrangel Island [English summary only]. Zoologicheskii Zhurnal 64(7): 1012-1023.

MacArthur, R.H., and J.H. Connell. 1966. The biology of populations. John Wiley & Sons, Inc., New York. 200 pp.

________, and E.O. Wilson. 1967. The theory of island biogeography. Princeton Univ. Press, Princeton. 203 pp.

MacInnes, C.D., R.A. Davis, R.N. Jones, B.C. Lieff, and A.J. Pakulak. 1974. Reproductive efficiency of McConnell River small Canada geese. J. Wildl. Manage. 38(4): 686-707.

Mackenthun, K.M. 1969. The practice of water pollution biology. U.S. Dep. Inter. Fed. Wat. Pollut. Control. Adm., Washington, DC. 281 pp.

MacLean, S.F. 1980. The detritus-based trophic system. Pages 411-457 *in* J. Brown, P.C. Miller, L.L. Tieszen, and F.L. Bunnell, eds. An arctic ecosystem: the coastal tundra at Barrow, Alaska. Dowden, Hutchinson & Ross, Inc., Stroudsburg, PA.

MacNally, R.C. 1983. On assessing the significance of interspecific competition to guild structure. Ecology 64(6): 1646-1652.

Maher, W.J. 1974. Ecology of pomarine, parasitic, and long-tailed jaegers in northern Alaska. Cooper Ornithol. Soc. Pacific Coast Avifauna No. 37. 147 pp.

Maltby, E. 1986. Waterlogged wealth: why waste the world's wet places. Int. Inst. for Environ. and Dev., London and Washington, DC. 200 pp.

Manville, R.H., and S.P. Young. 1965. Distribution of Alaskan mammals. U.S. Fish and Wildl. Serv. Bur. Sport Fish. and Wildl. Cir. 211. 74 pp.

Marsh, P., and M. Woo. 1979. Annual water balance of small high arctic basins. Pages 536-546 *in* Canadian Hydrology Symposium: 79 - Cold Climate Hydrology. Proc. Natl. Res. Counc. of Can., Ottawa.

Martin, P.D., and C.S. Moitoret. 1981. Bird populations and habitat use, Canning River Delta, Alaska. Rep. to U.S. Fish and Wildl. Serv. Arct. Natl. Wildl. Refuge, Fairbanks, AK. 188 pp.

McKendrick, J.D. 1986. Final cleanup at selected (1975-1981) wellsites, sampling and testing of waters and bottom muds in the reserve pits and the recording of tundra plant responses on the National Petroleum Reserve in Alaska (NPRA). Volume III: recording of tundra plant responses. Prepared by Nuera Reclamation Co. (Anchorage) for the U.S. Geol. Surv.. 225 pp.

McNaughton, S.J., and L.L. Wolf. 1973. General ecology. Holt, Rinehart, and Winston, Inc., New York. 710 pp.

Mech, L.D. 1970. The wolf: the ecology and behavior of an endangered species. Publ. for Am. Mus. Nat. Hist., Nat. Hist. Press, Garden City, NY. 384 pp.

_______, S.H. Fritts, G.L. Radde, and W.J. Paul. 1988. Wolf distribution and road density in Minnesota. Wildl. Soc. Bull. 16: 85-87.

Meehan, R. 1986*a*. Section I. Background information and assessment guidance for resource managers. 77 pp. *in* R. Meehan, P.J. Webber, and D. Walker, eds. Tundra development review: toward a cumulative impact assessment method. Prepared for U.S. Environ. Protection Agency by U.S. Fish and Wildl. Serv., Anchorage, AK.

_______. 1986*b*. Section II.C. Cumulative impacts on shorebirds in the Prudhoe Bay Oilfield, Alaska. 39 pp. *in* R. Meehan, P.J. Webber, and D. Walker, eds. Tundra development review: toward a cumulative impact assessment method. Prepared for U.S. Environ. Protection Agency by U.S. Fish and Wildl. Serv., Anchorage, AK.

_______. 1986*c*. Section III. Waterbird and surface impact annotated bibliographies. 95 pp. *in* R. Meehan, P.J. Webber, and D. Walker, eds. Tundra development review: toward a cumulative impact assessment method. Prepared for U.S. Environ. Protection Agency by U.S. Fish and Wildl. Serv., Anchorage, AK.

_______. 1986*d*. Section IV. Species accounts. 37 pp. *in* R. Meehan, P.J. Webber, and D. Walker, eds. Tundra development review: toward a cumulative impact assessment method. Prepared for U.S. Environ. Protection Agency by U.S. Fish and Wildl. Serv., Anchorage, AK.

_______, and T.W. Jennings. 1988. Characterization and value ranking of waterbird habitat on the Colville River delta, Alaska. Prepared for U.S. Environ. Protection Agency by U.S. Fish and Wildl. Serv., Anchorage. 105 pp.

_______, and P.J. Webber. 1986. Towards an understanding and assessment of cumulative impacts of Alaskan North Slope oil and gas development. 37 pp. *in* R. Meehan, P.J. Webber, and D. Walker, eds. Tundra development review: toward a cumulative impact assessment method. Prepared for U.S. Environ. Protection Agency by U.S. Fish and Wildl. Serv., Anchorage, AK.

Meltofte, H. 1985. Populations and breeding schedules of waders, Charadrii, in high arctic Greenland. Meddelelser om Gronland, Biosci. 16 pp.

