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Effects of forest harvesting disturbance on aquatic birds in the boreal forest of Alberta

by

Johanna Patricia Pierre ©

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degree of Doctor of Philosophy

in

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled 'Effects of forest harvesting disturbance on aquatic birds in the boreal forest of Alberta' submitted by Johanna Patricia Pierre in partial fulfillment of the requirements for the degree of Doctor of Philosophy in Environmental Biology and Ecology.

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Abstract

Effects of disturbances on some community characteristics may transcend habitat and taxonomic boundaries. For example, the intermediate disturbance hypothesis (IDH) purports that communities display their highest species richness at intermediate levels of disturbance. In the past, organisms sensitive to disturbance have been used as indicators of anthropogenic impacts on the environment. I examined aquatic bird communities in boreal Alberta, on 'harvested lakes' (forest harvesting closer than 450 m, within three years of my study) and 'unharvested lakes' (no harvesting within at least 450 m of the shore), to determine whether harvesting disturbance affected (i) species richness, following the IDH, (ii) community composition, and (iii) species densities. To investigate mechanisms linking harvesting disturbance to aquatic birds, I examined (i) community-environment and density-environment relationships, (ii) nest predation, and (iii) foraging patterns.

The composition of aquatic bird communities differed on harvested and unharvested lakes, although limnological variables (except conductivity) did not differ on these lake types. Species richness was higher on harvested lakes, because species that occurred sporadically tended to occur on these lakes. Densities of five of nine focal species (or species groups) differed before and after forest harvesting. However, only pre-/post-harvest decreases in scaup (*Aythya affinis, A. marila*) densities were maintained for two summers post-harvest.

Lake characteristics, including morphometry and water quality, were more important to communities and densities, than variation in lake characteristics attributable to harvesting. Artificial nests were depredated less in harvested areas than

in intact forest, suggesting that harvesting may not negatively affect nest success of cavity-nesting waterfowl, and thereby community composition and bird densities. Finally, foraging behaviour of common loon (*Gavia immer*) and bufflehead (*Bucephala albeola*) did not differ between harvested and unharvested lakes.

Differences in community composition between harvested and unharvested lakes may conform to the IDH, although the level of harvesting disturbance necessary to decrease species richness is unknown. Community composition and scaup densities may be useful indicators of disturbance related to forest harvesting, however mechanisms causing post-harvest differences remain obscure. Documented patterns of changes in communities suggest that increased permeability of harvested areas may facilitate colonisation of harvested landscapes by bird species more typical of the prairie parkland region.

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1.1 Introduction

Disturbance is an integral part of all ecological systems, and has been defined as 'any relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resources, substrate availability, or the physical environment' (Pickett and White 1985, p. 7). The effects of disturbances depend on their extent, in both space and time, and their intensity, as well as the persistence, resistance, and resilience of the ecological systems that are affected. Despite the obvious diversity in both disturbances, and systems that are affected by them, community-level patterns transcending habitat and taxonomic boundaries have been predicted to occur across ecological systems exposed to perturbations. For example, one of the best known hypotheses stipulates that communities display the highest species richness and diversity at intermediate levels of disturbance, whether disturbances are scaled spatially, temporally, or in terms of their intensity (Connell 1978). A second well known set of hypotheses purports, among other things, that stressed ecosystems, including disturbed systems, exhibit lower species richness or diversity, compared to systems that are not under stress (Odum 1985). Both these hypotheses have found wide support in empirical ecology (e.g. Schindler 1990, Wilcox and Meeker 1991, McNicol et al. 1995, Sommer 1995, Townsend et al. 1997).

Despite the practically limitless range of possible settings for disturbance studies, several characteristics of freshwater aquatic systems render these especially amenable to investigations of the effects of disturbance. Firstly, aquatic systems receive inputs from potentially extensive land bases. Thus, waterbodies represent much larger landscape areas than terrestrial sites of the same size. Secondly, waterbodies cover discrete areas, and thus their boundaries are readily apparent, at least above ground. Many organisms that live in, on, or around waterbodies cannot complete their lifecycles without these habitats. This dependence on waterbodies can render predominantly aquatic organisms easier to study than completely terrestrial species, because for at least part of their lifecycle, they are restricted to the relatively easily delineated habitats that waterbodies represent. Finally, the movement of water may reduce heterogeneity within aquatic systems, making some effects of disturbance more readily detectable than in terrestrial environments (Schindler 1990).

The biotic effects of disturbances occur via individuals responding to disturbance-induced environmental changes. The culmination of individual responses may then become apparent at the population and community levels. Changes in population characteristics in response to disturbances are fairly well documented in aquatic systems. For example, densities of macroinvertebrates can be reduced by acidification (Hall 1994), and fire (Rinne 1996), but can increase with forest harvesting (Murphy and Hall 1981). Decreases in fish populations are reported with acidification (Schindler 1990), and forest fire (Rinne 1996), but fish populations can increase with eutrophication (Mills and Chalanchuk 1987). Finally, aquatic bird populations can decrease in response to acidification (McNicol et al. 1995) and pesticides (Risebrough 1983). At the community level, acidification reduces the species richness, and therefore changes the composition of phytoplankton, zooplankton, macroinvertebrate, and fish communities (McNicol et al. 1987, Schindler 1990, Hall 1994). Also, eutrophication can change the composition of zooplankton, benthic invertebrate, and aquatic bird communities by changing species richness (Kauppinen and Väisänen 1993, Cardell et al. 1999, Leibold 1999).

Species, or communities, that are particularly sensitive to disturbances can be useful for indicating anthropogenic effects on the environment. In the animal kingdom, birds have been the most frequently recognised as effective indicators (Council on Environmental Quality 1972, cited in Morrison 1983). Aquatic birds may be effective indicator species because they are relatively large compared to other organisms in aquatic habitats, and they are also fairly conspicuous. Therefore, birds can be monitored more easily than other organisms occurring in aquatic systems. Also, aquatic birds are sensitive to a variety of habitat conditions. Obviously, the same habitat characteristics are not affected by all disturbances, however differing sensitivities among birds to various habitat characteristics, render different species, and groups of species, sensitive to different disturbances. Beyond studies formally investigating disturbance, the composition of aquatic bird communities, and abundances of various species of aquatic birds, have been linked to the landscape surrounding lakes, lake morphometry, water quality, and prey availability (Nilsson and Nilsson 1978, Kauppinen and Väisänen 1993, Newton 1994, Savard et al. 1994, Paszkowski and Tonn 2000).

In the boreal forest of western Canada, fire is the predominant natural disturbance (Rowe and Scotter 1973, Larsen 1980). Fire can disturb both aquatic and terrestrial habitats. Obviously, forest fires remove vegetation from the landscape. Thus, the occurrence of fire will change the abundance and distribution of terrestrial organisms (Crete et al. 1995). Following the loss of forest habitat due to fire, 'new', open habitat is created. Thus, for terrestrial birds for example, community composition changes after fire, due to colonisation of former forest patches by species characteristic of open landscapes, and those with specific associations with post-fire stands (Hobson and Schieck 1999, Imbeau et al. 1999).

In addition, aquatic systems can experience nutrient influx due to fires (Bayley et al. 1992, Hauer and Spencer 1998), and changes to their macroinvertebrate communities (Minshall et al. 1997). Also, fish populations are frequently reported to be negatively affected by forest fire, at least in the short-term (Gresswell 1999). The effects of forest fires on aquatic birds are unknown. Not surprisingly however, the burning of grasslands has been found to reduce the densities of some waterfowl nesting in these habitats (Kruse and Bowen 1996).

In contrast to wildfire, forest harvesting is an anthropogenic disturbance, but also changes terrestrial environments directly by removing vegetation. Commercial forestry was rare in the western boreal forest of Canada until 1993, when technological advances that rendered boreal hardwoods usable in the production of pulp and paper (Peterson and Peterson 1992) led to a rapid increase in harvesting activity. Like forest fires, harvesting can be expected to change the abundance and distribution of terrestrial fauna. Thus, terrestrial bird communities change after forest harvesting. Species more typical of open habitats are among post-harvest colonists, but birds depending on snags (including cavity-nesting species) tend to be absent from post-harvest stands (Hobson and Schieck 1999, Imbeau et al. 1999). The effects of forest harvesting on the terrestrial components of the lifecycles of aquatic birds are unknown, however waterfowl have been reported nesting in snags remaining in clearcuts after harvesting (R. G. Anderson and S. Woodley, pers. comm.). Terrestrial fauna affected by harvesting include predators of aquatic bird nests (Snyder and Bissonette 1987, Thompson et al. 1989). If harvesting affects nest predators, nest predation patterns may change in harvested landscapes. Increased avian nest predation is often reported in fragmented landscapes, and may be especially evident at habitat edges. However, in forest-dominated landscapes, edge effects are seldom reported (Paton 1994, Andrén 1995, Pöysä et al. 1997), and the effects of habitat destruction and fragmentation on cavity-nesting waterfowl remain unknown.

Again, like fire, forest harvesting can also affect aquatic habitats. Harvesting may cause elevated nutrient influx into lakes (Prepas et al. in press), which may lead to increases in primary productivity. Increased primary production may then affect invertebrate and fish populations (Mills and Chalanchuk 1987, Jorgenson et al. 1992). If the availability of aquatic bird food increases post-harvest, birds may increase their use of lakes in harvested drainage basins. However, if post-harvest changes in foraging conditions cause a reduction in prey availability, e.g. via decreased water clarity, aquatic birds may decrease their use of lakes in harvested landscapes. Alternatively, birds may compensate for changes in prey base by changing their foraging strategies. Aquatic bird foraging behaviour is known to change in response to prey type, availability, and density (Parker 1988, Wanless and Harris 1992, Uttley et al. 1994). Thus, if forest harvesting does change the availability of prey for aquatic birds, this may be indicated by changes in their foraging behaviour. If the use of lakes by aquatic birds is affected by forest harvesting, their populations and community composition may change.

Although the effects of forest harvesting on streams are better known, albeit from areas outside the western boreal forest (Campbell and Doeg 1989, Davies and Nelson 1994), research on how forest harvesting affects lakes, and lake biota, is sparse. In addition, boreal ecosystems in western Canada are relatively poorly studied in general, making it difficult to predict the effects of harvesting on the region. However, the utility of aquatic birds as indicators, and lakes as a venue for disturbance studies, point to lake-dwelling aquatic birds as an appropriate focal group for studies of ecological disturbances caused by forest harvesting.

Pickett and White (1985) divide disturbances into two general categories: destructive events, and environmental fluctuations, and recognise that disturbances often increase the amount of open space in the landscape, and alter the availability of resources. Forest harvesting is a member of the first general category of disturbances, i.e. it is a destructive event, and removal of tree biomass causes 'new' open spaces to be present on the landscape. Harvesting disturbance obviously changes the availability of resources in terrestrial environments, but can have this effect on aquatic environments as well, as described previously. Within this thesis, I investigate the effects disturbance, represented by forest harvesting, on aquatic birds occupying lakes in the boreal forest of Alberta. For the purposes of this thesis, I define forest harvesting disturbance as the anthropogenic removal of above-ground tree biomass, which may be coincident with, or followed by, changes in the physical, chemical, or biological properties of ecological systems.

My study is the first to examine aquatic bird communities in the boreal forest of Alberta from the ground. Therefore, to encompass the maximum number of species of aquatic birds, I investigated community responses to forest harvesting, and determined which environmental variables were the most important in structuring aquatic bird communities on boreal lakes. I report on my community-level investigations in Chapter 2 of this thesis. To determine the effects of forest harvesting and environmental variables on aquatic birds with finer resolution than is possible at the community-level, I examined the densities of nine of the most widespread species of aquatic birds. I determined which species appear the most likely to be effective indicators of ecological changes in lakes resulting from harvesting disturbance, and present the results of density analyses in Chapter 3. Following community- and population-level investigations, I report research on two mechanisms that may partially account for the effects of harvesting on aquatic birds. Firstly, I examine the potential effects of nest predation on cavity-nesting waterfowl. Then, I determine responses of birds to post-harvest changes in lakes, in terms of their foraging behaviour. In the final chapter of this thesis, I synthesise my results. To conclude, I offer recommendations for future research, and discuss management implications of my study.

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Chapter 2. Effects of disturbance associated with forest harvesting on aquatic bird communities in the boreal forest of Alberta.

2.1 Introduction

All ecological systems are affected by disturbances, which are generally considered disruptive to either the biotic environment, the abiotic environment, or both (Odum 1985, Pickett and White 1985). The effects of disturbances on ecosystems are determined by characteristics of both the systems, and the disturbances, involved. Important considerations include the spatial extent, temporal extent, and intensity of disturbances, and the persistence, resistance, and resilience of ecological systems and their components. The results of disturbances have been reported widely, for both aquatic and terrestrial ecosystems. However, freshwater aquatic systems, especially lakes, are a particularly appropriate venue for disturbance studies. This is because lakes can represent large landscape areas as they receive material from drainage basins that can cover extensive land bases. Thus, lakes represent larger areas of the landscape than if terrestrial sites of comparable sizes were studied. Also, waterbodies are enclosed within relatively discrete boundaries, above ground at least. Thus, delineating study areas is easier than in terrestrial locations. In addition, many organisms are restricted to living on, in, or around waterbodies and cannot live in surrounding terrestrial environments. Consequently, they are easier to study because of their confinement to the aquatic habitats that lakes provide. Finally, movement of water in aquatic ecosystems may reduce heterogeneity in these environments, compared to terrestrial systems, possibly making changes more detectable, including those induced by disturbance (Schindler 1990).

Biotic responses of ecological systems to disturbances begin with individuals reacting to environmental change. These individual reactions may then become apparent at higher levels of organisation. Thus, individual reactions to disturbances may be reflected by changes in populations and communities. Odum (1985) hypothesised that disturbed communities would exhibit lower species richness, and/or organism abundance, compared to undisturbed communities, unless initial richness, and/or abundance was low. When richness and/or abundance are low, he expected the reverse responses. Supporting this speculation, the species richness of phytoplankton, zooplankton, macroinvertebrate and fish communities are all reduced by acidification (McNicol et al. 1987, Schindler 1990, Hall 1994), and eutrophication is reported to cause decreases in the species richness of zooplankton and benthic invertebrates (Cardell et al. 1999, Leibold 1999). However, Connell (1978) purported that communities that experience intermediate levels of disturbance will display the greatest species richness, and this hypothesis has also found wide empirical support. For example, rocky intertidal organisms, phytoplankton, macroinvertebrates, and fish have all been found to attain the highest species richness at intermediate levels of different disturbances (Sousa 1979, Pearsons et al. 1992, Stanzer and Resh 1993, Sommer 1995).

Organisms with low resistance to changes in environmental conditions can be effective as indicators of disturbances, and may be used to assess anthropogenic effects on the environment. As a group, birds may be particularly effective indicators of environmental change because they occur widely, and different species occupy different habitat types. They are also relatively conspicuous organisms, and some species have been intensively studied. In addition, some birds appear more sensitive to anthropogenic environmental disturbance, e.g. contaminants, than other vertebrates (Morrison 1983). In freshwater aquatic systems, birds are large, relative to most other organisms. Consequently, they can be easier to monitor than other taxa occurring in freshwater systems, facilitating their use as environmental indicators. For example, based on studies of acidified lakes in eastern Canada, the use of both the common goldeneye (*Bucephala clangula*) and the common merganser (*Mergus merganser*) as indicators of acid stress has been advocated (McNicol et al. 1990).

Patterns in both the occurrences, and abundances, of aquatic birds have also been linked to features of the environment by researchers not specifically investigating disturbance. The nature of vegetation surrounding lakes, lake morphometry, water quality, and prey availability and detectability have all been related to the occurrences and abundances of aquatic birds (Nilsson and Nilsson 1978, Blancher et al. 1992, Kauppinen 1993, Kauppinen and Väisänen 1993, Hanson and Butler 1994, Hoyer and Canfield 1994, Newton 1994, Savard et al. 1994, Paszkowski and Tonn 2000a). Generally, community composition and species richness are most closely related to lake morphometry and nutrient levels. Identifying environmental characteristics that are important to aquatic birds should increase the likelihood that the effects of environmental change can be predicted accurately, including the effects of change caused by disturbances.