Mickelson, P.G. 1975. Breeding biology of cackling geese and associated species on the Yukon-Kuskokwim Delta, Alaska. Wildl. Monogr. 45:1-35.

Miller, F.L. 1982. Caribou. Pages 923-959 *in* J.A. Chapman and G.A. Feldhamer, eds. Wild mammals of North America: biology, management, and economics. John Hopkins Univ. Press, Baltimore and London.

Miller, M.C., R.T. Prentki, and R.J. Barsdate. 1980. Physics. Pages 51-75 in J.E. Hobbie, ed. Limnology of tundra ponds, Barrow, Alaska. Academic Press.

Miller, P.C., P.J. Webber, W.C. Oechel, and L.L. Tieszen. 1980. Biophysical processes and primary production. Pages 66-101 *in* J. Brown, P.C. Miller, L.L. Tieszen, and F.L. Bunnell, eds. An arctic ecosystem: the coastal tundra at Barrow, Alaska. Dowden, Hutchinson & Ross, Inc., Stroudsburg, PA.

Mindell, D.P., J.L.B. Albuquerque, and C.M. White. 1987. Breeding population fluctuations in some raptors. Oecologia 72(3): 382-388.

Mitsch, W.J., and J.G. Gosselink. 1986. Wetlands. VanNostrand Reinhold Co., New York. 537 pp.

Moore, J.J. 1981. Mires. Pages 35-37 *in* L.C. Bliss, O.W. Heal, and J.J. Moore, eds. Tundra ecosystems: a comparative analysis. Cambridge Univ. Press, Cambridge.

Morrison, R.I.G. 1984. Migration systems of some New World shorebirds. Pages 125-202 *in* J. Burger and B.L. Olla, eds. Shorebirds: breeding behavior and populations. Plenum Press, New York.

Muir, D., and D.M. Bird. 1984. Food of gyrfalcons at a nest on Ellesmere Island. Wilson Bull. 96(3): 464-467.

Myers, J.P. 1981*a*. Cross-seasonal interactions in the evolution of sandpiper social systems. Behav. Ecol. Sociobiol. 8: 195-202.

_______. 1981*b*. A test of three hypotheses for latitudinal segregation of the sexes in wintering birds. Can. J. Zool. 59: 1527-1534.

_______, P.G. Connors, and F.A. Pitelka. 1979. Territoriality in nonbreeding shorebirds. Stud. in Avian Biol. 2: 231-246.

_______, and F.A. Pitelka. 1980. Effect of habitat conditions of spatial parameters on shorebird populations. Rep. to Dep. Energy for 1975-1979. Univ. California, Berkeley. 82 pp.

Nagy, J.A., R.H. Russell, A.M. Pearson, M.C.S. Kingsley, and C.B. Larsen. 1983. A study of grizzly bears on the barren-grounds of Tuktoyaktuk Peninsula and Richards Island, Northwest Territories, 1974 to 1978. Can. Wildl. Serv., Edmonton. 136 pp.

Newton, I. 1980. The role of food in limiting bird numbers. Ardea 68(1-4): 11-30.

_______. 1988. Population regulation in peregrines: an overview. Pages 761-770 *in* T.J. Cade, J.H. Enderson, C.G. Thelander, and C.M. White, eds. Peregrine falcon populations: their management and recovery. The Peregrine Fund, Inc., Boise, ID.

_______, and R. Mearns. 1988. Population ecology of peregrines in South Scotland. Pages 651-665 *in* T.J. Cade, J.H. Enderson, C.G. Thelander, and C.M. White, eds. Peregrine falcon populations: their management and recovery. The Peregrine Fund, Inc., Boise, ID.

North, M.R. 1986. Breeding biology of yellow-billed loons on the Colville River Delta, arctic Alaska. M.S. Thesis. North Dakota State Univ., Fargo. 109 pp.

Nowak, R.M., and J.L. Paradiso. 1983. Walker's mammals of the world. Vol. 2. Fourth ed. Johns Hopkins Univ. Press, Baltimore and London. 1362 pp.

O'Brien, C.M. 1988. Characterization of muskox habitat in northeastern Alaska. M.S. Thesis. Univ. Alaska, Fairbanks. 114 pp.

Odum, E.P. 1971. Fundamentals of ecology, Third ed. W.B. Saunders Co., Philadelphia. 574 pp.

Oring, L.W., and D.B. Lank. 1984. Breeding area fidelity, natal philopatry, and the social systems of sandpipers. Pages 125-147 *in* J. Burger and B.L. Olla, eds. Shorebirds: breeding behavior and populations. Plenum Press, New York and London.

Ovsyanikov, N.G., and I.E. Menushina. 1986. Competition for food between the snowy owl (*Nyctea scandiaca*) and the arctic fox (*Alopex lagopus*) [English summary only]. Zoologicheskii Zhurnal 65(6): 901-910.

Packard, J.M., and L.D. Mech. 1983. Population regulation in wolves. Pages 151-174 *in* F.L. Bunnell, D.S. Eastman, and J.M. Peek, eds. Symposium on natural regulation of wildlife populations. Proc. Northwest Sect. The Wildl. Soc. For., Wildl. and Range Exp. Stn. Univ. Idaho, Moscow.

Page, G., and D.F. Whitacre. 1975. Raptor predation on wintering shorebirds. Condor 77: 73-83.

Paradiso, J.L., and R.M. Nowak. 1982. Wolves. Pages 460-474 *in* J.A. Chapman and G.A. Feldhamer, eds. Wild mammals of North America: biology, management, and economics. John Hopkins Univ. Press, Baltimore and London.

Patterson, I.J. 1980. Territorial behavior and the limitation of population density. Ardea 68: 53-62.

Peek, J.M., and D.S. Eastman. 1983. Factors which naturally control moose populations. Pages 175-193 *in* F.L. Bunnell, D.S. Eastman, and J.M. Peek, eds. Symposium on natural regulation of wildlife populations. Proc. Northwest Sect. The Wildl. Soc. For., Wildl. and Range Exp. Stn., Univ. Idaho, Moscow.

Peterson, R.M., Jr., and G.O. Batzli. 1984. Activity periods and energetic reserves of the brown lemming in northern Alaska. Holarct. Ecol. 7(2): 245-248.

Phillips, M.K. 1986. Behavior and habitat use of grizzly bears in northeastern Alaska. M.S. Thesis. Univ. Alaska, Fairbanks. 115 pp.

Pitelka, F.A. 1973. Cyclic pattern in lemming populations near Barrow, Alaska. Pages 199-215 *in* M.E. Britton, ed. Alaskan arctic tundra. Arct. Inst. North Am. Tech. Pap. No. 25.

_______, R.T. Holmes, and S.F. Maclean, Jr. 1974. Ecology and evolution of social organization in arctic sandpipers. Am. Zool. 14:185-204.

_______, P.Q. Tomich, and G.W. Treichel. 1955. Ecological relations of jaegers and owls as lemming predators near Barrow, Alaska. Ecol. Monogr. 25:85-117.

Prentki, R.T., M.C. Miller, R.J. Barsdate, V. Alexander, J. Kelley, and P.Coyne. 1980. Chemistry. Pages 76-178 *in* J.E. Hobbie, ed. Limnology of tundra ponds, Barrow, Alaska. Academic Press.

Pruitt, W.O., Jr. 1978. Boreal ecology. The Inst. of Biol., Stud. in Biol. No. 91. Edward Arnold Limited, London. 73 pp.

*Radforth, J.R. 1972. Analysis of disturbance effects of operations of off-road vehicles on tundra. ALUR 1971-72, Dep. Indian Aff. and Northern Dev., Canada. 77 pp.

Ratcliffe, D.A. 1988. Human impacts on the environment in relation to the history and biological future of the peregrine, Pages 813-820 *in* T.J. Cade, J.H. Enderson, C.G. Thelander, and C.M. White, eds. Peregrine falcon populations: their management and recovery. The Peregrine Fund, Inc., Boise, ID.

Raveling, D.G. 1989. Nest predation rates in relation to colony size of black brant. J. Wildl. Manage. 53(1):87-90.

Reed, A., R. Stehn, and D. Ward. 1989. Autumn use of Izembek Lagoon, Alaska, by brant from different breeding areas. J. Wildl. Manage. 53(3):720-725.

Reynolds, H.V. 1980. North Slope grizzly bear studies. Alaska Dep. Fish and Game, Fed. Aid Wildl. Rest. Rep. Proj. W-17-11, Jobs 4.14-4.15R, Juneau. 75 pp.

Reynolds, P.E. 1989. Muskox population and distribution in northeastern Alaska. Oral Presentation. 69th Ann. Meet. Am. Soc. Mammal. Abstracts. Univ. Alaska, Fairbanks.

R & M. 1982. Placer mining wastewater settling pond demonstration project. Prepared for Alaska Dep. of Environ. Conserv. by R & M Consultants, Inc., Fairbanks. 60 pp. + 4 appendices.

Roberts, J.L., and N. Bowman. 1986. Diet and ecology of short-eared owls *Asio flammeus* breeding on heather moor. Bird Stud. 33:12-17.

Robertson, S.B. 1987. The Alaska arctic coast: wetland or desert. Pages 5295-5307 *in* O.T. Magoon, H. Converse, D. Miner, L.T. Tobin, D. Clark, and G. Domurat, eds. Proc., Coastal Zone '87, fifth symposium on coastal and ocean management, May 26-29, 1987, Seattle.

Robus, M.A. 1984. Summer food habits of muskoxen in northeastern Alaska. Biol. Pap. Univ. Alaska Spec. Rep. No. 4: 81-85.

Roulet, N.T., and M. Woo. 1986*a*. Hydrology of a wetland in the continuous permafrost region. J. Hydrol. 89:73-91.

_______, and _______. 1986*b*. Low arctic wetland hydrology. Can. Wat. Resour. J. 11(1):69-75.

Ryden, B.E. 1981. Hydrology of northern tundra. Pages 115-137 *in* L.C. Bliss, O.W. Heal, and J.J. Moore, eds. Tundra ecosystems: a comparative analysis. Cambridge Univ. Press, Cambridge.

Sanville, W. 1988. Response of an Alaskan wetland to nutrient enrichment. Aquatic Bot. 30:231-243.

Sather, J.H., and R.D. Smith. 1984. An overview of major wetland functions. U.S. Fish and Wildl. Serv. FWS/OBS-84/18. 68 pp.

Schamel, D.L. 1974. The breeding biology of the Pacific eider (*Somateria mollissima* V-*nigra* Bonaparte) on a barrier island in the Beaufort Sea, Alaska. M.S. Thesis. Univ. Alaska, Fairbanks. 95 pp.