The dominant natural disturbance in the western boreal forests of Canada is fire (Rowe and Scotter 1973, Larsen 1980). Forest fire removes vegetation from the landscape, and can eutrophy aquatic systems (Hauer and Spencer 1998). Fires in forests surrounding waterbodies can also change macroinvertebrate and fish populations and communities (Minshall et al. 1997, Gresswell 1999, Scrimgeour et al. 2000), although the effects of wildfire on aquatic bird communities are unknown. In the boreal forests of Alberta, forest harvesting began to accelerate rapidly in 1993, due to technology making boreal forest hardwoods available for pulp and paper production (Peterson and Peterson 1992). Consequently, large areas of this forest have recently become available to commercial foresters for harvesting. Forest harvesting has some similar environmental effects as forest fire, superficially at least. Harvesting disturbs terrestrial habitat directly by removing vegetation. Forest removal changes the distribution and abundance of organisms on the terrestrial landscape (Saunders et al. 1991), and reduces the availability of nest sites for birds, including some aquatic species (Newton 1994). If nutrient influx increases post-harvest, as reported by Prepas et al. (in press), forest harvesting may also change the amount of primary production in aquatic systems. In addition, water clarity may decrease due to increased algal growth resulting from elevated nutrient influx. Changes in the availability of invertebrate and fish prey for aquatic birds may result from increased primary production, due to changes in prey populations, species composition of prey communities, and detectability of prey (Eriksson 1984, 1985, Campbell and Doeg 1989, Growns and Davis 1991, Davies and Nelson 1994).

The effects of forest harvesting on streams, including some stream biota, have been studied, albeit predominantly in areas outside the western boreal forest (Campbell and Doeg 1989, Davies and Nelson 1994). However, the effects of harvesting on lakes, and lake biota including aquatic birds, are poorly known. Also, ecological systems are not well studied on the boreal plain of western Canada. These key knowledge deficits make it difficult to predict the nature and extent of the ecological effects that harvesting will have on lentic systems in this region. However, based on the sensitivity of aquatic birds to habitat disturbance, and their consequent utility as indicator species, I hypothesise that aquatic bird communities are not resistant to forest harvesting disturbance. Therefore, I predict that the composition of these communities differs on lakes disturbed by harvesting, and undisturbed boreal lakes. Secondly, following the intermediate disturbance hypothesis (Connell 1978), species richness is predicted to be higher in moderately disturbed habitats than essentially undisturbed or very disturbed environments. Thus, I hypothesise that the lack of resistance of aquatic bird communities to forest harvesting will result in elevated species richness of aquatic bird communities on lakes disturbed by harvesting versus undisturbed lakes, due to increased food availability resulting from post-harvest nutrient influx. Therefore, species predominantly feeding on primary producers are expected to increase their use of lakes the most rapidly (within the first growing season after harvesting, e.g. green-winged teal *Anas crecca*, northern shoveler *Anas clypeata*, and ring-necked duck *Aythya collaris*), followed by those that consume invertebrates and fish (e.g. common loon *Gavia immer*, lesser scaup *Aythya affinis*, red-necked grebe *Podiceps grisegena*) the first or second growing season after harvesting. (In undisturbed and very disturbed lakes, decreased abundance and/or diversity of food resources (e.g. Cardell 1999) is expected to reduce foraging opportunities for some species, and decrease their use of lakes).

Finally, based on the results of previous studies investigating bird-habitat relationships, I predict that the most important environmental variables determining the species richness and composition of aquatic bird communities on western boreal lakes are lake morphometry and lake productivity. Lake morphometry will remain unaffected by harvesting disturbance. However, as described above, post-harvest increases in lake productivity are expected to affect bird communities.

2.2 Methods

2.2.1 Study lakes

Censuses of aquatic birds were conducted on 30 study lakes in the boreal mixedwood forest of north-central Alberta, between latitudes 54°59' and 56°49', and longitudes 110°02' and 116°27' (Figure 2.1). Aquatic birds were defined as non-passerine species that feed at waterbodies, including on lakeshores. Lakes ranged in size from 8.6-165.9 ha, and were meso- to hypereutrophic (Prepas et al. in press, Table 2.1). Twelve of the study lakes were part of the TROLS (Terrestrial and Riparian Organisms, Lakes and Streams) project, a large scale experimental study using different forest harvesting regimes around these lakes to determine the effectiveness of buffer strips in protecting boreal systems from ecological change caused by harvesting. Fourteen study lakes were part of the Network of Centres of Excellence in Sustainable Forest Management (NCE) research initiative, which includes a large scale lake survey designed to investigate the ecological effects of harvesting and wildfire disturbance. Four study lakes were independent of both larger projects, therefore I refer to these as 'independent study lakes' hereafter. Lakes were selected based on criteria that included forest harvesting schedules, composition of forest around lakes, lake level in the landscape (headwater lakes were preferred), lake morphometry, and lake accessibility (Prepas et al. in press).

Forest surrounding study lakes was dominated by trembling aspen (*Populus tremuloides*), balsam poplar (*Populus balsamifera*), white spruce (*Picea glauca*), black spruce (*Picea mariana*) and jack pine (*Pinus banksiana*). Forest harvesting in the study area is carried out in 2-3 passes 10 years apart, creating a mosaic landscape of harvested patches of various ages and unharvested stands. Harvested areas average approximately 30 ha in size and contain 5-20 residual trees per hectare. After forest harvesting, forest buffer strips 20-200 m wide remained between harvested areas and the lakeshore. When riparian vegetation separated the forest edge from the lakeshore, buffer strips were measured from harvested areas to the interface of the forest and riparian vegetation. Forest blocks were removed from around 16 'harvested' study lakes once between September 1995 and April 1997. Harvesting removed forest from approximately 4-40% of the drainage basins of these lakes ($\bar{x}$=18.7, SE=2.4, for 14/16 lakes. The drainage basins of the two independent harvested lakes were not delineated. However, forest was harvested from 9% and 19% of the land area within 800 m of these lakes, substantially more than any unharvested lakes). During my study, there was no forest harvesting within at least 800 m of 11/14 'unharvested' study lakes. The three remaining lakes (LLB800, R5, and R26) were harvested within 800 m of the lakeshore before my study began. However, <3% of the forest within this area was harvested in these cases, to between 450-800 m from the lakeshore. Thus, these three lakes were retained in the 'unharvested' category. Harvesting removed forest from 0-11% of the drainage basins of unharvested lakes ($\bar{x}$=1.3, SE=1.0). TROLS and independent study lakes are named with respect to their location and buffer strip width, e.g. LLB20 is situated in the cluster of lakes occurring east of Lac La Biche, and has a forest buffer strip 20 m wide. Lakes in the NCE study are labelled by their disturbance status followed by a code number, e.g. R20 is an unharvested (Reference) lake, whereas C21 is a harvested (Cut) lake. Thus, lakes with names ending in 800, or starting with R, are considered undisturbed (unharvested) sites. All other lakes are disturbed (harvested) sites. These names are retained throughout this paper to facilitate comparisons with other studies.

2.2.2 Bird censuses

Aquatic bird censuses were conducted from a boat rowed around the perimeter of study lakes. On three occasions, a small motor was used during censuses when rowing became impossible due to very strong winds. I conducted censuses on TROLS lakes and the four independent study lakes in 1996-1998, and 1997-1998, respectively. I conducted censuses once between 29 May-14 July, and again between 31 July-16 August, each year. Censuses on NCE lakes were conducted once only between 1-27 August 1996 or 26 June-27 July 1997. All birds seen were identified, and their sexes and ages determined when possible. All non-passerine birds that feed on lakes or at the lake edge, and breed in the study area (Semenchuk 1992) were included in analyses. Some species of aquatic birds were grouped in analyses, due to the difficulty of making precise identifications at a distance, or rarity of occurrence (Appendix 2.2).

2.2.3 Environmental data collection

Each year that bird censuses were conducted, euphotic zone water samples were collected. Water samples were taken from at least one location on lakes, 1-6 times in July. Maximum depth and Secchi depth were also determined when water samples were collected. Frequency of sampling varied according to the schedules of the TROLS and NCE projects. The means of measurements were calculated for the month of July, and means used in statistical analyses corresponded to the years bird censuses were conducted. The depth of the euphotic zone was determined using light meter readings (LiCor Li 1000 or LiCor Quantum Sensor meter) or Secchi depth (Wetzel 1983). Euphotic zone samples were collected using a composite hose. Total phosphorus was measured using persulphate oxidation (Menzel and Corwin 1965, as modified by Prepas and Rigler 1982). Conductivity was determined using the CDM210 conductivity meter lab (Radiometer Copenhagen), and pH using PC-Titrate (Man-Tech Associates Inc.) and the Accumet pH meter 25 (Fisher Scientific). Exceptions to this sampling schedule were for NCE lakes C18 and C19, which were not sampled for conductivity in 1996. Therefore, I used July 1997 conductivity values. Also, seven other NCE lakes were not sampled for conductivity until August 1996. Maximum depth was determined on NCE and independent study lakes using the bottom depth feature of a fish finder (Humminbird or Eagle), and recording the bottom depth while traversing lakes according to predetermined transects. On TROLS lakes, the deepest part of lakes was determined by measuring depth along transects using a weighted, graduated string (Silins 1994). During my study, the deepest area of each lake was revisited after ice-off in spring each year, and the deepest point determined by weighted, graduated string, and marked by a float. On subsequent visits, maximum depth was measured as the depth of water at this float. Lake area was determined once using planimetry or a geographic information system (GIS). The amount of forest harvested within 800 m of study lakes was determined for the 19/30 lakes for which digital data were available, also using GIS (ArcView 3.1, Environmental Systems Research Institute Inc. 1992-1998).

To investigate relationships between aquatic birds and fish, species composition of fish assemblages was determined using overnight sets of Gee minnow traps and multi-mesh gillnets (mesh size: 6.25-75.0 mm, net size: 42.0x1.5 m). Net and trap locations were determined according to a stratified random design (Tonn and Danylchuk unpubl.). Composition of fish assemblages in 4/12 TROLS lakes was determined in 1997, and the other 8/12 lakes in 1996. Fish were sampled on NCE lakes, and independent study lakes, the same year bird surveys were conducted. I included presence or absence of fish in analyses, as abundance data were not available for all lakes. I dichotomised fish as either large- or small-bodied, due to differences in the perceived impact of these two categories on birds. Small-bodied fish are primarily food sources for birds, although they may compete with birds for some invertebrate foods, as both groups include insectivores (Ehrlich et al. 1988, Nelson and Paetz 1992). Large-bodied fish can act as prey, and competitors for food, but they also depredate aquatic birds (Johnsgard 1987, Eadie et al. 1995). Their larger size means they can consume much larger prey items than small-bodied fish species. Also, large-bodied fish are more susceptible to being exterminated from lakes or having their populations reduced by winterkill, due to their higher oxygen requirements. Large-bodied fish in my study lakes included perch (*Perca flavescens*), pike (*Esox lucius*), and white sucker (*Catostomus commersoni*). Small-bodied species were brook stickleback (*Culaea inconstans*), fathead minnow (*Pimephales promelas*), finescale dace (*Phoxinus neogaeus*), and pearl dace (*Semotilus margarita*). Lakes tended to be occupied by assemblages of either large- or small-bodied fish; both large- and small-bodied fish were present in only 6/30 study lakes.

2.2.4 Statistical analysis

I conducted both direct and indirect ordinations in CANOCO 4.0 (Ter Braak and Smilauer 1998), to explore aquatic bird community composition, and relationships between aquatic bird communities and environmental characteristics. Ordination operates by maximally dispersing study sites along a series of orthogonal axes which represent hypothetical (indirect ordination) or actual (direct ordination) recombinations of environmental variables. To determine if aquatic bird occurrence on lakes could be accounted for best by linear or unimodal response models, I conducted detrended correspondence analysis (DCA). The gradient length of the first DCA axis rendered both linear and unimodal techniques appropriate (Ter Braak and Prentice 1988). Consequently, I chose to conduct indirect ordinations of aquatic bird community composition using correspondence analysis (CA), and direct ordinations investigating relationships of aquatic birds and environmental variables using canonical correspondence analysis (CCA).

I used presence/absence data to represent aquatic bird species in ordinations. I used presence/absence, rather than abundance, to reduce potential inaccuracies in abundance caused by conducting censuses of aquatic birds at different times during the May-August period. For example, conducting surveys in June probably reduced detections of nesting female ducks. Also, in August, young-of-the-year and adult females of some species were difficult to distinguish at a distance. Therefore, abundance values obtained in August may have included young-of-the-year, and may not have accurately reflected populations of adults resident on lakes through the summer. Finally, the use of presence/absence, rather than abundance, removed the potential for observer bias in counting birds. I eliminated bird species present on only one lake prior to conducting ordination analyses and downweighted rare species, to prevent them having disproportionately large effects in ordinations (Ter Braak and Smilauer 1998).

Both year and geographic location of lakes can affect aquatic bird community composition, e.g. due to climatic conditions and geographic gradients in species richness, respectively (Brown and Gibson 1983, Johnson and Grier 1988, Wiens 1989). To assess the importance of interannual variation in aquatic bird community composition, I compared scores from the first two axes of CA analyses of aquatic bird occurrences from 1996 with 1997 and 1998, and from 1997 with 1998, for lakes sampled in all these years, using PROTEST analysis (Jackson 1995). PROTEST, developed by Jackson and Harvey (1993), determines the degree and significance of concordance between two matrices, via randomisation testing based on Procrustean matrix rotation. The method gives similar results to Mantel tests (Mantel 1967), without the issue of selecting an appropriate distance measure, which can introduce subjectivity into Mantel procedures. PROTEST may also be more powerful than Mantel tests (Peres-Neto and Jackson unpubl.). Birds were surveyed on 12 common lakes in 1996-1998, and 16 common lakes in 1997-1998. PROTEST analysis revealed no significant differences between species composition of aquatic bird communities in 1996 and 1997 (PROTEST $P=0.16$), and 1996 and 1998 (PROTEST $P=0.22$), unlike 1997 and 1998 (PROTEST: $P=0.003$). Due to the lack of significant differences in community composition between 1996 and 1997 and because not all lakes were surveyed for birds in all years of the study, I created a composite data set from lakes sampled in 1996 and 1997 to maximise the number of lakes in subsequent analyses. This composite data set included more lakes than could have been analysed for any one year. I included TROLS lakes sampled in 1997, NCE lakes sampled in either 1996 or 1997, and independent study lakes sampled in 1997 in the composite data set. Forest harvesting on all sites occurred prior to summer of 1997. Thus, the data set I used best represented disturbed lakes, but without the potentially confounding effects of significant interannual variation, which may have resulted from inclusion of 1998 data. Also, fewer lakes were sampled in 1998. Thirty lakes (16 harvested, 14 unharvested, see above) were included in the composite data set. Twenty eight aquatic bird species, or species groups were included in subsequent ordination analyses (Appendix 2.2).

To determine the effect of geographic location on bird community composition, I compared latitude and longitude (in decimal degrees), with scores from the first two CA axes of aquatic bird presence/absence on the 30 study lakes in the composite data set described, using PROTEST analysis. I also conducted Pearson correlations of log of species richness per hectare, with latitude and longitude, in SPSS 8.0 (SPSS Inc. 1997). PROTEST showed that geographic location did not significantly affect species composition of aquatic bird communities, in the composite data set ($P=0.10$). However Pearson correlation analyses showed that latitude affected species richness ($r=-0.41$, $P=0.02$, $n=30$), although the effect of longitude on richness was not significant ($r=0.004$, $P=0.98$, $n=30$). To be conservative, I used both latitude and longitude (entered as decimal degrees) as covariates when appropriate, in CAs and CCAs, including partial CCAs.

Before conducting CCAs, I examined the environmental data set for collinearity, by ensuring that no variables were strongly correlated ($P<0.05$) with Pearson correlation coefficients of $|r|>\pm0.65$. I used SPSS 8.0 for Pearson correlations (SPSS Inc. 1997). Prior to conducting both these correlations, and ordinations, I log transformed environmental variables, when appropriate. Environmental variables included in analyses were log lake area, log maximum depth, conductivity, pH, log Secchi depth, and log euphotic zone total phosphorus. I also included categorical variables representing the presence or absence of large- and small-bodied fish. I used biplot scaling in CAs and CCAs, which is more suitable than other scaling methods for gradients of the length produced from my data (Ter Braak and Smilauer 1998). After conducting CAs, I examined the relationship between various environmental variables and site scores using the first four axes of CAs with Pearson correlations conducted in SPSS 8.0 (SPSS Inc. 1997). I used Bonferroni α adjustments when conducting multiple correlations with elements of the same data set (Miller 1981).