Schell, D.M. 1983. Carbon-13 and carbon-14 abundances in Alaskan aquatic organisms: delayed production from peat in arctic food webs. Science 219:1068-1071.

_______, and P.J. Ziemann. 1983. Accumulation of peat carbon in the Alaska Arctic Coastal Plain and its role in biological productivity. Pages 1105-1110 *in* Permafrost: Fourth Inter. Conf. Proc., 17-22 July 1983, Fairbanks, AK. Natl. Acad. Press, Washington, DC.

Schoen, J.W. 1990. Bear habitat management: a review and future perspective. Int. Conf. Bear Res. and Manage. 8: In Press.

Schoener, T.W. 1968. Sizes of feeding territories among birds. Ecology 49(1):123-141.

Schultz, A.M. 1974. The tundra as a homeostatic system (1969). Pages 327-334 *in* J.A. Bailey, I.W. Elder, and T.D. McKinney, eds. Readings in wildlife conservation. The Wildl. Soc., Washington, DC. [Excerpted from: A study of an ecosystem: the arctic tundra. G.M. VanDyne, ed. The ecosystem concept in natural resource management. Academic Press, Inc., New York. 383 pp.]

Seastedt, T.R., and S.F. MacLean, Jr. 1979. Territory size and composition in relation to resource abundance in Lapland longspurs breeding in arctic Alaska. Auk 96: 131-142.

Senner, R.G.B. 1989. Effects of petroleum operations in Alaskan wetlands. Rep. by Robert Senner and Co. for ARCO Alaska, Inc. and BP Exploration (Alaska) Inc., Anchorage. 138 pp.

Senner, S.E., and M.A. Howe. 1984. Conservation of neararctic shorebirds. Pages 379-421 *in* J. Burger and B.L. Olla, eds. Shorebirds: breeding behavior and populations. Plenum Press, New York and London.

Serie, J.R., and D.E. Sharp. 1989. Body weight and composition dynamics of fall migrating canvasbacks. J. Wildl. Manage. 53(2): 431-441.

Shideler, R.T. 1986. Impacts of human developments and land use on caribou: a literature review. Volume II: Impacts of oil and gas development on the Central Arctic Herd. Alaska Dep. Fish and Game Habitat Div. Tech. Rep. No. 86-3. 128 pp.

_______, M.H. Robus, J.F. Winters, and M. Kuwada. 1986. Impacts of human developments and land use on caribou: a literature review. Volume I: A worldwide perspective. Alaska Dep. Fish and Game Habitat Div. Tech. Rep. No. 86-2. 219 pp.

Sinclair, A.R.E. 1979*a*. Dynamics of the Serengeti ecosystem: process and pattern. Pages 1-30 *in* A.R.E. Sinclair and M. Norton-Griffiths, eds. Serengeti: dynamics of an ecosystem. Univ. of Chicago Press, Chicago.

_______. 1979*b*. The eruption of the ruminants. Pages 82-103 *in* A.R.E. Sinclair and M. Norton-Griffiths, eds. Serengeti: dynamics of an ecosystem. Univ. of Chicago Press, Chicago.

Sjölander, S., and G. Ågren. 1976. Reproductive behavior of the yellow-billed loon, *Gavia adamsii*. Condor 78: 454-463.

Skoog, R.O. 1968. Ecology of the caribou (*Rangifer tarandus granti*) in Alaska. Ph.D. Dissertation. Univ. California, Berkeley. 699 pp.

Slaughter, C.W., and D.L. Kane. 1979. Hydrologic role of shallow organic soils. Pages 380-389 *in* Canadian Hydrology Symposium: 79 Proc. Natl. Res. Counc. of Can., Ottawa.

Smith, A.G., J. H. Stoudt, and J.B. Gollop. 1964. Prairie potholes and marshes. Pages 39-50 *in* J.P. Linduska, ed. Waterfowl tomorrow. U.S. Fish and Wildl. Serv. Gov. Printing Off., Washington, DC

Smith, D.G., and D.H. Ellis. 1989. Snowy owl. Pages 97-105 *in* Northeast Raptor Manage. Symp. and Workshop. Natl. Wildl. Fed. Sci. and Tech. Ser. No. 13.

Smith, R.H., F. Dufresne, and H.A. Hansen. 1964. Northern watersheds and deltas. Pages 51-66 *in* J.P. Linduska, ed. Waterfowl tomorrow. U.S. Fish and Wildl. Serv. Gov. Printing Off., Washington, DC.

Smith, R.L. 1966. Ecology and field biology. Harper & Row, New York. 686 pp.

**Smith, W.T., and R.D. Cameron. 1985*a*. Factors affecting pipeline crossing success of caribou. Pages 40-46 *in* A.M. Martell and D.E. Russell, eds. Proc. First North Am. Caribou Workshop, Whitehorse. Can. Wildl. Serv. Spec. Publ., Ottawa.

**_______, and _______. 1985*b*. Reactions of large groups of caribou to a pipeline corridor on the Arctic Coastal Plain of Alaska. Arctic 38(1): 53-57.

Sonerud, G. 1986. Effect of snow cover on seasonal changes in diet, habitat, and regional distribution of raptors that prey on small mammals in boreal zones of Fennoscandia. Holarct. Ecol. 9: 33-47.

*Spindler, M.A., P.A. Miller, and C.S. Moitoret. 1984. Terrestrial bird populations and habitat use on coastal plain tundra of the Arctic National Wildlife Refuge. Pages 211-291 *in* G.W. Garner and P.E. Reynolds, eds. 1983. Update report, baseline study of the fish, wildlife, and their habitats. U.S. Fish and Wildl. Serv., Anchorage, AK.

Summers, R.W. 1986. Breeding production of dark-bellied brent geese *Branta bernicla bernicla* in relation to lemming cycles. Bird Stud. 33: 105-108.

_______, and L.G. Underhill. 1987. Factors related to breeding production of brent geese *Branta b. bernicla* and waders (Charadrii) on the Taimyr Peninsula. Bird Stud. 34: 161-171.

Tarnocai, C., and S.C. Zoltai. 1988. Wetlands of arctic Canada. Pages 28-53 *in* National Wetlands Working Group, eds. Wetlands of Canada. Ecol. Land Classification Ser. No. 24. Sustainable Dev. Branch, Environ. Can., Ottawa.

Taylor, E.J. 1986. Foods and foraging ecology of oldsquaw (*Clangula hyemalis* L.) on the Arctic Coastal Plain of Alaska. M.S. Thesis. Univ. Alaska, Fairbanks. 130 pp.

Tener, J.S. 1965. Muskoxen in Canada: A biological and taxonomic review. Can. Dep. of Northern Affairs and Natl. Resourc. Queens Printer, Ottawa. 166 pp.

The Conservation Foundation. 1988. Protecting America's wetlands: an action agenda. Final Rep. Natl. Wetlands Policy Forum. Conserv. Found., Washington, DC. 69 pp.

Tieszen, L.L., P.C. Miller, and W.C. Oechel. 1980. Photosynthesis. Pages 102-139 *in* J. Brown, P.C. Miller, L.L. Tieszen, and F.L. Bunnell, eds. An arctic ecosystem: the coastal tundra at Barrow, Alaska. Dowden, Hutchinson & Ross, Inc., Stroudsburg, PA.

Tiner, R.W. 1989. An update of federal wetland delineation techniques. 11 pp. *in* D.W. Fisk, ed. Wetlands: concerns and successes. Symp. Proc. Am. Wat. Resourc. Assoc., Bethesda, MD.

Wielgolaski, F.E. 1986. Production-ecology and functioning of polar and alpine ecosystems. Pages 12-34 *in* N. Polunin, ed. Ecosystem theory and application. John Wiley & Sons, New York.

Wiens, J.A. 1977. On competition and variable environments. Am. Sci. 65: 590-597.

Wiklund, C.G., and J. Stigh. 1986. Breeding density of snowy owls *Nyctea scandiaca* in relation to food, nest sites and weather. Ornis Scandinavica 17(3): 268-274.

Williams, J.R., and R.O. van Everdingen. 1973. Groundwater investigations in permafrost regions of North America: a review. Pages 435-446 *in* Permafrost - North Am. Contrib. to Second Int. Conf. on Permafrost, Yakutsk, Siberia, July 13-18, 1973. Natl. Acad. Sci., Washington, DC.

Wilson, E.O. 1975. Sociobiology: the new synthesis. Belknap Press of Harvard Univ. Press, Cambridge, MA. 697 pp.

Winters, J.F. 1990. Goose Green Gulch: fish and wildlife habitat in a former gravel mine site. Alaska Dep. Fish and Game Habitat Div. Tech. Rep. No. 90-1. 27 pp.

Woo, M. 1986. Permafrost hydrology in North America. Atmos. - Ocean 24(3):201-234.

_______, R. Heron, and P. Steer. 1981. Catchment hydrology of a high arctic lake. Cold Reg. Sci. and Technol. 5:29-41.

_______, and P. Steer. 1983. Slope hydrology as influenced by thawing of the active layer, Resolute, NWT. Can. J. Earth Sci. 20(6):978-986.

_______, and _______. 1986. Runoff regime of slopes in continuous permafrost areas. Can. Wat. Resour. J. 11(1):58-68.

Woodward, D.F., E. Snyder-Conn, R.G. Riley, and T.R. Garland. 1988. Drilling fluids and the arctic tundra of Alaska: assessing contamination of wetlands habitat and the toxicity to aquatic invertebrates and fish. Arch. Environ. Contam. Toxicol. 17:683-697.

Young, E.C. 1989. Ecology and conservation of the polar regions. Ambio 18(1):23-33.

Zoltai, S.C. · 1988. Wetland environments and classification. Pages 2-26 *in* National Wetlands Working Group, eds. Wetlands of Canada Ecol. Land Classification Ser. No. 24. Sustainable Dev. Branch, Environ. Can., Ottawa.

*These citations are to annotations contained in Meehan (1986c).

** These citations are to annotations contained in Shideler (1986).

CORRIGENDUM

Roulet, N.T., and M. Woo. 1988. Runoff generation in a low arctic drainage basin. J. Hydrol. 101:213-226.

*Troy, D.M. 1985. Tundra bird monitoring program. Annual Report of the Prudhoe Bay Waterflood Environmental Monitoring Program, U.S. Army Corps Eng., Alaska Dist., Anchorage, AK. 163 pp.

_______. 1988. Bird use of the Prudhoe Bay Oil Field during the 1986 nesting season. Rep. by LGL Alaska Res. Assoc., Inc. for Alaska Oil and Gas Assoc., Anchorage, AK. 96 pp.

Village, A. 1982. The home range and density of kestrels in relation to vole abundance. J. Anim. Ecol. 51: 413-428.