In CCAs, I conducted automatic forward selection to assess the importance of environmental variables in capturing variation in species data. To test the significance of forward-selected variables, I used 1,000 Monte Carlo permutations. I also tested the significance of the first two canonical ordination axes, again using 1,000 Monte Carlo permutations. To assess the relative importance of (i) the geographic location of lakes, (ii) lake morphometry, (iii) lake water quality, (iv) the nature of fish assemblages in lakes, and (v) the occurrence of forest harvesting disturbance in the landscape surrounding lakes, in capturing variation in aquatic bird community composition, I conducted partial CCAs (Borcard et al. 1992). Geographic location of lakes was represented by latitude and longitude in decimal degrees. Lake morphometry was represented by log lake area, and log maximum depth. Attributes of lake water quality included in analyses were log Secchi depth, and euphotic zone conductivity, pH, and log total phosphorus. I used the first two components of a Principal Components Analysis (PCA) to summarise these four variables in partialling analyses, to eliminate the possibility that water quality captured more variation than other sets of variables purely because it was described by four measures, instead of two (Kent and Coker 1992, Borcard et al. 1992). Fish assemblages were characterised categorically as containing large- and/or small-bodied species. Disturbance status of lakes was also represented categorically. I did not include disturbance status of lakes in partial CCAs examining (i)-(iv), above. Instead, I conducted an additional set of partialling analyses on the aforementioned variables, and disturbance status, because I wanted to examine the amount of variation attributed to the different suites of variables described in (i)-(iv), in the absence of any consideration of disturbance effects.

To assess the effect of disturbance on aquatic bird community composition and environmental characteristics of lakes, I used a Multi-Response Permutation Procedure (MRPP) (Zimmerman et al. 1985). MRPP is a non-parametric technique used to test null hypotheses of no differences between groups, which are identified *a priori*. I conducted MRPP analyses using the composite data set, with lakes categorised as harvested or unharvested, as before. For species analyses, I excluded birds present on only one lake. For environmental analyses, variables used included lake morphometric characteristics, and water quality variables, described for CCAs above. I conducted MRPP analyses using the Euclidean distance measure, recommended by Zimmerman et al. (1985). This analysis may have been confounded by the underlying effects of geographic location (see above). Therefore, after analysing the data set as a whole, I divided lakes into groups. Northern versus southern lakes were divided at 55°30' latitude, and eastern versus western lakes at 113° longitude. There were 11 and 19 lakes in the northern and southern groups, and 17 and 13 in the eastern and western groups, respectively. I then compared disturbed lakes with undisturbed lakes within each of these four groups. When environmental characteristics of lakes did not differ with respect to disturbance status, according to multivariate MRPP tests (see Results), I sought to confirm the lack of differences by conducting t tests on individual environmental variables, comparing the two lake types. I log-transformed lake area, maximum depth, total phosphorus, and Secchi depth, prior to conducting t tests in SPSS 8.0 (SPSS Inc. 1997).

To further identify whether there were differences in aquatic bird communities on disturbed versus undisturbed lakes, beyond species composition, I conducted simple linear regressions of log species richness versus log area on each of the two lake types, using SPSS 8.0 (SPSS Inc. 1997). I used the composite data set for these analyses, as well as species of aquatic birds that were present on only one lake. I included species present on only one lake in richness regressions because these species did not affect these regressions as they may have affected ordinations (by having disproportionately large effects on analyses, see above). I also regressed log species richness against log lake area for an additional set of 41 lakes located south of my study sites, in Athabasca County around 54°37', 113°20', sampled by C.A. Paszkowski in 1993 (Paszkowski and Tonn 2000a, Paszkowski and Tonn 2000b). These lakes represented an extreme level of disturbance (due to forest removal and agriculture), compared to TROLS, NCE and independent study lakes. Forest has been cleared from approximately 50% of land in the area around 'Athabasca' study lakes. Thus, I was able to test whether species richness declined in aquatic bird communities occupying very highly disturbed habitats, as predicted by Connell (1978). Study lakes in Athabasca County were circumneutral-basic, with euphotic zone total phosphorus concentrations of 11.0-500.0 μgL^{-1} ($\bar{x}$=73.5, SE=14.3). Lake areas ranged from 2.7-273.0 ha ($\bar{x}$=81.9, SE=12.8), and maximum depths from 0.6-22.8 m ($\bar{x}$=6.2, SE=1.2). However, aquatic bird censuses were comparable to my study lakes because surveys were conducted the same way. Composition of aquatic bird communities on these lakes was described by Paszkowski and Tonn (2000a) and Paszkowski and Tonn (2000b). I followed regressions of log species richness versus log area by comparing regression slopes and intercepts between the three sets of lakes, using F statistics, and conducting multiple comparisons using Tukey procedures (Zar 1996).

Also using my composite data set of 30 harvested and unharvested lakes, I examined the frequency of occurrences of seven of the most widespread species on disturbed versus undisturbed lakes, using G tests (Zar 1996). Scaup and ring-necked duck were analysed separately in G tests, using data from 25 lakes on which they were effectively discriminated. Occurrences of other species were examined across all 30 lakes in these tests.

2.2.5 Natural disturbance comparisons

Finally, although my study focussed on the effects of forest harvesting disturbance in the boreal forest, the NCE study included 10 lakes in drainage basins that were disturbed by forest fire (Figure 2.1, B identifies these lakes). Therefore, I was able to compare the effects of natural disturbance versus forest harvesting disturbance on aquatic bird communities. From 8.1-44.2% of the drainage basins of these study lakes were burnt ($\bar{x}=22.8$, SE=4.2), in summer of 1995. 'Burnt' lakes had euphotic zone total phosphorus concentrations ranging from 27.5-142.5 μgL^{-1} ($\bar{x}=52.0$, SE=11.4), and pHs from slightly acidic to basic. Lakes were 38.8-205.9 ha in size ($\bar{x}=88.6$, SE=17.3) with maximum depths of 1.5-11.6 m ($\bar{x}=3.1$, SE=1.0). Aquatic bird censuses were conducted as described previously, between 9 July-19 August 1996, and 2-23 July 1997. I compared the composition of aquatic bird communities on lakes disturbed by forest harvesting, and undisturbed lakes from my composite data set described earlier, with community composition on burnt lakes, using MRPP. As before, I excluded bird species present on only one lake. I did not include burnt lakes in species richness comparisons described earlier because the degree of disturbance represented by fire is not clear, compared to forest harvesting or harvesting followed by agriculture. Thus, including burnt lakes in richness comparisons was not useful in addressing the hypotheses of my study.

2.3 Results

The number of resident species of aquatic birds present on harvested and unharvested study lakes ranged from 3-17 ($\bar{x}=8.2$, SE=0.7). Species assemblages on lakes always included common loons. Other 'core' species occurring on >50% of lakes were red-necked grebe, mallard, bufflehead and common goldeneye. Either ring-necked duck, scaup or both also occurred on >50% of study lakes. Species occurring on 25-50% of lakes were American white pelican, belted kingfisher, blue-winged teal, double-crested cormorant, great blue heron, and spotted sandpiper. Bonaparte's or Franklin's gulls were also in this category. Finally, there were 15 species or species groups that were present on up to 25% of study lakes. These were American wigeon, bald eagle, black tern, canvasback, common snipe, gadwall, green-winged teal, horned grebe, northern pintail, short-billed dowitcher, and solitary sandpiper. Composite species categories included in this group were mergansers, scoters, and California, ring-billed and herring gulls, and yellowlegs. (See Appendix 2.1 for patterns of occurrence and life history information on birds occurring on study lakes, Appendix 2.2 for scientific names, and Appendix 2.3 for a complete list of all birds identified on study lakes).

Differences in species composition of aquatic bird communities approached significance on harvested versus unharvested lakes, for all lakes combined (MRPP: P=0.07). When I divided lakes geographically, and compared harvested and unharvested lakes within each geographical group, MRPP distinguished significantly different communities on disturbed versus undisturbed sites for southern lakes only (MRPP, southern lakes: P=0.03; northern lakes: P=0.34; eastern lakes: P=0.27; western lakes: P=0.18). Differences in environmental characteristics also approached significance for harvested versus unharvested lakes, for all lakes combined (MRPP: P=0.07). However, when lakes were grouped geographically, there were no significant differences in environmental factors due to disturbance (MRPP, southern lakes: P=0.80; northern lakes: P=0.14; eastern lakes: P=0.13; western lakes: P=0.37). In t tests of individual environmental variables, only conductivity differed significantly with respect to disturbance status (conductivity: $t_{28}=2.10$, P=0.03; pH: $t_{28}=1.51$, P=0.21; total phosphorus: $t_{28}=0.69$, P=0.47; Secchi depth: $t_{28}=0.28$, P=0.27), and there were no coincidental differences in morphometry between the two lake types (lake area: $t_{28}=-1.41$, P=0.85; maximum depth: $t_{28}=1.56$, P=0.53).

The occurrences of seven species of aquatic birds present on 13-22 of 30 study lakes (25 for ring-necked duck, and scaup) were not affected by forest harvesting disturbance (G tests: red-necked grebe, bufflehead, common goldeneye, ring-necked duck, scaup, mallard, and Bonaparte's or Franklin's gulls, range of $G_2=0.02$-2.48, all P>0.05). Similarly, aquatic bird species did not appear to form assemblages with respect to harvesting patterns in ordination plots (Figures 2.2, 2.3). However, species richness per unit area tended to be higher on lakes disturbed by harvesting versus undisturbed lakes in my study ($q_{2,26}=7.82$, P<0.05, Figure 2.4). Disturbed lakes in my study also accrued more species per unit area, than undisturbed lakes ($q_{2,26}=3.82$, P<0.05). When the highly disturbed lakes from Athabasca County were included in analyses, they displayed higher species richness per hectare than both the disturbed and undisturbed lakes in my original group of 30 study lakes ($F_{2,79}=33.06$, P<0.05; Athabasca lakes versus disturbed lakes in the original composite data set: $q_{2,53}=5.78$, P<0.05; Athabasca lakes versus undisturbed lakes in the original composite data set: $q_{2,51}=15.48$, P<0.05, Figure 2.4). These very highly disturbed systems gained a similar number of species, per unit area, as my original disturbed lakes, but significantly more species per unit area than undisturbed lakes in my study ($F_{2,65}=3848.12$, P<0.001; Athabasca lakes versus disturbed lakes in the original composite data set: $q_{2,26}=1.87$, P>0.10; Athabasca lakes versus undisturbed lakes in the original composite data set: $q_{2,51}=3.82$, P<0.05).

Species occurring sporadically were more likely to be found on lakes disturbed by forest harvesting. For example, American bittern, black tern, Canada goose, common snipe, gadwall, green-winged teal, killdeer, northern pintail, ruddy duck, short-billed dowitcher, and Wilson's phalarope occurred exclusively at 1-4 disturbed lakes. American wigeon, belted kingfisher, double-crested cormorant, and solitary sandpiper occurred on 4-8 lakes, of which all but one were disturbed. In contrast, there were only four species (or species groups) that occupied undisturbed lakes only. These were common or Forster's tern, eared grebe, redhead, and osprey, and all occurred on only one lake. Finally, all but one of the four lakes occupied by scoters were undisturbed.

In CA of aquatic bird communities occurring on lakes in the composite data set, the first four CA axes captured 45.3% of the variation in the species data, with individual axes accounting for 8.9-13.1%. Eigenvalues ranged from 0.13-0.19 (Table 2.2). Correlations between CA axes and environmental variables were not significant, after Bonferroni α adjustments. The strongest correlations, which were significant prior to Bonferroni α adjustments, were between CA axis 1, and the amount of forest harvested around the 19 study lakes for which these data were available, and CA axis 4, and the presence of large-bodied fish (Table 2.3). Bird assemblages from disturbed and undisturbed lakes did not form distinct clusters in CA plots (Figure 2.2).

CCA accounted for 33.9% of the variation in the species composition of aquatic bird communities on 30 lakes, with the first four axes capturing 18.4% (Table 2.4). Of the variation in species data captured by the first four axes, 68.3% was explained by environmental variables. Eigenvalues ranged from 0.05-0.10 for the first four axes of the ordination (Table 2.4). Species-environment correlations on axes 1-4 were moderate (Table 2.4), suggesting that the environmental variables entered were reasonably effective at explaining variation in species data, overall.

When entered stepwise using forward selection, environmental variables were not statistically significant in accounting for the variation in species data. Conductivity, pH, and total phosphorus entered forward selections first (Table 2.5). Also, ordination plots show that the first two CCA axes were most strongly related to conductivity and maximum depth, and lake area and Secchi depth, respectively (Figure 2.3). Monte Carlo permutations determined that the first canonical axis, and all canonical axes, were not significant (significance of CCA Axis 1: P=0.85; significance of all CCA axes: P=0.84). Aquatic bird assemblages did not appear tightly linked to lake disturbance status (Figure 2.3).

Partial CCAs demonstrated that when all other variables were controlled for, those reflecting lake morphometry (lake size and maximum depth) and water quality (represented by the first two components of a PCA of Secchi depth, and euphotic zone total phosphorus, pH, and conductivity) accounted for the majority of explained variation in the species data set (Table 2.6). Fish community composition (represented as the presence or absence of large- or small-bodied fish) and geographic location of lakes explained slightly less variation. However, the geographic location of study lakes was important for both species composition of aquatic bird communities and environmental variables. This is indicated by the relatively large amount of variation that geographic location captures that is common to species assemblages and the environment, as well as the responses of species to aspects of the environment that are spatially structured (column B, Table 2.6). The amount of variation in the species data that is common to water quality, and other environmental characteristics was also relatively high. When I conducted an additional set of partial CCAs including disturbance status of lakes, this categorical variable captured 4.0% of the variation in the species data, i.e. 15.0% of the explained variation. An additional 1.3% of the total variation, i.e. 5.0% of the explained variation, was captured by disturbance status combined with other environmental variables, leaving 72.9% of the variation in the species data unexplained.

Finally, the composition of aquatic bird communities occupying lakes subjected to natural disturbance, represented by forest fire, did not differ from harvested or unharvested lakes (MRPP: P=0.10). Communities on burnt lakes were more different from those on harvested lakes (MRPP: P=0.08), than those on unharvested lakes (MRPP: P=0.70).

2.4 Discussion

2.4.1 Community patterns

Aquatic bird communities on my study lakes consisted of a core of commonly occurring, and therefore frequently coexisting species, augmented by less widespread species, discussed below. Some core species present on my study lakes are also among the most widespread in other boreal regions. For example, common loon, common goldeneye, and ring-necked duck are species that frequently co-occur in the boreal forests of eastern Canada (McNicol et al. 1995), and common goldeneye and mallard co-occur widely in boreal Finland (Kauppinen and Väisänen 1993). Also, the core species on my study lakes were almost identical to core species identified in an agricultural-boreal forest transitional landscape, located south of my study lakes, and communities appeared to accrue species similarly in both areas (Paszkowski and Tonn 2000a). For example, Paszkowski and Tonn (2000a) identified aerially-foraging piscivorous species as entering communities after core species. My results suggest the same trend, with American white pelican, belted kingfisher, double-crested cormorant, great-blue heron, and small gulls forming part of the species group present on 25-50% of lakes. In my study, these lakes were typically deeper, more productive, with higher pHs, and more frequently occupied by small-bodied species of fish, compared to other lakes. Species occurring the most sporadically, i.e. on <25% of lakes, included some that are most frequently found in prairie or parkland habitats, e.g. American wigeon, gadwall, horned grebe, northern pintail, and canvasback (Semenchuk 1992). There were also some sporadically-occurring species that are more commonly recorded in the boreal forest than prairie or parkland regions, but are linked to mudflats which were not available to the same extent on all lakes. These were yellowlegs, solitary sandpiper, short-billed dowitcher, and common snipe (Semenchuk 1992).

2.4.2 Effects of disturbance

As predicted, aquatic bird communities were not resistant to forest harvesting disturbance; differences in community composition were significant between disturbed and undisturbed lakes in the southern part of my study area. Differences in aquatic bird communities were due to species that occurred more sporadically tending to occupy lakes disturbed by forest harvesting. Thus, lakes disturbed by forest harvesting were more species rich than undisturbed lakes. There was a slight tendency for sporadically-occurring species on unharvested lakes to be carnivorous (e.g. common and/or Forster's tern, eared grebe, and surf or white-winged scoter, Appendix 2.1), whereas those on harvested lakes were more likely to be herbivorous (e.g. American wigeon, green-winged teal, and northern pintail, Appendix 2.1). However, contrary to my prediction, this seems unlikely to be due to post-harvest increases in food availability, due to the lack of differences in total phosphorus levels (and consequent productivity) between harvested and unharvested lakes.

When I compared species richness of my study lakes in forest-dominated landscapes, to lakes that I considered very highly disturbed by forest removal and agriculture, species richness continued to increase with increasing disturbance. Elevated species richness at disturbed versus undisturbed lakes is contrary to the hypothesis that species richness decreases with disturbance (Odum 1985). However, it may coincide with the intermediate disturbance hypothesis (Connell 1978), which suggests that the highest levels of species richness are attained at intermediate levels of disturbance. Similar to my results, elevated species richness of aquatic bird communities has been recorded in Finnish boreal systems eutrophied by agriculture, relative to non-eutrophied systems (Kauppinen 1993). Elevated species richness has also been found in other taxa occurring in aquatic habitats disturbed by eutrophication, e.g. macrophytes and fish (Growns et al. 1998, Thiebaut and Muller 1998). Assuming I identified the degree of disturbance appropriately, the lakes in landscapes subjected to forestry and agriculture, which I considered very highly disturbed, were not sufficiently beyond 'intermediate' levels of disturbance that aquatic bird species richness demonstrated the decrease predicted by Connell (1978). Therefore, levels of disturbance sufficiently large to cause this decrease remain to be identified. Perhaps lakes must occur in almost entirely deforested landscapes before the species richness of aquatic bird communities declines. If disturbance-induced changes in aquatic habitats are less important than habitat requirements that are linked to terrestrial landscape characteristics (e.g. access to nest sites for cavity-nesting birds), this may be the case.