_______. 1987. Numbers, territory-size and turnover of short-eared owls *Asio flammeus* in relation to vole abundance. Ornis Scandinavica 18: 198-204.

Walker, D.A., E.F. Binnian, N.D. Lederer, E.A. Nordstrand, R.H. Meehan, M.D. Walker, and P.J. Webber. 1986. Cumulative landscape impacts in the Prudhoe Bay Oil Field 1949-1983. 51 pp. + 3 appendices *in* R. Meehan, P.J. Webber, and D. Walker, eds. Tundra development review: toward a cumulative impact assessment method. Prepared for U.S. Environ. Protection Agency by U.S. Fish and Wildl. Serv., Anchorage, AK.

_______, D. Cate, J. Brown, and C. Racine. 1987. Disturbance and recovery of arctic Alaskan tundra terrain: a review of recent investigations. U.S. Army Cold Reg. Res. Eng. Lab Rep. 87-11. Hanover, NH. 62 pp. + appendix.

________, K.R. Everett, P.J. Webber, and J. Brown. 1980. Geobotanical atlas of the Prudhoe Bay Region, Alaska. U.S. Army Cold Reg. Res. Eng. Lab. Rep. 80-14. Hanover, NH. 47 pp. + 2 appendices.

Walker, H.J. 1978. Lake tapping in the Colville River Delta, Alaska. Pages 223-238 *in* Proc. Third Int. Conf. on Permafrost. Vol. 1. Natl. Resour. Counc. Can., Edmonton, Alberta.

________. 1983. Guidebook to permafrost and related features of the Colville River Delta, Alaska. 34 pp. *in* Fourth Int. Conf. on Permafrost, July 18-22, 1983, Univ. Alaska, Fairbanks.

Walker, W. 1977. Chlorinated hydrocarbon pollutants in Alaska gyrfalcons and their prey. Auk 94(3): 442-447.

Watson, A., and R. Moss. 1970. Dominance, spacing behavior and aggression in relation to population limitation in vertebrates. Pages 167-218 *in* A. Watson, ed. Animal populations in relation to their food resources. Symp. Br. Ecol. Soc., Blackwell Sci. Publ., Oxford and Edinburgh.

West, R.L., and E. Snyder-Conn. 1987. Effects of Prudhoe Bay reserve pit fluids on water quality and macroinvertebrates of arctic tundra ponds in Alaska. U.S. Fish and Wildl. Serv. Biol. Rep. 87(7). 48 pp.

White, R.G., F.L. Bunnell, E. Gaare, T. Skogland, and B. Hubert. 1981. Ungulates on arctic ranges. Pages 397-483 *in* L.C. Bliss, O.W. Heal, and J.J. Moore, eds. Tundra ecosystems: a comparative analysis. Cambridge Univ. Press, Cambridge.

_______, and J. Trudell. 1980. Patterns of herbivory and nutrient intake of reindeer grazing tundra vegetation. Pages 180-195 *in* E. Reimers, E. Gaare, and S. Skjenneberg, eds. Proc. 2nd Int. Reindeer/Caribou Symp., Roros, Norway, 1979. Direktoratet for vilt og ferskvannsfisk, Trondheim.

Whittaker, R.H., S.A. Levin, and R.B. Root. 1973. Niche, habitat, and ecotope. Am. Nat. 107(955):321-338.

APPENDIX A: HABITAT

Senner (1989), citing Whittaker et al. (1973), narrowly defines "habitat" as location-specific physical features used by a species, and he excludes "processes" affecting a species from his definition, citing Leopold (1933). This is inappropriate since Leopold (1933) does not define habitat but instead discusses predation, hunting, disease, and regional climate as factors affecting game populations. Although it is true that Whittaker et al. (1973) narrowly define habitat, they do so in order to clarify the concepts of niche, habitat, and ecotope as parts of a conceptual system that Senner does not discuss. This omission places the definition of Whittaker et al. (1973) out of context as applied to wetland fills in the Arctic (or to what is commonly called "habitat loss" in any environment).

Whittaker et al. (1973) define "habitat" in the following way:

> The m variables of physical and chemical environment that form spatial gradients in a landscape or area define as axes a habitat hyperspace. The part of this hyperspace a given species occupies is its habitat hypervolume. The species' population response to habitat variables within this hypervolume, as expressed in a population measure, describes its habitat. The environment of a particular community in the landscape is a community habitat or biotope.

These authors constrained habitat to the physical and chemical environment in order to separate habitat from "niche" described as follows:

> The n variables by which species in a given community are adaptively related define as axes a niche hyperspace. The part of this hyperspace in which a species exists is its niche hypervolume, or realized niche in the sense of Hutchinson. The species' population response within its niche hypervolume describes its niche.

Whittaker et al. (1973) thus incorporate the biotic environment in their niche concept. They go on to combine habitat and niche to define the "ecotope" of a species as follows:

> The variables of habitats and niches may be combined to define as axes an (m + n')-dimensional ecotope hyperspace. The part of this hyperspace to which a given species is adapted is its ecotope hypervolume. When a population measure is superimposed on this hypervolume, the ecotope of the species is described.

Thus, what some authors would define as habitat has been defined as an ecotope by Whittaker et al. (1973).

Habitat loss, in the vernacular, occurs when a portion of the environment becomes unsuitable for occupancy by a particular species or group of species. Unsuitability may derive from altered physical and chemical conditions (habitat *sensu* Whittaker et al. [1973]) or from altered community structure (niche relationships *sensu* Whittaker et al. [1973]); therefore, a precise definition of the vernacular "habitat loss" would be "ecotope reduction." This terminology would be consistent with the conceptual system of Whittaker et al. (1973); however, Senner did not use it. Accordingly, we refrain from using the terminology of Whittaker et al. We do so with the explicit understanding that the effects of rendering a portion of the biosphere unsuitable for specific forms of life are the same regardless of the conceptual constructs used to describe those effects.

Most ecologists define habitat simply as the place where an organism lives, including both biotic and abiotic components of the environment (Smith 1966:13, Odum 1971:234-239, McNaughton and Wolf 1973:5). Some authors take an even broader view, including substances and forces affecting an organism, directly or indirectly, in their definition of habitat (McNaughton and Wolf 1973:5). Processes such as predation, hunting, disease, and climate appear to be components of habitat in the latter definition. Harris (1984) and Harris and Kangas (1988) have refined the habitat concept by distinguishing between primary, secondary, and tertiary habitats. Primary habitat for a species is that area containing all the requirements necessary to support a viable population through time (i.e., a population large enough to have a low probability of extirpation as a result of stochastic processes); secondary habitat is that area containing all the requirements necessary to support a few individuals or a subpopulation in the near term but too small to maintain a viable population through time; and tertiary habitat is that area used by a species but not continuously providing all the requirements for survival and reproduction (Harris and Kangas 1988). Ecologists rather arbitrarily fix the boundaries of habitats (Andrewartha and Birch 1984:223), based on their knowledge of the species under study. Incomplete autecological knowledge implies some uncertainty about what areas are actually habitable by a given species. With this caution, we follow the usage common among biologists and consider a species' habitat as the place where it is found, including biotic and abiotic factors, and interpret this to include regional climate, prey density, predator density, forage availability, etc.

Senner, without citation, further excludes the possibility of an animal "community" having a habitat, limiting his definition to single species, a practice at variance with fundamental ecological concepts. Most ecologists view biological communities as occupying habitats. Krebs (1972:379), for example, defines a community as "any assemblage of populations of living organisms in a prescribed area or habitat." Smith (1966:12-13) and Odum (1971:140-143) share similar definitions of community. Likewise, biologists commonly refer to "stream habitat" or "wetland habitat" and understand this to mean the habitat of the ecological community occurring in the referenced stream or wetland. Indeed, Elton, a pioneer in animal ecology, described a community "as the complex of animals that are usually found living together in a 'habitat'" (Andrewartha 1971:4). Elton further defined habitat "as an area that seems to possess a certain uniformity with respect to physiography, vegetation, or some other quality that the ecologist decides is important (or easily recognized)" (Andrewartha 1971:4). Even Whittaker et al. (1973), cited by Senner for his definition of habitat, specifically state, "The environment of a particular community in the landscape is a community habitat or biotope." Based on the preceding discussion, it is apparent that ecologists view communities as occupying habitats. Therefore, we follow ecological convention and accept the concept of community habitats.

Senner uses a narrow view of habitat and exclusion of habitat from the ecological concept of community throughout his report to support conclusions that cannot be reached in a broader ecological context. The definition of habitat is thus central to understanding its functional value to fish and wildlife populations.

APPENDIX B: CARRYING CAPACITY

Senner's (1989) view of "carrying capacity" is narrow and inflexible and does not fully account for the host of factors determining animal abundance or account for variation of those factors over time. He equates carrying capacity with forage availability, a concept sometimes used when discussing ungulates or range management (Edwards and Fowle 1974) but consistent neither with Leopold's (1933:50-51,450) original definition nor with current usage in scientific literature (e.g., Bergerud 1983). Carrying capacity, as originally conceived by Leopold (1933:50-51), a pioneer of wildlife management, "is a property of a unit of range" defined as "the maximum density [of a wildlife species' breeding population] which a particular . . . range is capable of supporting." He contrasted carrying capacity with the "saturation point" of a species, the species-specific, intrinsic maximum density achievable "in the most favorable local environments," explicitly recognizing that carrying capacity differs on different ranges in response to local environmental conditions. Leopold (1933:22-29) preceded his definition of carrying capacity with a detailed discussion of the factors that control wildlife populations: hunting, predation, starvation, disease and parasites, accidents, food, water, cover, and special requirements such as mineral licks. He included drainage, cultivation, cuttings, weather, fire, and grazing as "influences" that affect the previously listed factors and thus indirectly act on wildlife populations. Although Leopold did not explicitly define carrying capacity (Edwards and Fowle 1974), each unit of range has characteristic values for the factors and influences he described as controlling populations. Further, Leopold (1933:208-355) devoted several chapters to methods for modifying these factors to increase game production. Thus, it is reasonable to assume that Leopold viewed carrying capacity as being set by his population-controlling factors.