The differences between species richness of aquatic bird communities may have been most pronounced on disturbed and undisturbed southern lakes in my data set due to the proximity of these lakes to a colonising source of 'non-boreal' species, i.e. those more typical of the prairie parkland region. The invasion of new species into disturbed habitats is a commonly cited result of habitat fragmentation (Saunders et al. 1991). Thus, harvesting may assist the percolation of non-boreal species into what was previously relatively intact boreal habitat. This may be because newly harvested areas may resemble prairie environments, given that they are more open than neighbouring forest. Unfortunately, there were fewer disturbed lakes, compared to undisturbed lakes, in the north in my study area (Figure 2.1), which may have reduced the detectability of disturbance effects in this geographic area.

The penetrability of boreal habitats, irrespective of forest harvesting, is demonstrated by interannual variation in bird communities, which can occur in response to climatic conditions. When prairie habitats are dryer than normal, fewer birds than usual are able to occupy this region. Those unable to secure prairie habitat may move up to the boreal forest, changing populations, and potentially the composition of aquatic bird communities in this region (Johnson and Grier 1988). In 1996 and 1997, spring precipitation on the Canadian prairies was above the long-term average, by 17% and 6% respectively. However, in 1998, precipitation on the prairies was 2% below the long-term average (Environment Canada unpubl.). Thus, differences in composition of aquatic bird communities on my study lakes between 1997 and 1998 could result from aquatic birds being displaced from the prairies by drought. However, why this effect was not detected in comparisons between 1996 and 1998 is unknown.

2.4.3 Community-environment relationships

Although aquatic bird communities differed significantly between lakes disturbed by harvesting and undisturbed lakes in my study, how these differences related to differences in lake environments is not clear. Only conductivity differed significantly between the two lake types. Also, the relative similarity of eigenvalues within CA and CCA axes produced from my study lakes demonstrates that environmental gradients separating the sites and their respective assemblages of aquatic birds, are complex, rather than being dominated by one or two variables (Belland and Vitt 1995). Lack of significance in correlations between CA axes and environmental variables, forward selection procedures in CCA, and the results of partial CCAs all support this conclusion. However, despite lack of statistical significance, the amount of variation captured by environmental variables entered in direct ordinations was not trivial (Table 2.6).

The prominence of conductivity and total phosphorus in forward selection, and of water quality variables in partialling analyses, probably reflects the importance of lake productivity in structuring aquatic bird communities. Productivity reflects the amount of food for aquatic birds, and previous studies also report its importance in accounting for the composition of aquatic bird communities (Kauppinen and Väisänen 1993), as well as species richness and bird abundance and biomass (Nilsson and Nilsson 1978, Hoyer and Canfield 1994, Suter 1994). Similar my results, Paszkowski and Tonn (2000a) found that conductivity, which reflects productivity, captured the most variation in their aquatic bird communities, after lake morphometry. Thus, even if current levels of harvesting are not affecting primary productivity of lakes (Prepas et al. in press), this may be one mechanism by which harvesting could affect birds in the future.

In my study however, the importance of morphometry and water quality in capturing variation in community composition were more similar than expected. This may be due to the lack of morphometric diversity displayed by study lakes. Lake area was not related to maximum depth in my study, precluding bird communities separating along a continuum from relatively large, deeper lakes, to relatively small, shallower lakes. However, study lakes were relatively shallow overall, with only 1/30 exceeding 10 m in depth. Many authors have found that the area of lakes is an important determinant of aquatic bird community composition or species richness (e.g. Kauppinen 1993, Hoyer and Canfield 1994, Savard et al. 1994, Paszkowski and Tonn 2000a, b), and this is expected from species-area relationships (Williams 1943). In my study, species richness did increase with lake area as expected, although community composition was better explained by lake depth than lake area, according to forward selection. Aquatic birds are limited by water depth when foraging (Gauthier 1993, Austin et al. 1998, Hohman and Eberhardt 1998). Lake depth may therefore affect community composition more strongly than lake area if it provides a better indication of the amount of foraging habitat available to aquatic birds.

Fish assemblage captured slightly less variation in aquatic bird community composition than water quality and lake morphometry, when these variables were controlled for by partialling. This may be partly due to categorical representation of fish communities. Ordinations using fish biomass in each category may have captured more variation in bird communities, however, these data were not available for all lakes or years required. The greater sensitivity of large-bodied fish to winterkill, compared to small-bodied species, may become more important in structuring fish assemblages in the future, if nutrient influxes resulting from continued harvesting increase lake productivity, and therefore oxygen demand. The effects of the two types of species on aquatic birds are also expected to differ, as described previously (see Methods).

Given that fish are only one component of the food base of aquatic birds, the amount of variation in community composition captured by fish communities was unexpectedly high. Overall, invertebrates are expected to be more important to aquatic birds than fish or aquatic plants, because 13/28 of the focal species (and species groups) included in ordinations resulting from the composite data set can be primarily insectivorous, compared to eight that can be primarily piscivorous, and another eight that are predominantly herbivorous (Ehrlich et al. 1988). Also, birds that are typically predominantly herbivorous as adults can be more dependent on invertebrates as young birds, or when breeding (Ehrlich et al. 1988, Hohman and Eberhardt 1998). Quantifying the food base would better illustrate the importance of these other lake biota to birds. Then also, the vulnerability of birds to potential post-harvest changes in prey base could be assessed much more effectively.

The disturbance status of lakes also captured a relatively large proportion of variation in the composition of aquatic bird communities. This occurred despite the fact that disturbance status was represented categorically. Incorporating the amount of forest removed from around lakes may have accounted for more variation, however these quantitative data were not available for all lakes. The disturbance status of lakes captured only slightly less variation than lake morphometry, water quality, and fish community composition. Thus, based on partialling analyses, it appears that lake characteristics overall have only slightly stronger effects on aquatic bird composition than the aspects of lake characteristics that can be specifically associated with disturbance. Also, any direct effects of disturbance (e.g. removal of trees) on aquatic bird communities may be only slightly smaller than would result from disturbance-induced changes in other variables, e.g. water quality. As previously mentioned however, at current levels of harvesting, water quality characteristics were not consistently different between disturbed and undisturbed lakes. Only conductivity did differ significantly, and this difference was not associated with significant differences in phosphorus levels as was expected due to post-harvest nutrient influxes.

2.4.4 Conclusions

Currently, forest harvesting practices in North America are in a state of transition, from more traditional high-yield, short rotation logging, to more holistic and ecologically based approaches (Maser 1994). Inherent in this transition is the consideration of natural disturbance processes of the areas slated for harvesting. In the boreal forest of Alberta, wildfire is the dominant natural disturbance (Rowe and Scotter 1973, Larsen 1980). The effects of fire on aquatic bird communities are poorly known, but it appears they could operate via similar mechanisms to the effects of harvesting. However, the composition of aquatic bird communities on the lakes I examined that occupied burnt drainage basins did not differ from either undisturbed or harvested lakes. This may have been because only 10 lakes were examined, and communities on these lakes were very different from each other. Also, burnt lakes were located in the northern portion of my study area. Thus, if forest harvesting is currently affecting bird communities by opening up the landscape to invading species, burnt lakes may have been sufficiently far from a source of invading 'non-boreal' species that sites remained unaffected by invasions. However, if natural disturbance regimes are to be considered in the formulation of harvesting protocols, extending studies of fire to determine its effects on aquatic birds (beyond these preliminary results) is required.

According to my results, forest harvesting does affect aquatic bird communities in the boreal forest of Alberta. Currently, these changes involve the addition of species to communities, but the mechanisms driving these effects are not clear. Thus, aquatic bird communities should not be used as indicators of disturbance until mechanisms causing disturbance effects are clarified. This is particularly important when community composition may change considerably between years, due to factors unrelated to harvesting, e.g. climate (Johnson and Grier 1988). However, if retaining aquatic bird communities in their pre-harvest state is desirable, the addition of species due to forest harvesting disturbance must be considered negative.

Disturbance of the landscape by harvesting may change aquatic bird communities by facilitating percolation of species more typical of less forested habitats into disturbed areas. If this is the case in my study, pre-harvest aquatic bird communities might be preserved in boreal landscapes by concentrating forest harvesting into discrete areas, rather than spreading out harvesting across the landscape. Longer term studies, encompassing climatic extremes that may affect community composition, are required to corroborate this speculation, and determine the amount of undisturbed land needed to maintain pre-harvest aquatic bird communities in regions disturbed by harvesting.

Table 2.1. Summary of characteristics of 30 study lakes. Area=lake area, ZMax=maximum depth, Cond=conductivity, Secc=Secchi depth, TP=euphotic zone total phosphorus, Harvest=area of cutblocks within 800 m of lakes. (For harvested lakes, statistics on the amount harvested within 800 m represent 13/16 lakes, due to lack of availability of digital data for the other lakes).

	Environmental variable						
	Area (ha)	Zmax (m)	Cond (μScm^{-1})	pH	Secc (m)	TP (μgL^{-1})	Harvest (ha)
Harvested lakes:							
Mean±SE	54.7±10.5	5.1±0.7	235.1±29.5	7.6±0.2	1.7±0.2	102.7±26.0	71.0±13.3
Range	8.6-156.5	1.1-11.1	51-450	6.7-9.4	0.4-3.8	18.0-355.3	8.0-192.6
Unharvested lakes:							
Mean±SE	79.7±15.3	3.5±0.5	152.6±25.0	7.1±0.3	1.5±0.2	83.1±27.5	2.5±1.4
Range	15.2-165.9	1.8-8.3	11.0-300.0	4.7-9.3	0.7-2.7	20.3-365.8	0-15.4

Table 2.2. Results of correspondence analysis applied to 30 lakes with 28 species of aquatic birds in boreal Alberta. Latitude and longitude entered as covariables.

Axis	1	2	3	4	
Eigenvalues	0.19	0.18	0.16	0.13	
Cumulative percentage variance of species data	13.1	25.5	36.4	45.3	
Sum of all unconstrained eigenvalues					1.48
Total inertia					1.63

Table 2.3. Results of Pearson correlations between the first four axes of correspondence analysis of aquatic bird assemblages on boreal lakes in Alberta, and environmental variables characterising lakes. All variables were measured on 30 lakes, except the amount of harvesting within 800 m of lakes, which was determined for 19 lakes. Variables that were log transformed are indicated by asterisks. The amount of harvesting within 800 m of lakes was log x+1 transformed prior to correlation analysis. No correlations were statistically significant after Bonferroni α adjustments. Correlation coefficients are shown. [a] Marked coefficients are $P<0.05$ prior to Bonferroni α adjustment; $P=0.045$ in both cases.

Environmental variable	Axis 1	2	3	4
Lake area*	0.11	-0.05	0.20	-0.05
Maximum depth*	0.14	0.31	-0.03	-0.04
Total phosphorus*	-0.12	-0.03	-0.21	-0.05
Conductivity	0.03	0.25	-0.17	0.06
pH	-0.06	0.07	-0.06	-0.27
Secchi depth*	0.12	0.26	0.20	-0.16
Presence of large-bodied fish	0.11	-0.06	0.03	-0.37[a]
Presence of small-bodied fish	-0.15	0.02	-0.18	0.20
Amount of harvesting within 800 m of lakes	0.44[a]	0.32	0.26	0.32

Table 2.4. Results of canonical correspondence analysis of 30 lakes, 28 species, and 8 environmental variables in boreal Alberta. Latitude and longitude entered as covariables.

Axis	1	2	3	4	
Eigenvalues	0.10	0.07	0.06	0.05	
Species-environment correlations	0.84	0.81	0.84	0.70	
Cumulative percentage variance of species data	6.6	11.5	15.3	18.4	
Cumulative percentage variance of species-environment relation	24.6	42.8	56.6	68.3	
Sum of unconstrained eigenvalues after fitting covariables					1.48
Sum of canonical eigenvalues					0.40
Total inertia					1.63

Table 2.5. Results of forward selection procedure in canonical correspondence analysis of 30 lakes, 28 species of aquatic birds, and 8 environmental variables in boreal Alberta. Latitude and longitude entered as covariables. Marginal effect=amount of variation captured by environmental variables if each variable was the only one in the CCA; Cumulative fit=amount of variation captured by each environmental variable, in addition to those listed previously.

Environmental variable	Marginal effect	Cumulative fit	P
Conductivity	0.05	0.05	0.50
Total phosphorus	0.05	0.10	0.57
Maximum depth	0.05	0.15	0.56
Presence of small-bodied fish	0.05	0.21	0.32
Secchi depth	0.04	0.26	0.57
pH	0.04	0.31	0.65
Lake area	0.05	0.36	0.59
Presence of large-bodied fish	0.05	0.40	0.78

Table 2.6. Importance of geographic location, lake morphometry, water quality, and fish assemblages, in accounting for variation in aquatic bird communities in boreal Alberta, determined by partial canonical correspondence analyses. Analyses included 28 species on 30 lakes. Values given are percent of explained variation. A=Variation in species data captured uniquely by focal environmental variables (fraction a in Borcard et al. (1992)), B=Variation in species data captured by focal environmental variables that is shared by other environmental variables, due to underlying processes structuring all these (fraction b in Borcard et al. (1992)). Unexplained variation and stochastic fluctuations accounted for 71% of variation in aquatic bird communities. [a] Latitude and longitude, [b] Maximum depth, lake area, [c] First two principal components from PCA of euphotic zone total phosphorus, pH, conductivity, and Secchi depth, [d] Presence of large- and small-bodied fish, [e] Latitude and longitude included in analyses as covariables.

Source of variation	A: Uniquely captured variation	B: Variation shared with other variables
Lake morphometry[be]	24.73	2.90
Water quality[ce]	24.48	8.51
Fish assemblage[de]	20.85	1.06
Geographic location[a]	20.57	12.56