Edwards and Fowle (1974) thoroughly reviewed the carrying-capacity concept, including its origin with Leopold (1933). They found general agreement in the literature that only finite densities of animals could exist in given environments and concluded that the concept of carrying capacity had evolved from a single-factor, stable view to a multiple-factor, variable view in which populations were seen as interacting with their ecosystems. Animal density is ultimately limited by ecosystem productivity and intrinsic characteristics of the population under consideration, such as individual body mass, metabolic rate, and trophic level (Odum 1971:163). Natural populations, however, tend to exist at densities less than their theoretical maxima. MacArthur and Connell (1966:130) state, "In natural populations, r [observed rate of population increase] fluctuates around zero. If r were continuously positive or negative for a protracted period, the population would either become dangerously high, exhaust its resources, and 'crash,' or else it would decrease to extinction. Therefore, natural selection must act to prevent protracted positive or negative values of r." Some authors have suggested that animals regulate their numbers through behavioral mechanisms at densities sufficiently low to prevent starvation whereas other authors point to predation and parasitism as mechanisms regulating populations (MacArthur and Connell 1966:132-142). Lower limits on animal density in stable ecosystems are established by homeostatic mechanisms (Odum 1971:163). Thus, the preceding discussion of animal densities is consistent with the views of Edwards and Fowle (1974) that carrying capacity is determined by the interactions of populations with their ecosystems.

Populations interact with their ecosystems in many ways. In nature, animal populations fluctuate (MacArthur and Connell 1966:120,130,132; Odum 1971:188-195) about characteristic levels of abundance for particular regions in response to both density-independent and density-dependent factors. In some species these fluctuations are random, or at least aperiodic, and in some species they are cyclic (Lidicker 1988), especially at high latitudes. Examples of the latter include lemmings (Schultz 1969, Batzli 1981), snowshoe hares (Keith and Windberg 1978), and lynx (Odum 1971:191-192). Thus, at any given time, one might find a population that appeared to be low in relation to available forage (or prey). Nevertheless, because carrying capacity is determined by all the factors controlling a population and varies in time (Edwards and Fowle 1974), one must not assume the population is always low in relation to forage. Stochastic patterns in the environment (Odum 1971:154,194) may at times allow populations to increase sufficiently to be forage-limited (or limited by some other resource), even if they are generally controlled by other factors such as predation. For example, Gasaway et al. (1983) state that "natural mechanisms must exist that allow ungulate populations to eventually escape antiregulatory control by wolves (the antiregulatory process leads to extirpation if not checked)." They further state, "The prerequisite for escape is an abundant food supply." Habitat loss reduces ungulate food supply and thus maximum carrying capacity, reducing the future population ceiling. Similar habitat relationships exist for other species.

Ecosystem interactions are much more complex than just forage availability or weather and encompass population-regulating factors such as predation. Given that predation, disease, harvest, nutrition, and other factors act to set carrying capacity, Edwards and Fowle (1974) state that "we may regard carrying capacity as represented by the minimum number of animals of given species and quality [i.e., nutritional condition] that can in a given ecosystem survive through the least favorable environmental [i.e., physical and biotic] conditions occurring within a stated time interval." This directly contradicts Senner's belief that most, if not all, arctic species exist in numbers well below the carrying capacities of their ecosystems, since Edwards and Fowle would say that in many cases populations represent carrying capacities. These authors qualify their statement by excluding cases where "time has been insufficient to enable increase when it is possible and . . . where the distribution of the animals is such as to leave some parts of inhabitable environment vacant." Large arctic vertebrates may fall into these categories because their intrinsic rates of increase are low and they do not necessarily occupy all suitable range over the 1-year interval suggested by Edwards and Fowle for assessing carrying capacity. Caribou, for example, exhibit long-term shifts in distribution and abundance (Skoog 1968:312-328), and muskoxen are occupying new range in Alaska following reintroduction to the ANWR (Reynolds 1989). Migratory species using arctic-wetland habitats present a complex picture with regard to carrying capacity for several reasons. Species such as waterbirds use the tundra during summer but are absent during winter. Edwards' and Fowle's (1974) measure of carrying capacity for resident animals cannot be extrapolated to these migrants, at least over a 1-year interval, because the minimum density over the year is zero, yielding a zero carrying capacity. Although there is a certain logic to assigning this value to a species not able to overwinter in the Arctic, it yields no useful information and is not consistent with the annual return of the species to tundra habitats. One potential solution to this dilemma is to measure the carrying capacities of arctic wetlands for waterbirds only over the summer season, since Edwards and Fowle allow time scales appropriate to species characteristics. Edwards and Fowle's key point remains: carrying capacity varies in space and time as a result of the interactions between organisms and their ecosystems.

Ecological evidence from the world's other biomes argues against the simple assumption that arctic habitat is different and can be removed from production without producing population-level effects. Justifying habitat alteration or loss simply by claiming a population is below carrying capacity is incorrect, as is defining carrying capacity to exclude ecosystem interactions such as predation (McNaughton and Wolf 1973:198-199). Predation and human harvest are two interactions between organisms and their ecosystems that potentially determine carrying capacity (Bergerud 1983). Both can vary. Population increases occurring when predation or harvest are relaxed are finite. Nutrition, behavior, and other factors then potentially determine carrying capacity. For a resident (non-migratory) species, if the population is stable, it is by definition at carrying capacity, even though forage may not be a limiting factor (Edwards and Fowle 1974). If the population is rapidly increasing, we may not know what the carrying capacity will be or what factor (e.g., forage, prey base, predation rate, weather, social structure, etc.) or combination of factors will control the population at that point. For example, previously vacant range may be occupied during population highs, as is the case for caribou (Skoog 1968:312-317); therefore, we cannot say that habitat loss will not diminish carrying capacity. Habitat loss may permanently reduce maximum populations of fish and wildlife achievable when factors such as predation or harvest are relaxed. Carrying-capacity arguments thus do not provide sufficient information to predict that population-level effects will not occur for species resident in arctic wetlands subjected to habitat loss.