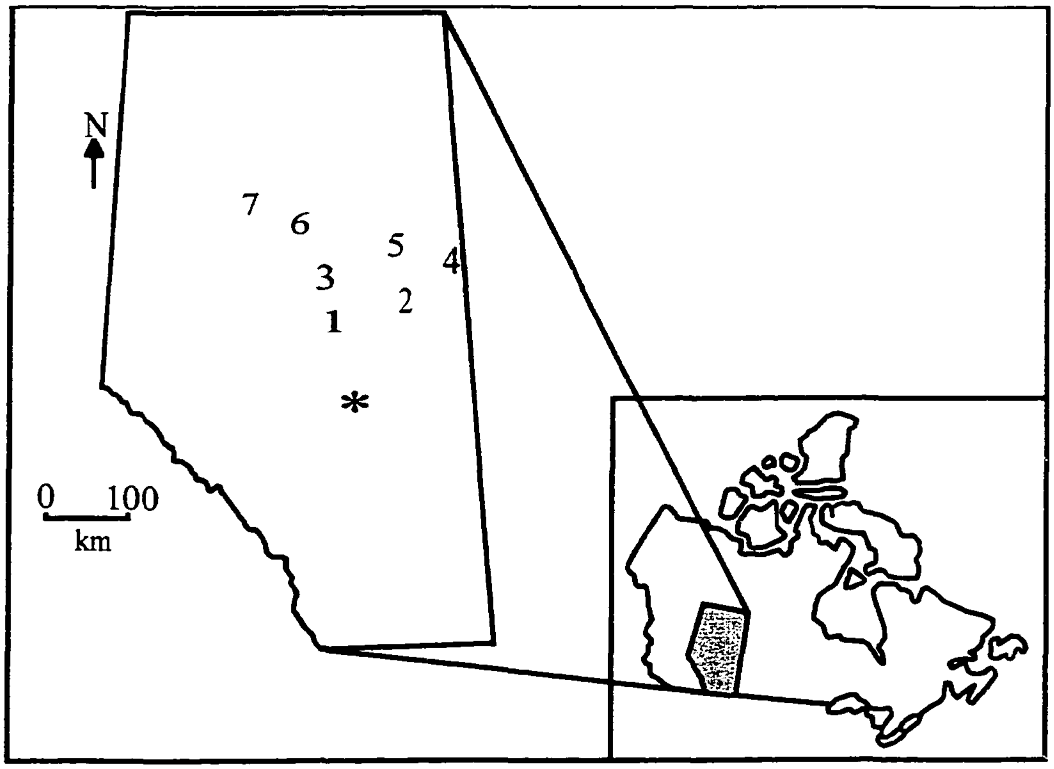
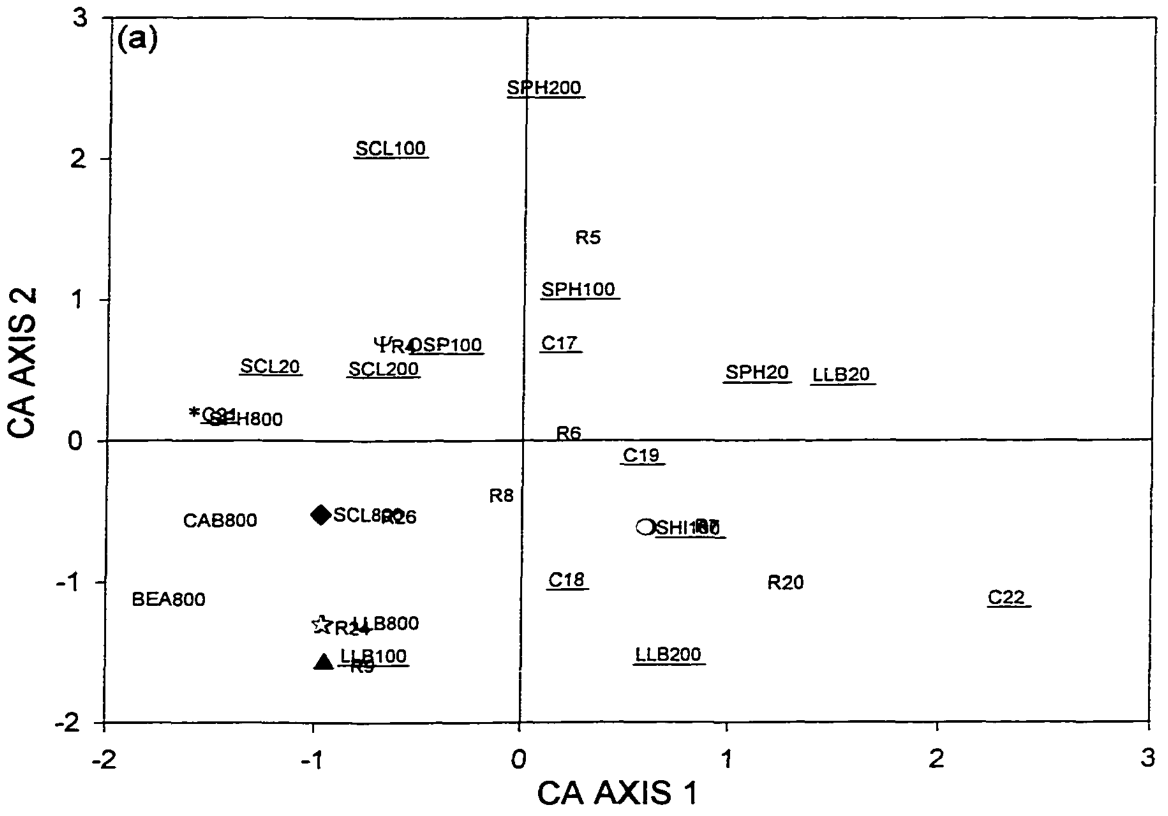


Figure 2.1. Location of clusters of study lakes (numbered) in Alberta, Canada (inset). Asterisk marks Edmonton. 1=SCL20, SCL100, SCL200, SCL800, R20, 2=LLB20, LLB100, LLB200, LLB800, SHI100, OSP100, CAB800, BEA800, C18, C19, 3=SPH20, SPH100, SPH200, SPH800, C21, 4=R4, R5, B1, B2, B3, 5=R6, R7, R8, R9, C17, B10, B12, B13, B14, B15, 6=C22, R24, 7=B25, R26, B27. See text for explanation of lake names.


(a)
SPH200
SCL100
R5
SPH100
ΨR4
OSP100
C17
SCL20
SCL200
SPH20
LLB20
*C21
SPH800
R6
C19
R8
CAB800
◆SCL800
R26
○SHI100
R7
C18
R20
C22
BEA800
☆R24
LLB800
▲LLB100
R9
LLB200
3
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CA AXIS 2
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3
CA AXIS 1

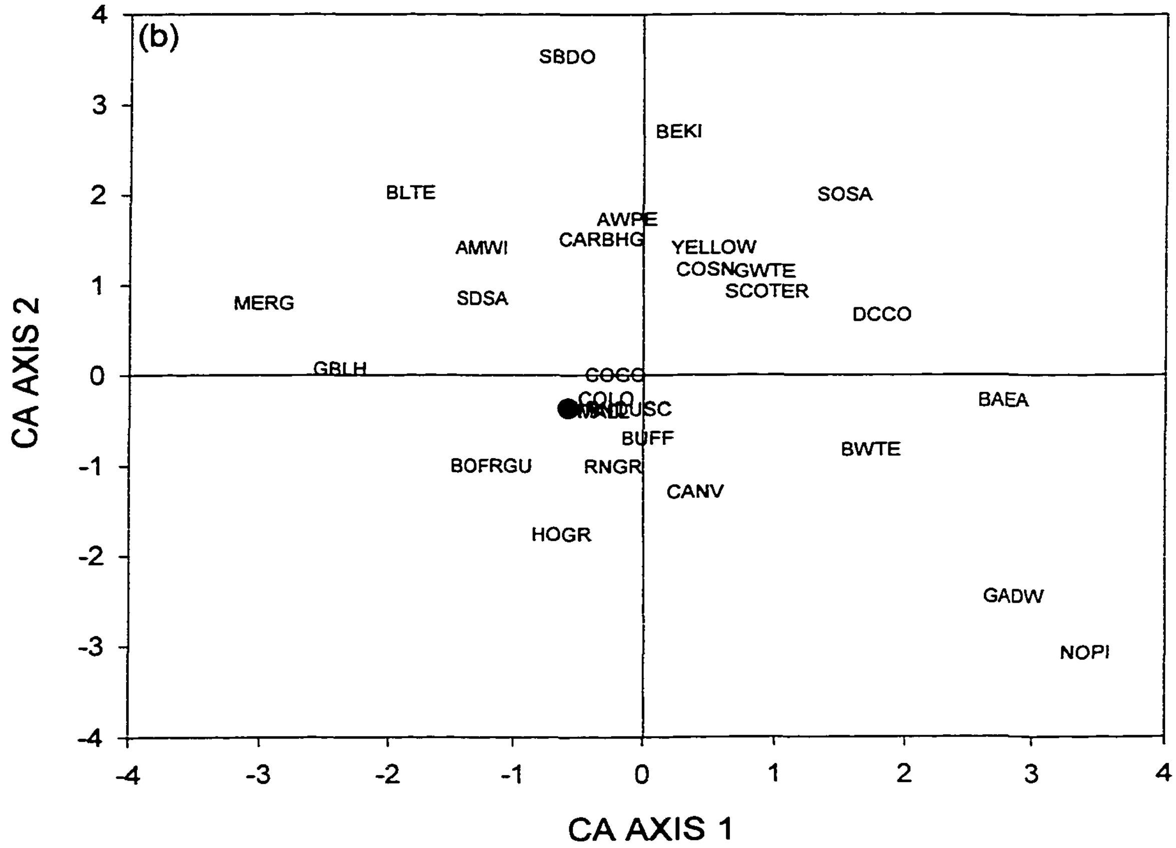
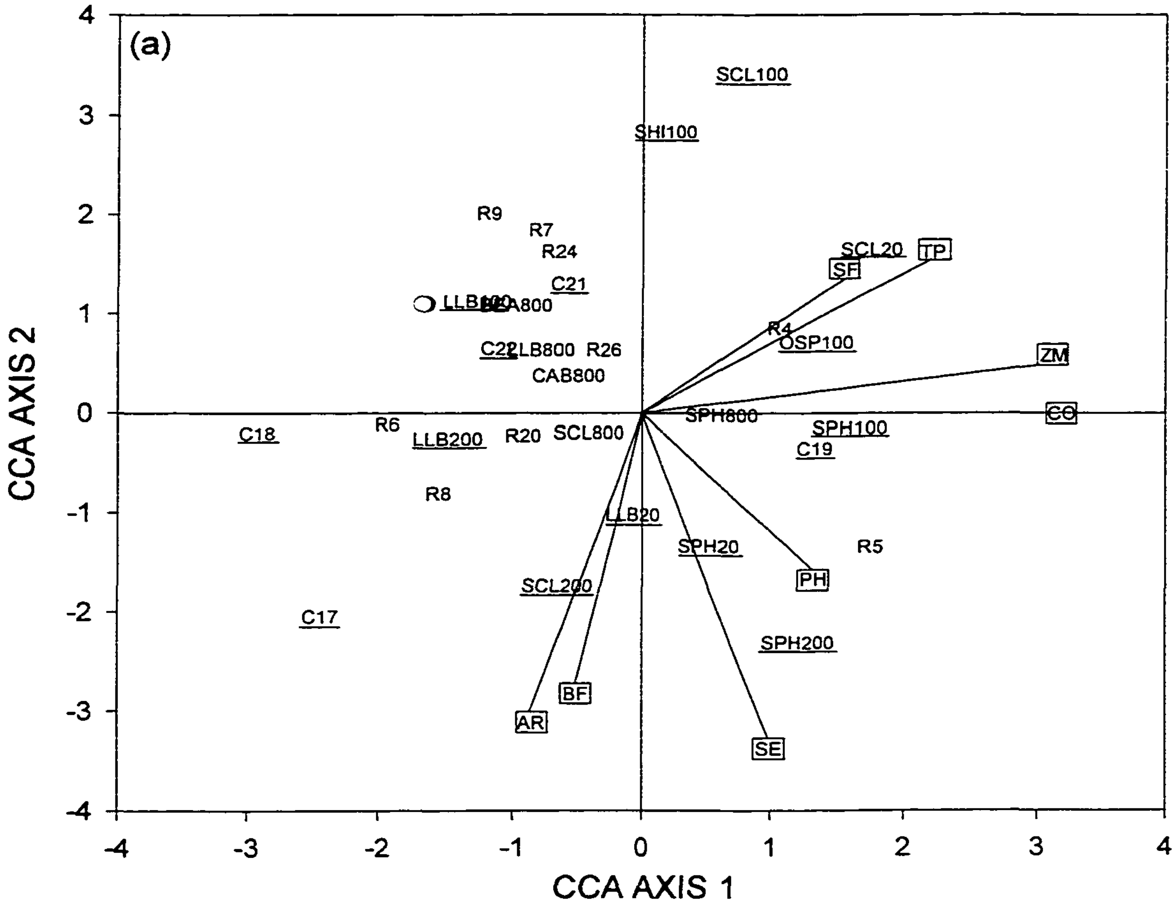


Figure 2.2. Plots of correspondence analysis of (a) 30 lakes and (b) 28 species of aquatic birds in boreal Alberta. Latitude and longitude entered as covariables. See text for explanation of lake names, and Appendix 2.2 for species codes. Disturbed lakes are underlined. Symbols identify overlapping cases. In (a), Ψ=R4, OSP100, *=C21, SPH800, ◆=SCL800, R26, ☆=R24, LLB800, ▲=LLB100, R9, and ○=SHI100, R7. In (b), ●=COLO, MALL, RNDUSC.


(a)
SCL100
SHI100
R9
R7
R24
C21
LLB100
A800
SCL20
TP
SF
R4
OSP100
ZM
C22
LLB800
R26
CAB800
CO
SPH800
SPH100
C19
C18
R6
LLB200
R20
SCL800
R8
LLB20
SPH20
R5
PH
SCL200
C17
SPH200
BF
AR
SE
CCA AXIS 2
4
3
2
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CCA AXIS 1

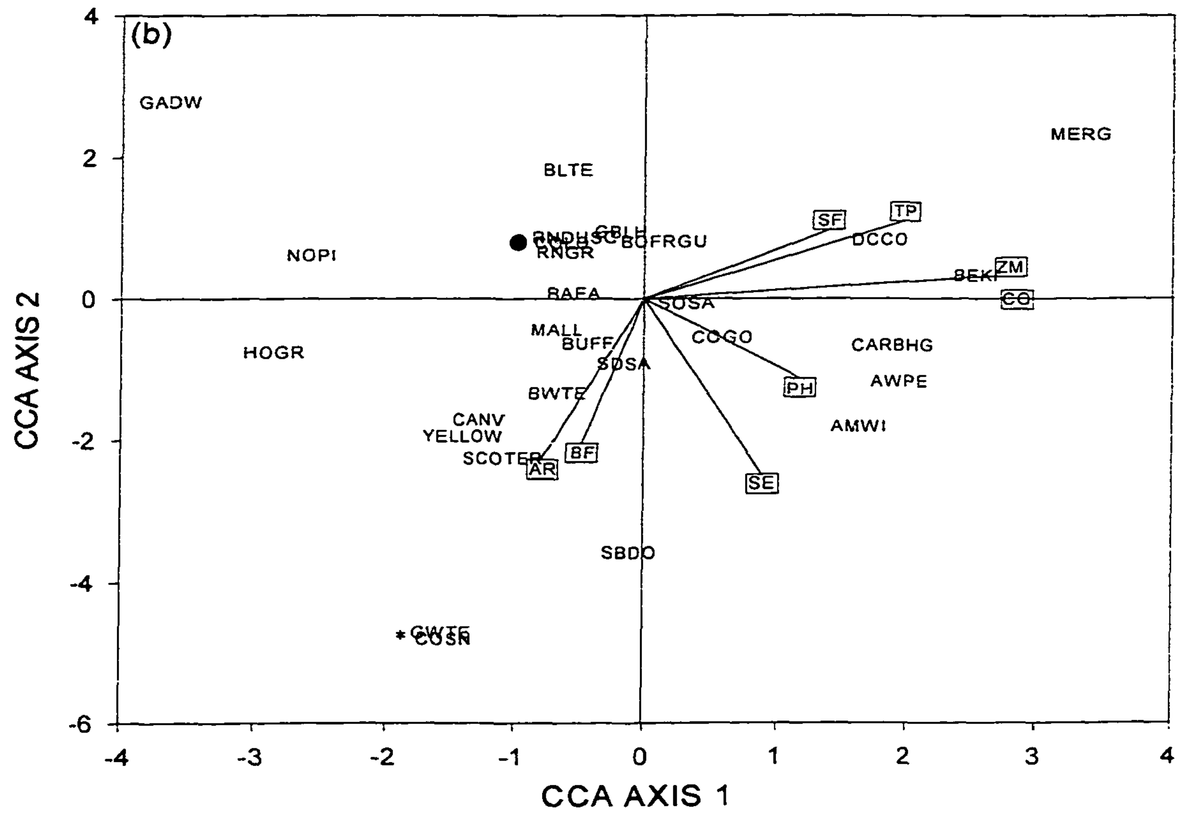

Figure 2.3. Biplots of canonical correspondence analysis of 30 lakes, based on 28 species of aquatic birds, and eight environmental variables in boreal Alberta; (a) Lake-environment biplot (b) Species-environment biplot. Latitude and longitude entered as covariables. AR=lake area, ZM=maximum depth, CO=conductivity, PH=pH, SE=Secchi depth, TP=euphotic zone total phosphorus, SF=presence of small-bodied fish, BF=presence of large-bodied fish. See text for explanation of lake names, and Appendix 2.2 for species codes. Disturbed lakes are underlined. Symbols identify overlapping cases. In (a), O=LLB100, BEA800. In (b), ●=RNDUSC, GBLH, COLO, RNGR, *=GWTE, COSN.

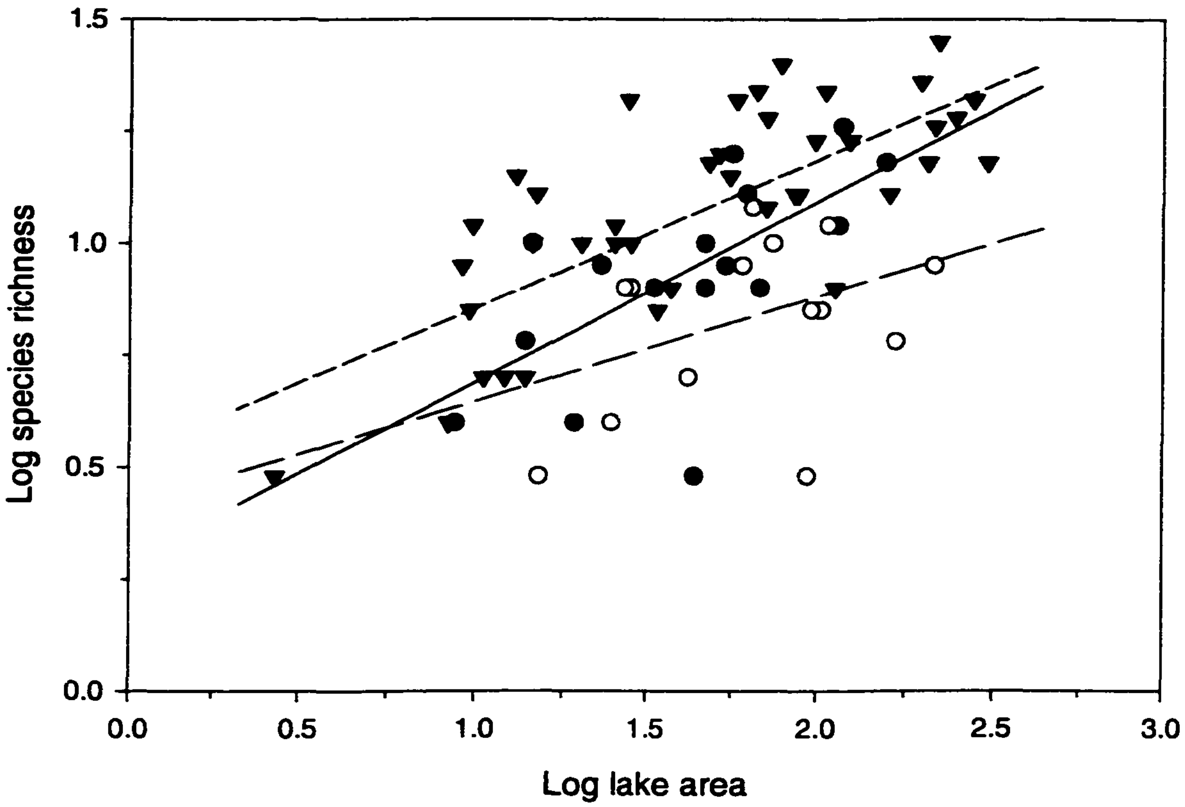

Figure 2.4. Log species richness versus log lake area for undisturbed lakes (○), and disturbed lakes (●) in forest-dominated landscapes, and disturbed lakes in agricultural landscapes (▼). Simple linear regression lines are shown. Long dashed line=undisturbed lakes in forest-dominated landscapes, solid line=disturbed lakes in forest-dominated landscapes, short dashed line= disturbed lakes in agricultural landscapes.

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Chapter 3. Relationships between environmental factors and aquatic bird densities on boreal lakes in Alberta

3.1 Introduction

Disturbance is a key process in all ecological systems, and it is usually viewed as disruptive to the biotic environment, the abiotic environment, or both (Odum 1985, Pickett and White 1985). The consequences of disturbances are determined by their spatial extent, temporal extent, and intensity, together with the persistence, resistance, and resilience of ecological systems. Consequences of disturbance have been studied in aquatic and terrestrial systems. However, freshwater aquatic systems are especially amenable to disturbance studies, for several reasons. Firstly, freshwater aquatic systems receive material from drainage basins that can cover very large areas. Thus, waterbodies represent larger landscape areas, and consequently integrate the effects of disturbance over broader spatial scales, than terrestrial areas the same size. Also, the boundaries of lakes and streams are readily apparent, at least above ground. Many organisms inhabiting waterbodies cannot live in terrestrial environments. Thus, aquatic organisms can be easier to study than terrestrial species because of their confinement to specific aquatic habitats. Finally, water movements can reduce the heterogeneity of lakes, which may facilitate the detection of disturbance effects (Schindler 1990).

Following disturbance, biotic properties of aquatic systems change due to the reactions of individual organisms to changes in their environment. Individual reactions may then be reflected in changes in population characteristics. For example, the densities of some macroinvertebrate species are reduced by acidification (Hall 1994), debris flow (Lamberti et al. 1991), fire (Rinne 1996), and forest harvesting around streams (Davies and Nelson 1994). Fish populations are reported to increase when lakes are anthropogenically eutrophied (Mills and Chalanchuk 1987), but can decrease with acidification (Schindler 1990), and forest fire (Rinne 1996). Finally, aquatic bird populations can be negatively affected by acidification (McNicol et al. 1995), pesticides (Risebrough 1983), and forestry (Newton 1994).

Species populations that change in response to disturbance may be useful in indicating the magnitude and extent of anthropogenic effects on the environment. Aquatic birds can be useful indicators, as they tend to be relatively large, and conspicuous, and therefore they can be easier to monitor than other members of aquatic ecosystems. They can also facilitate detection of the effects of different types of disturbances, due to the sensitivity of different species, or groups of species, to different habitat characteristics. For example, the foraging requirements of the common goldeneye (*Bucephala clangula*) and the common merganser (*Mergus merganser*) resulted in these species being proposed as indicators of acid stress in lakes (McNicol et al. 1990).

The presence of aquatic bird species, and their abundance, have also been related to environmental characteristics in studies that have not specifically investigated disturbance. The composition of the landscape surrounding study lakes, the size, depth, productivity, pH, and clarity of lakes, and prey availability have all been linked to the presence and abundance of aquatic birds (Eriksson 1984, Blancher et al. 1992, Hanson and Butler 1994, Kauppinen 1993, Newton 1994, Savard et al. 1994, Austin et al. 1998, Paszkowski and Tonn 2000). The most important environmental factors differ among species and habitats. However, typically lake morphometry and productivity are the key determinants of aquatic bird densities, due to their direct effects on the number of birds lakes can support through the availability of space and food. The categorisation of aquatic birds into foraging guilds has been used widely by investigators relating aquatic birds to their environment. The most common way waterfowl species are divided for these analyses is into dabbling species, that forage by skimming food from the surface of the water, upending, or immersing their heads and necks, versus diving species, that submerge completely and swim underwater to find food (Ehrlich et al. 1988). Guilds identified via foraging method can be expected to respond to environmental conditions similarly, due to at least some habitat requirements being common across guild members. Thus, grouping species into guilds may facilitate identification of habitat requirements, and foraging guilds have been used in investigations of the effects of disturbance on other taxa, e.g. stream macroinvertebrates and lake fish (Hawkins et al. 1982, Matthews 1998). Identifying the key habitat associations of aquatic birds may facilitate predictions of the effects of environmental changes on populations, including changes induced by disturbances.

Forest harvesting is an anthropogenic disturbance that changes the terrestrial environment directly by removing forest. Thus, harvesting changes the distribution and abundance of terrestrial organisms, including predators of aquatic bird eggs (Kirkland 1977, Snyder and Bissonette 1987, Thompson et al. 1989). Removing forest also removes nest sites for species of aquatic birds that use cavities (Newton 1994). Effects of forest harvesting on aquatic systems can vary with lake morphometry and stratification regimes (Prepas et al. in press). However, effects may include increased nutrient influx after harvesting (Prepas et al. in press), which can increase primary production. Increased primary production may be reflected by decreased water clarity due to increased algal growth. Changes in primary production may be expected almost immediately after nutrient influx resulting from forest harvesting, due to the rapid generation of primary producers, specifically phytoplankton, and non-planktonic algae (Gabor et al. 1994, Murkin et al. 1994). Increased primary production may also affect invertebrate and fish populations and biomass (Mills and Chalanchuk 1987, Jorgenson et al. 1992). Changes in these organisms could occur in the first or second growing season after nutrient enrichment resulting from winter harvesting (Mills and Chalanchuk 1987, Jorgenson et al. 1992, Kiesling 1999). Through these trophic interactions, harvesting may affect the availability of prey for aquatic birds (Eriksson 1984, 1985, Campbell and Doeg 1989, Growns and Davis 1991, Davies and Nelson 1994).

If the availability of food increases for aquatic birds after forest harvesting, use of lakes by these birds is expected to increase. Increases in density should occur the fastest for bird species feeding on primary producers, as primary producers are expected to track post-harvest nutrient influxes the most closely. If nutrient influxes cause invertebrate biomass to increase, birds including invertebrates in their diets may be expected to increase their use of lakes in harvested landscapes. Finally, if post-harvest nutrient influxes cause fish biomass to increase, piscivorous birds may increase their use of lakes. However, benefits accrued to piscivores may be accompanied by costs to insectivores, as fish consume invertebrates, thereby possibly competing with birds for food (Eadie and Keast 1982, Winfield and Winfield 1994). Large-bodied fishes may also depredate young birds (Erskine 1972, Johnsgard 1987, McIntyre 1994).

While the effects of forest harvesting on biotic and abiotic characteristics of streams have been studied (Campbell and Doeg 1989, Davies and Nelson 1994), the effects of harvesting on lakes are poorly known. However, the suitability of aquatic birds as indicators of disturbance, and the amenability of lakes to disturbance studies, suggests that aquatic birds are an appropriate focal group for studies of ecological disturbance caused by forest harvesting around lakes. In the boreal forest of western Canada, forest fire is the dominant natural disturbance (Rowe and Scotter 1973, Larsen 1980), and oil and gas operations were the major anthropogenic disturbance until 1993. However, in 1993, commercial forest harvesting began to accelerate rapidly due to technological developments making boreal forest hardwoods usable in pulp and paper production (Peterson and Peterson 1992). Consequently, much of this forest is relatively newly available to commercial harvesters.

Because boreal ecosystems in western Canada are poorly studied, and relationships between aquatic birds and habitat characteristics are poorly known, the effects of habitat disturbance, including forest harvesting, on aquatic birds are difficult to predict precisely. However, based on what is known about aquatic birds, and studies of disturbances in other ecosystems, the objectives and hypotheses of my study are:

(i) Objective: To identify the importance of different landscape and physical, chemical, and biological characteristics of boreal lakes in determining aquatic bird densities.

Hypothesis: Lake morphometry and nutrient levels are more important than landscape and other lake characteristics in determining aquatic bird densities on boreal lakes in Alberta, for all focal species, regardless of foraging method, i.e. dabbling or diving.

(ii) Objective: To determine whether low-level forest harvesting affects the densities of aquatic birds on boreal lakes in Alberta, in the first and second summers after harvesting.

Hypothesis: Forest harvesting affects the densities of aquatic birds on boreal lakes. Effects are most rapidly demonstrated by species that are tightly linked to forest. Thus, I expect decreased use of lakes by cavity-nesting species beginning the first summer after harvesting. Secondly, because primary productivity is expected to increase immediately after post-harvest nutrient influxes, I expect the densities of bird species feeding on the primary producers to increase the first growing season after harvesting. Increases in these species are expected to precede increases in densities of species feeding on invertebrates and fish, which may occur later in the first growing season, or in the second growing season after harvest.

3.2 Methods

3.2.1 Study lakes

I conducted censuses of aquatic birds on 14 study lakes in the boreal mixedwood forest of north-central Alberta, between latitudes 55°5'30"-55°25', and longitudes 111°38'30"-113°46'45" (Figure 3.1). Lakes were selected based on criteria including the composition of the surrounding forest, landscape position (headwater lakes preferred), morphometry, accessibility, and harvesting schedules (Prepas et al. in press). Lakes ranged in size from 8.6-156.5 ha, and were meso- to hypereutrophic (Prepas et al. in press, Table 3.1). Twelve of the study lakes were part of the TROLS

(Terrestrial and Riparian Organisms, Lakes and Streams) project, a large scale experimental study using different forest harvesting regimes to determine the effectiveness of buffer strips adjacent to waterbodies in protecting systems from ecological change caused by forest harvesting. Two study lakes were independent of this larger project, but were close by the Lac La Biche cluster of TROLS study lakes. I refer to these as 'independent' study lakes hereafter.

Study lakes were surrounded by forest dominated by trembling aspen (*Populus tremuloides*), balsam poplar (*Populus balsamifera*), white spruce (*Picea glauca*), black spruce (*Picea mariana*) and jack pine (*Pinus banksiana*) (Silins 1994, Strong and Leggat 1992). Forest in the study area is harvested in 2-3 passes, 10 years apart, which creates a mosaic landscape of harvested areas of different ages and unharvested stands. Harvested areas are approximately 30 ha in size, on average, and contain 5-20 residual trees per hectare. Forest blocks were removed from around 11 'harvested' study lakes (nine TROLS lakes and two independent study lakes) once between September 1995 and April 1997. Due to the very small amount harvested the previous winter (4% of the drainage basin), one TROLS study lake sustained a small amount of additional harvesting between September 1997 and April 1998. Harvesting removed forest from approximately 4-40% ($\bar{x}$=15.9, SE=3.8) of the drainage basins of TROLS study lakes. Drainage basins of independent study lakes were not delineated, however forest was removed from 9% and 19% of land within 800 m of these lakes. This is a substantially larger proportion of land than was cleared from around 'unharvested' lakes (see below). After forest harvesting around study lakes, experimental buffer strips of vegetation 20-200 m wide remained between harvested areas and riparian vegetation adjacent to lakes. (Current operational guidelines for forestry in Alberta recommend that buffer strips 100 m in width remain around waterbodies the size of my study lakes (Alberta Environment 1994)). Forest within 450 m of three 'unharvested' study lakes was undisturbed by harvesting in all years of my study. In fact, forest within 800 m of two of these three lakes was undisturbed. Less than 3% of the forest within 800 m of the third lake was harvested to 450 m, in 1994. Eleven percent of the drainage basin of this lake was harvested. Forest was harvested from 0-5% of the drainage basins of other unharvested lakes.

3.2.2 Bird censuses

I conducted aquatic bird censuses from a boat rowed around the perimeter of study lakes twice each summer, (once between 29 May-14 July, and once between 30

July-16 August), from 1996-1998 for TROLS lakes, and 1997-1998 for independent study lakes. Aquatic birds were identified as they were seen, and their sexes and ages were determined when possible. I included non-passerine species that feed on lakes or at the lakeshore in surveys. Bird communities consisted of 4-24 species ($\bar{x}$=11.7, SE=0.7).

I determined bird abundance as the maximum number of adults present in either of the two surveys conducted each summer, and used abundance per hectare, multiplied by 100, as the density measure, after log (x+1) transformation. I multiplied abundance per hectare values by 100 to make data easier to handle via elimination of very small values, and transformed data using log (x+1) to address lack of normality, and abundance values of zero. Focal diving species included in statistical analyses were common loon, red-necked grebe, bufflehead, common goldeneye, ring-necked duck, and lesser and greater scaup. Focal dabbling species were American wigeon, blue-winged teal, and mallard. (See Appendix 3.1 for scientific names, and life history characteristics of these species). These were nine of the most frequently occurring species (or species groups in the case of scaup) on study lakes. When determining abundances, I combined lesser and greater scaup into one category due to the difficulty of reliably distinguishing them from a distance. However, greater scaup are expected to be rare in my study area (National Geographic Society 1987), and I refer to these two species simply as 'scaup' hereafter. I excluded male buffleheads, common goldeneyes, and mallards from abundance calculations, due to their early departure from the breeding grounds, and consequently infrequent detection in surveys. Among focal species in which both males and females remain on the breeding site all summer, the biggest range in densities, and the highest mean densities, occurred in the red-necked grebe (Table 3.2). Of species in which males leave the breeding grounds relatively early in the breeding season (i.e. buffleheads, common goldeneyes, and mallards), mallards displayed the greatest range, and common goldeneyes the highest mean densities (Table 3.2).

3.2.3 Lake characteristics

Lake characteristics included in analyses were selected based on their suspected or confirmed biological importance, and inclusion in other studies that aim to identify habitat characteristics influencing densities of aquatic birds (see previous references). Each year that bird censuses were conducted, euphotic zone water samples were collected. Water samples were taken from at least one location on lakes, 1-6 times in

July. Yearly means of these measurements used in statistical analyses corresponded to years in which bird censuses were conducted. The depth of the euphotic zone was determined using the LiCor Li 1000 or LiCor Quantum Sensor light meters, or Secchi depth (Wetzel 1983). Euphotic zone water samples were collected using a weighted composite hose. Total phosphorus was determined using persulphate oxidation (Menzel and Corwin 1965, modified by Prepas and Rigler 1982). Conductivity was measured using the CDM210 conductivity meter lab (Radiometer Copenhagen), and pH using the Accumet pH meter 25 (Fisher Scientific) and PC-Titrate (Man-Tech Associates Inc.). Lake area was quantified once using planimetry or a geographic information system (ArcView 3.1, Environmental Systems Research Institute Inc. 1992-1998). Maximum depth was determined on independent study lakes by recording lake depth along predetermined transects across lakes, using an Eagle fish finder. On TROLS lakes, the deepest area of lakes was determined before my study began by traversing lakes, again along predetermined transects, and measuring lake depth along transects using a weighted, graduated string (Silins 1994). Between 1996-1998, maximum depth was determined after ice-off within the area initially identified as harbouring the deepest point of each lake, again by measuring depth with a weighted, graduated string. The deepest point was then marked with a float, and measured on subsequent visits to lakes.

Species composition of fish assemblages was also determined, using overnight sets of Gee minnow traps and multi-mesh gillnets (mesh size: 6.25-75.0 mm, net size: 42x1.5 m). Nets and traps were located following a stratified random design (Tonn and Danylchuk unpubl.). Composition of fish assemblages in eight of 12 TROLS lakes was determined in 1996 and 1998; four of 12 TROLS lakes were sampled yearly. I determined composition of fish assemblages in independent study lakes in both 1997 and 1998. I included presence or absence of large- or small-bodied fish in statistical analyses, as abundance data were not available for all lakes. I categorised fish as large- or small-bodied, because these two groups are expected to affect aquatic birds differently. Small-bodied fish in my study lakes (brook stickleback (*Culaea inconstans*), fathead minnow (*Pimephales promelas*), and finescale dace (*Phoxinus neogaeus*)) probably influence bird communities most strongly as prey organisms, although they may consume some of the same prey as birds (Ehrlich et al. 1988, Nelson and Paetz 1992). Large-bodied fish, including yellow perch (*Perca flavescens*), northern pike (*Esox lucius*), and white sucker (*Catostomus commersoni*) in my study lakes, are also consumed by aquatic birds. However, in addition, these fish feed on much larger invertebrates than small-bodied fish. They also consume small-bodied fish, and the young of aquatic birds (Johnsgard 1987, Eadie et al. 1995). Also, large-bodied fish are much more susceptible to winterkill than small-bodied species.

3.2.4 Landscape characteristics

I included landscape properties in analyses to ascertain whether environmental characteristics beyond the lake level could effectively capture variation in aquatic bird densities. For example, Kauppinen (1993) suggested that birds may use vegetation surrounding lakes as a cue indicating lake characteristics. I used a geographic information system (ArcView 3.1, Environmental Systems Research Institute Inc. 1992-1998) to quantify characteristics of the landscape around study lakes, using digital data from the Alberta Vegetation Inventory. I defined an 800 m-wide strip around lakes and within that area determined the amount of land covered by conifer-dominated forest, deciduous-dominated forest, open water, vegetated wetland (i.e. with no open water), non-treed land (e.g. seismic lines and clearings from the oil and gas industries), and cutblocks resulting from forest harvesting. I chose 800 m as this was the width of unharvested forest around reference undisturbed lakes, as defined by the TROLS project (Prepas et al. in press). In preliminary analyses, I used these descriptors, after combining vegetated wetland and non-treed land (excluding cutblocks) into one category, due to difficulty distinguishing the two based on some digital data. In analyses presented here, I excluded the amount of deciduous forest, and vegetated wetland/non-treed land within 800 m of lakes, due to strong correlations of these variables with other landscape variables and lake area. I calculated the area of land covered by cutblocks separately, rather than including them in the area of non-treed land, as I was specifically interested in the effects of forest harvesting.

3.2.5 Statistical analysis

To identify environmental factors that may be affecting abundance of aquatic birds on lakes, I conducted linear regressions. Focal bird species used in linear regression analyses are listed above; these are aquatic bird species excluding shorebirds, that were present on ≥ 7 lakes. I also conducted regressions of total densities of diving and dabbling aquatic birds. When conducting regression analyses using all individuals of diving aquatic bird species, I included canvasback, common, hooded, and red-breasted merganser, double-crested cormorant, horned grebe, pied-billed grebe, ruddy duck, and white-winged scoter as well as focal species of diving birds listed earlier. When conducting regression analysis using all individuals of dabbling species, I included Canada goose, cinnamon teal, green-winged teal, northern pintail, and northern shoveler, along with focal species that dabble, mentioned previously. (See Appendix 3.1 for scientific names, and life history characteristics of species included in analyses). Shorebirds were excluded from analyses because the mudflat areas they occupied were not available to the same extent on all lakes. Physical features of lakes included in regression analyses were lake area and maximum depth of lakes. Euphotic zone conductivity, pH, and total phosphorus, Secchi depth, and the occurrence of large- and small-bodied fish were included because they indicate lake productivity, and food availability. I also included latitude and longitude (in decimal degrees) in regressions, because geographic trends in abundance of some bird species are well documented in Alberta (Semenchuk 1992). Landscape variables included in linear regression analyses were area of conifer-dominated forest (which may reflect lake conditions (Kauppinen 1993)), open water (potentially reflecting habitat availability), and cutblocks (indicating disturbance levels) within 800 m of study lakes.

I log-transformed both environmental and landscape variables (except area of cutblocks) when appropriate. Variables log-transformed in 1996 were the amount of conifer-dominated forest, and open water within 800 m of lakes, lake area, maximum depth, and total phosphorus. In 1997, Secchi depth was also log-transformed, and the area of cutblocks within 800 m of lakes was log (x+1) transformed. In 1998, the amount of conifer-dominated forest, and open water within 800 m of lakes, lake area, total phosphorus, and Secchi depth were log transformed, and the area of cutblocks within 800 m of lakes was log (x+1) transformed. I used log (x+1) transformation when attempting to normalise the amount of cutblocks within 800 m of study lakes in analyses of 1997 and 1998 data, due to zero values in the data. In analyses of 1996 data, transforming the area of cutblocks within 800 m of lakes did not improve normality of the data, because almost all lakes were undisturbed. Therefore, I did not transform these data.

In 1996, the 12 TROLS study lakes were included in regression analyses. In 1997, 12 TROLS lakes were included, as well as the two independent study lakes. In 1998, 11 TROLS lakes were included in analyses, alongside the two independent study lakes. One TROLS lake was excluded from regression analyses in 1998 due to the lack of digital landscape data recording harvesting which occurred between September 1997 and April 1998. In both regression analyses, and ANOVA described below, I analysed data from two post-harvest years (1997 and 1998) to investigate changes in the relationships detected between aquatic birds and their habitats over time, and beyond one year post-harvest.

Initially, I conducted exploratory simple linear regressions on transformed abundance per hectare values, and individual environmental variables. I compensated for conducting separate regressions of each environmental variable on species densities by using Bonferroni α adjustment to maintain $\alpha=0.05$. I then conducted multiple forward stepwise linear regressions using α levels of 0.20 and 0.25 for entry and elimination respectively (Hosmer and Lemeshow 1989). To assess significance of multiple linear regressions, I applied analysis of variance. I executed both simple and multiple linear regressions, and associated significance tests, in SPSS 8.0 (SPSS Inc. 1997).

Finally, to investigate the effects of harvesting on populations of aquatic birds, I conducted repeated measures analysis of variance on bird densities before and after forest harvesting on the same lakes. I used TROLS lakes disturbed by harvesting between September 1996-April 1997 in these analyses, and determined bird abundance as the maximum number of adults of the focal species present in either of the two surveys conducted each summer (1996-1998). I used the same focal species as in multiple linear regressions, although two species (blue-winged teal and American wigeon) were not present on $\geq$7 lakes in all years that were used in ANOVAs. I conducted analyses in SPSS 8.0 (SPSS Inc. 1997), and used abundance per hectare values, transformed prior to analysis by log (x+1). I examined the sphericity of the data using Mauchly's test. When the assumption of sphericity was not met, I used the Greenhouse-Geisser adjustment (von Ende 1993). I conducted simple contrasts in repeated measures analyses to compare abundances between years, and thus identify which of the two post-harvest years differed from the pre-harvest year for each focal species. Because the number of study lakes was small (nine lakes), and therefore statistical power relatively low, I set α at 0.1 (Day and Quinn 1989).

When presenting the results of regressions, I divide environmental variables into those that are independent of disturbance (latitude, longitude, lake area, maximum lake depth and area of open water within 800 m of study lakes), those that are sensitive to disturbance (area of conifer-dominated forest within 800 m of study lakes, conductivity, pH, Secchi depth, total phosphorus, fish community composition), and the area of cutblocks within 800 m of lakes, which represents disturbance directly. I also describe results in terms of dabbling versus diving aquatic bird species. These are the two modes of foraging employed by focal species, and within these groups birds may respond similarly to the environment, as mentioned previously. However, due to the small number of dabbling species and regression models for these species, relationships between dabblers and the environment reported here should be interpreted cautiously.

Serendipitously, my study coincided with two seasons that were wetter than average, and one that was dryer than average, on the Canadian prairies. In 1996, the pre-harvest year of my study, spring precipitation was 17% higher than the long-term (1951-1980) average on the prairies. Spring of 1997 was also wetter than average, by 6%. However, in 1998, spring precipitation was 2% below the long-term average (Environment Canada unpubl.). Interannual variation in climate, such as this, can affect aquatic bird populations, via drought-induced displacement of aquatic birds from the prairie habitats they normally occupy, and changes in offspring production (Johnson and Grier 1988, Ferguson 2000). Displaced birds may settle in the boreal region in dry years. In my study therefore, bird densities may have been affected by climate, as discussed below. Spring precipitation also differed from long-term averages (1985-1994 for LLB, and 1971-1994 for SCL and SPH study regions) in my study area (Environment Canada unpubl.). Spring precipitation was 14% higher than average in 1996, and 26% and 48% lower than average in 1997 and 1998, respectively. These differences probably affected lake environmental characteristics (Webster et al. 1996), and may therefore alter relationships between bird densities and lake characteristics as detected by regressions.

3.3 Results

3.3.1 Multiple linear regressions

In multiple linear regressions of total divers and dabblers, R^2 values varied widely between 0.52-0.99, however these regressions were all significant, or close to significant at $\alpha=0.05$, with P values ranging from 0.08-<0.001 (Tables 3.3, 3.4). For single focal species, multiple linear regressions fitted the data at least relatively well, with R^2 values ranging from 0.4-1.0. In fact, 61% of R^2 values were greater than 0.60 for multiple regressions of individual focal species (Tables 3.3, 3.4). Also, all but four multiple regression models for single species were significant at $P<0.05$, and three of the remaining four models resulted in $P\leq0.06$. In 1996, ring-necked ducks were weakly related to environmental variables, such that no variables were included in regression models at P(entry)≤0.20.

Latitude was included in the fewest multiple regression models of densities of focal species, of all the variables used in analyses. Lake area was the variable that most frequently entered single species regression models, even though I used bird densities in regression analyses. The number of variables included in regression models varied widely, from zero (see above) to 11, and different variables were important in capturing variation in densities in different years of the study. In addition, the direction of relationships (i.e. positive or negative) often differed between years of the study. This was also the case in simple linear regressions. At the individual species level, models of dabbling duck densities appeared to be more affected by the amount of conifer-dominated forest within 800 m of study lakes, and the presence of fish, compared to divers. In contrast, models of diving bird densities featured lake area more frequently, as well as the amount of open water around lakes. For dabblers overall, Secchi depth, conductivity, and fish presence featured most frequently in models, compared to longitude, amount of open water surrounding lakes, lake area, maximum depth, and presence of large-bodied fish, which all appeared in two of three models of total diver densities (Tables 3.3, 3.4).

3.3.2 Environmental variables independent of disturbance

Variables representing geographic location were among the least important explanatory variables influencing aquatic bird abundance per hectare on lakes, and entered 7/44 multiple regression models for focal species (Tables 3.3, 3.4). In contrast, lake morphometry, represented as lake area and maximum depth, was relatively important in capturing variation in aquatic bird densities. In fact, lake area produced the only statistically significant simple linear regression result recorded (common loon densities, 1997: R^2=0.67, P<0.001). In multiple linear regressions, lake area entered models of densities of seven species, and maximum depth was included in models for six species (Tables 3.3, 3.4). Finally, the area of open water within 800 m of study lakes was included in nine multiple regression models of focal species' densities (Tables 3.3, 3.4).

3.3.3 Environmental variables sensitive to disturbance

The amount of conifer-dominated forest in the landscape surrounding study lakes appeared in nine multiple regression models, for four species (Tables 3.3, 3.4).

Environmental variables associated with lake water quality entered regression models for all species except red-necked grebes. Total phosphorus was included in more multiple regressions than any other variable indicating water quality (Tables 3.3, 3.4). The composition of fish assemblages appeared important to all focal species, except common goldeneye and American wigeon (Tables 3.3, 3.4).

3.3.4 Direct effects of disturbance and density changes after forest harvesting

Simple linear regressions of bird densities and area harvested within 800 m of lakes were weak, and were not statistically significant (Table 3.5). Based on multiple linear regression models, the area of cutblocks appeared less important than other landscape variables (area of conifer-dominated forest, and open water surrounding study lakes) in accounting for aquatic bird densities on study lakes. The area of cutblocks within 800 m of study lakes entered multiple linear regression models of six species, but did not enter models of total diver and total dabbler density (Tables 3.3, 3.4).

3.3.4.1 Diving aquatic birds

There were no differences in the densities of common loon, red-necked grebe, and common goldeneye before compared to after forest harvesting (common loon: ANOVA: $F_{2,16}$=0.16, P=0.85; red-necked grebe: ANOVA: $F_{2,16}$=0.17; P=0.84; common goldeneye: ANOVA: $F_{1.27,10.10}$=0.24, P=0.69). However statistical power was low for analyses of the densities of these species (range of 1-β=0.13-0.14). In contrast, bufflehead densities differed before and after forest harvesting (ANOVA: $F_{2,16}$=3.10, P=0.07). Densities decreased the first summer post-harvest (Simple contrasts, pre-harvest vs. the first summer post-harvest: $F_{1,8}$=4.24, P=0.07), but there were no differences in densities before harvesting compared to two summers after harvesting (Simple contrasts, pre-harvest vs. the second summer post-harvest: $F_{1,8}$=2.52, P=0.15). Also, densities of ring-necked duck differed between years (ANOVA: $F_{2,16}$=4.24, P=0.03). Densities were higher the first post-harvest summer, compared to pre-harvest (Simple contrasts, pre-harvest vs. the first summer post-harvest: $F_{1,8}$=11.10, P=0.01), but did not differ significantly between the second summer post-harvest versus pre-harvest (Simple contrasts, pre-harvest vs. the second summer post-harvest: $F_{1,8}$=2.12, P=0.18). Finally, densities of scaup were significantly lower in both post-harvest summers, compared to before harvesting (ANOVA: $F_{2,16}$=7.81, P=0.004; Simple contrasts, pre-harvest vs. the first summer post-harvest: $F_{1,8}$=8.95, P=0.02, Simple contrasts, pre-harvest vs. the second summer post-harvest: $F_{1,8}$=15.84, P=0.004).

3.3.4.2 Dabbling aquatic birds

Mallard densities did not differ significantly post-harvest, compared to pre-harvest (ANOVA: $F_{2,16}$=2.29, P=0.13), although statistical power was not high ($1-\beta$=0.54). However, the densities of American wigeon differed significantly both post-harvest summers, compared to pre-harvest (ANOVA: $F_{1.08,8.65}$=6.75, P=0.03). Densities of wigeon were slightly lower the first summer post-harvest, compared to pre-harvest (Simple contrasts, pre-harvest vs. the first summer post-harvest: $F_{1,8}$=4.74, P=0.06). Wigeon also occurred on fewer lakes the first summer post-harvest (one lake) compared to pre-harvest (five lakes). Densities of wigeon were highest the second summer post-harvest, compared to pre-harvest (Simple contrasts, pre-harvest vs. the second summer post-harvest: $F_{1,8}$=5.79, P=0.04), again with birds occurring on five lakes. Densities of blue-winged teal also differed after forest harvesting, compared to before (ANOVA: $F_{2,16}$=8.67, P=0.003), though not in the first summer post-harvest (Simple contrasts, pre-harvest vs. the first summer post-harvest: $F_{1,8}$=0.02, P=0.90). However, densities the second summer after harvesting were significantly higher than pre-harvest densities (Simple contrasts, pre-harvest vs. the second summer post-harvest: $F_{1,8}$=10.04, P=0.01).

3.5 Discussion

One objective of my study was to identify characteristics of lake environments, and landscapes surrounding lakes, that were important in determining the densities of aquatic birds on boreal lakes in Alberta. That only one simple linear regression was statistically significant suggests that a small number of (non-interacting) environmental variables of those measured are not determining species densities. Thus, a complex of environmental factors appears important in determining densities of aquatic birds, as it is for determining community composition (Chapter 2 of this thesis).

3.5.1 Environmental variables independent of disturbance

Overall, geographic location was less important than other environmental variables in accounting for variation in the densities of focal aquatic bird species. This is probably due to the relatively small area that lakes occupied (~7,250 km^2).

Geographic location of lakes is more important in determining occurrences and densities of birds over larger areas (Chapter 2 of this thesis, Brown and Gibson 1983). I expected the geographic location of lakes to affect densities of dabbling aquatic birds more strongly than diving birds, because focal dabbling species are more typical of prairie environments that occur closer to more southerly study lakes (Semenchuk 1992). However, geographic location of lakes entered a greater proportion of the regression models of focal diving species, compared to dabblers, as well as entering models of total diver densities in two years.

Lake area entered regression models of the densities of diving species more frequently than dabbling species, possibly because the former category includes more species that can be territorial, i.e. common loon, red-necked grebe, common goldeneye, and bufflehead (McIntyre 1994, Johnsgard 1987, Gauthier 1993, Eadie et al. 1995). Thus, although all but one of the relationships between the densities of birds, and lake area, were not statistically significant at the univariate level, the more relaxed α levels employed in multiple regressions permitted area to enter multiple regression models. In fact, lake area entered more multiple regression models than any other variable used in analyses, supporting its importance in accounting for bird densities. Calculating densities is the method most widely employed by researchers to remove the effect of lake area on aquatic bird abundances, and in my study, it was successful in reducing area effects on abundances to below conventional statistical significance levels (α=0.05) in almost all cases. However, as shown by the inclusion of lake area in multiple regression models, the effect of this variable on bird abundances was not completely removed.

Dabbling species were expected to be more strongly affected by lake depth than diving species because they are confined to shallower water when foraging. However, maximum depth was included in one of three regression models of total dabbler density and two of three models of total diver density. Also, maximum depth was only included in one of five models of individual focal species of dabbling ducks, for blue-winged teal. Similar to this result, Savard et al. (1994) found densities of blue-winged teal were negatively correlated with mean pond depth, which was strongly correlated with maximum depth. The relationships between focal species of diving waterfowl and maximum depth appeared stronger in my study than reported by Savard et al. (1994), possibly because of the greater range of depths found in my study lakes.

Although the effects of the area of open water surrounding study lakes were expected to be similar for dabbling and diving aquatic birds, this variable was included more frequently in models of the densities of diving species, although the biological significance of this is not clear. Similar to my study, Gauthier (1993) reported that buffleheads were more likely to occur on less hydrologically connected waterbodies, but he did not speculate why. Common goldeneyes have also been found to prefer more isolated lakes, specifically when breeding, and this has been related to food availability (Mallory et al. 1993, Pöysä and Virtanen 1994). In my study, most of the strongest relationships between bird densities and the amount of water in the landscape were negative. For aquatic bird species that move between waterbodies, a landscape with many waterbodies could enhance feeding opportunities, as has been reported for common loons (McIntyre 1994, Alvo et al. 1988, Parker 1988). Thus, if birds are selecting the most desirable habitats, they may occur at lower densities on lakes surrounded by more open water, because they are spreading out to take advantage of the greater availability of preferred habitat.

3.5.2 Environmental variables sensitive to disturbance

Dabbling duck densities were more closely related to the amount of conifer-dominated forest around study lakes, than densities of diving aquatic birds. However, the biological significance of the amount of conifer in the landscape is expected to be similar for both categories of aquatic birds. Kauppinen (1993) suggested that aquatic birds use vegetation surrounding study lakes as a cue of lake characteristics. For example, he proposed that uncultivated, wooded shorelines in his study area indicated more oligotrophic lakes, compared to lakes occurring in a cultivated matrix. In my study area, conifer-dominated landscapes can reflect less productive environments (Strong and Leggat 1992). Thus, vegetation composition is one possible cue by which birds may assess lake characteristics, including productivity, which is expected to be an important determinant of bird densities (Hoyer and Canfield 1994, Suter 1994).

Overall, variables related to water quality entered fewer multiple regression models than expected, based on the strong relationships between lake productivity and bird densities, reported in other studies (Nilsson and Nilsson 1978, Hoyer and Canfield 1994, Suter 1994). This may be partly because landscape variables were included in regression models more frequently than expected, and landscape characteristics may reflect lake productivity (Kauppinen 1993). Similar to the results of Savard et al. (1994), in my study, conductivity featured in more models of dabbling duck densities compared to diving aquatic birds. However, the range of conductivities on their ponds was two orders of magnitude greater than on my study lakes, and included values indicative of saline waterbodies (Mitchell and Prepas 1990). Although the biological significance of conductivity is difficult to explain unless it is extreme, as in saline lakes (Campbell and Prepas 1986), the effects of pH and nutrient levels, which contribute to conductivity, are easier to elucidate (see below).

Multiple regression models including pH captured densities of dabbling and diving birds with about the same frequency. On anthropogenically acidified lakes, pH has been linked to changes in invertebrate and fish populations and communities (Schindler 1990). Thus, aquatic birds and pH may be related via prey base. However, the pHs found in my study lakes did not overlap those found in acidified lakes experiencing biological change, and do not appear sufficiently extreme to cause organisms stress (Schindler 1990, Matthews 1998). Thus, how pH affects aquatic birds on my study lakes is unknown.

I expected relationships between total phosphorus and both dabbling and diving bird densities to be strong, and positive, as this variable represents lake productivity, which may indicate prey biomass for aquatic birds (Smith 1979, Hanson and Leggett 1982). Also, overall bird densities have been found to increase with total phosphorus concentrations in other studies (Nilsson and Nilsson 1978, Hoyer and Canfield 1994, Suter 1994). However, total phosphorus entered fewer regression models than expected, for both dabbling and diving species. This could be because other variables that capture variation in productivity had already entered regression models, e.g. conductivity and Secchi depth.

Although I predicted positive relationships between phosphorus levels, and bird densities overall, I also suspected that foraging by diving species might be affected by differences in water quality brought about by increasing total phosphorus more than dabbling birds, specifically changes in water clarity. Secchi depth entered models for three diving species, compared to two species of dabblers. Secchi depth was also included in two of three models of total dabbler densities, and one of three models of total diver densities. However, relationships between aquatic bird densities and increasing Secchi depth tended to be negative, if non-significant, in simple linear regressions, for almost all years and all species. Thus, phosphorus levels were apparently more important than water clarity in determining bird densities over the ranges examined, and water clarity was not sufficiently low to restrict foraging activities by diving species that can forage visually. However, if continued forest harvesting causes sustained eutrophication of lakes, foraging conditions dictated by water clarity may become more important to diving birds foraging visually. If harvesting is not sustained, nutrient influxes may not be detectable by the second growing season after harvesting (Prepas et al. in press). In this case, post-harvest changes in water clarity should not be sustained beyond initial influxes. If post-harvest changes in prey base occur, these should not persist beyond cohorts exposed to initial nutrient influxes. Finally, Secchi depth may also appear important in multiple regression models because it is correlated with maximum depth.

I expected relationships between dabbling bird densities and the presence of fish to be weak, as these species are predominantly herbivorous (Ehrlich et al. 1988). In contrast, I expected stronger relationships between divers and fish, because most divers eat fish and/or invertebrates that are also consumed by fish, and it has been suggested that the two taxa compete for invertebrate food (Eadie and Keast 1982, Winfield and Winfield 1994). However, these expectations were the reverse of what my results showed. Competition between fish and birds in my study lakes may be weak, or food supply plentiful, in part accounting for these unexpected results. Also, no species in my study were exclusively piscivorous. Consequently, dietary flexibility may have weakened links between fish occurrence and bird densities. Using biomass of fish in each of the two body size categories may have given stronger regression relationships. However, this information was not available for all lakes, or all years. It is not known whether harvesting affected fish in my study lakes. However, when productivity increases due to anthropogenic eutrophication, populations of omnivorous fishes can increase the first season that nutrient influx is elevated (Kiesling 1999). Populations of carnivorous fishes, feeding on zooplankton and larger invertebrates, and fish, can respond the first growing season after nutrient influxes increase (Mills 1985). Occurrences of increases may also vary between cohorts within species, for example, for fish that have a different diet early versus later in life, e.g. yellow perch (Nelson and Paetz 1992).

3.5.3 Direct effects of disturbance and density changes after forest harvesting

The second major objective of my study was to identify whether forest harvesting affected densities of aquatic birds on boreal lakes. I expected the densities of dabbling species, and aquatic birds most tightly linked with forests (i.e. cavity-nesting species), to respond to harvesting the most rapidly. I predicted that dabbling species would increase in density because of increased food availability resulting from increased primary production by macrophytes. I expected cavity-nesting species would respond to loss of nest sites due to forest removal. The area of cutblocks in the landscape around harvested lakes produced weak simple linear regressions, which showed that common loon and ring-necked duck were most strongly related to harvesting. The amount of harvesting around lakes captured sufficient variation to be included in the multiple regression models of five of six diving species, two of which are cavity-nesters, and one of three dabbling species. Despite this, it is difficult to account for the relationships demonstrated between these birds, and forest harvesting. For example, although common loons have been described as sensitive to disturbance (McIntyre 1994), it is unlikely that birds are disturbed directly by the process of harvesting, as it is conducted when they are not present on lakes. However, environmental change at the landscape level may affect aquatic birds, for example, they may perceive lakes in harvested landscapes as less desirable (Kauppinen 1993).

Similarly, how harvesting affected common goldeneye densities is not clear. It was expected that this cavity-nesting species would be negatively affected by forest harvesting due to a post-harvest decrease in the availability of nest sites (Newton 1994). However, common goldeneye densities were positively related to the amount of forest harvested around lakes. Also, the strong relationships between forest harvesting and red-necked grebe and mallard densities were unexpected. Both species are habitat generalists (Kauppinen 1993, Nummi et al. 1994, Savard et al. 1994), and both occupy lakes in much more open habitats, and more disturbed landscapes, than those examined in this study.

The amount of harvesting accounted for sufficient variation in the densities of bufflehead and scaup, to be included in multiple regression models. These species also occurred at significantly different densities before and after forest harvesting. Buffleheads occurred at reduced densities the first summer after harvesting, and returned to their pre-harvest densities the second post-harvest summer. Scaup occurred at reduced densities both summers post-harvest. Mechanisms mediating these differences in densities are unknown. Buffleheads, which nest in cavities, breed in much more open landscapes than those in my study, including in parkland (Gauthier 1993). Therefore, as long as sufficient nest sites are available, it seems unlikely that breeding is affected by changes to habitat characteristics caused by forest harvesting. Also, harvesting is currently occurring at relatively low levels, and the common goldeneye, which is the other common species of cavity-nesting bird in the study area, was not negatively affected by harvesting. It is possible that buffleheads returning to lakes in newly harvested landscapes are unable to locate nest sites identified the previous summer, causing a temporary decline in bufflehead use of harvested lakes.

New female buffleheads may colonise disturbed sites the second breeding season after harvesting, having located nest sites there the year before (Eadie and Gauthier 1985). However, this is highly speculative, and again, why common goldeneyes are not affected the same way is unknown. Scaup are ground nesters, thus, it is unlikely that forest harvesting affects the availability of their nest sites. However, their responses to anthropogenic disturbances have not been studied, and they do appear sensitive to nest predation (Austin et al. 1998). Nest predation patterns may change post-harvest depending on the responses of predators to harvesting (Kirkland 1977, Snyder and Bissonette 1987, Thompson et al. 1989). Finally, scaup appear to be undergoing a continental decline in North America, for unknown reasons (Austin et al. 1998, Wilkins et al. 2000).

As well as scaup and bufflehead, the densities of ring-necked duck, American wigeon, and blue-winged teal differed significantly before and after forest harvesting. Ring-necked ducks attained higher densities in the first summer post-harvest, compared to pre-harvest. Densities remained elevated the second summer after harvesting, but not significantly so. Ring-necked ducks are considered more generalised in feeding habits, than other species of diving ducks (Hohman and Eberhardt 1998). Thus, they may readily occupy habitats left vacant by other species including those negatively affected by harvesting. Their generalist nature has been linked to range expansion previously (Hohman and Eberhardt 1998). Interspecific interactions may also be important in determining the density of ring-necked ducks, as they are subordinate to other species of waterfowl (Hohman and Eberhardt 1998).

American wigeon densities were lower the first summer post-harvest, compared to pre-harvest, and both American wigeon and blue-winged teal densities were significantly higher the second summer post-harvest, compared to pre-harvest levels. However, changes in densities of these two dabbling species were probably mediated by climate, rather than forest harvesting. In dry years, fewer birds than usual may find suitable habitat on the prairies, due to the shrinkage and loss of waterbodies. These birds may therefore fly over the prairies, on to other regions, including the boreal forest (Johnson and Grier 1988). As mentioned previously, in spring of 1996, the pre-harvest year of my study, precipitation was 17% higher than average on the Canadian prairies. In 1997, this value was 6% higher. In 1998, spring precipitation on the prairies was 2% below the long-term average (Environment Canada unpubl.). Thus, higher densities of American wigeon and blue-winged teal the second summer after harvesting may represent their drought-induced displacement from prairie habitats.

Because so few undisturbed lakes were sampled in pre- and post-harvest years of my study, these were not included in statistical analyses. However, changes in densities on the three undisturbed TROLS lakes sampled yearly during my study did not parallel significant changes detected on disturbed lakes. Both the lack of availability of accessible undisturbed lakes in my study area, and field schedules in 1996, precluded the inclusion of more undisturbed lakes in my study. However, I recommend that future studies encompass more undisturbed lakes to better indicate interannual variability in bird densities that is unrelated to harvesting disturbance.

3.5.4 Conclusions

Increases in total phosphorus concentrations were significant on TROLS study lakes in 1997, the first growing season after forest harvesting, compared to pre-harvest levels (combined measure from 1995 and 1996, Prepas et al. in press). However, total phosphorus levels were significantly below pre-harvest levels the second growing season after harvesting. Despite post-harvest elevated total phosphorus levels in the euphotic zone, there were no significant increases in chlorophyll a in the water column (Prepas et al. in press). However, changes in primary production by other producers, e.g. macrophytes, and non-planktonic algae were not assessed. Therefore, it is not possible to determine whether changes in primary productivity due to forest harvesting had any effects on the food base utilised by aquatic birds on my study lakes. Quantifying primary production more completely would assist future studies investigating the effects of harvesting disturbance (and other disturbances) on lake biota.

Insight into the sensitivity of aquatic birds to environmental conditions and disturbances may also be garnered from studies in other areas. However, results of other studies should be extrapolated to the western boreal forest with care, as patterns in other areas do not always apply to this region (e.g. common loon habitat characterised by McIntyre and Barr 1997, compared to Gingras and Paszkowski 1999). Thus, results of correlative studies only indicate where birds were found among sites sampled, not habitat requirements. Further, extrapolating the results of correlative type studies beyond the range of variables recorded within studies may be tenuous. Variables may erroneously appear unimportant, or important, to birds, due to the range of values sampled. Also, although regression analyses imply a cause and effect relationship, significant regression results do not demonstrate this. Thus, mechanisms causing effects may act via other variables, which may be related to or interact with focal variables in regression. For example, climatic variation can simultaneously cause both ionic concentrations of lake water (Webster et al. 1996) and bird abundances (Johnson and Grier 1988) to vary significantly, as mentioned previously. Thus, interannual variation may cause detection of statistically important, but biologically unimportant relationships, via regression analyses. Finally, regressions of the densities of individual species do not examine the interspecific relationships of birds, e.g. territoriality or competition, which may change abundance and distribution patterns regardless of environmental conditions.

The relative conspicuousness of aquatic birds, combined with the demonstrated sensitivity of some species to environmental change, render them potentially useful as indicators of the ecological effects of disturbances. However, due to the apparent sensitivity of American wigeon and blue-winged teal to climate, I would not recommend use of these species, or the dabbling foraging group overall, to indicate disturbance effects in the boreal forests of Alberta. Also, based on my results showing variable relationships with environmental characteristics between species within feeding groups, use of the diving foraging guild as a whole appears inadequate to indicate disturbance effects. Further, although it is a diving species that occurred at significantly different densities before and after forest harvesting, the generalist nature of the ring-necked duck precludes its use as an indicator species. Instead, the results of my study suggest that bufflehead and scaup, which are focal diving birds, may be the most at risk from forest harvesting. However, if buffleheads only respond to low-level harvesting the first year after it occurs, as my results show, they may not represent effective long-term indicators of the effects of disturbance. Thus, scaup appear to be the best potential indicator. Before scaup can be considered an effective indicator, mechanisms causing changes in densities must be identified, and the sensitivity of scaup to forest harvesting must be confirmed over longer time periods than were covered by this study.

Table 3.1. Summary of characteristics of study lakes, determined as described in the text. Decid=Amount of deciduous-dominated forest within 800 m of study lakes, Conif=Amount of conifer-dominated forest within 800 m of study lakes, Cut=Amount of land covered by cutblocks within 800 m of study lakes, Nontree=Amount of non-treed land, including vegetated wetlands, industrial clearings, and roads, within 800 m of study lakes, Open=Amount of land covered by open water within 800 m of study lakes, Area=lake area, ZMax=maximum depth, Cond=conductivity, Secc=Secchi depth, TP=euphotic zone total phosphorus.

	Environmental variable										
	Decid (ha)	Conif (ha)	Cut (ha)	Nontree (ha)	Open (ha)	Area (ha)	Zmax (m)	Cond (μScm^{-1})	pH	Secc (m)	TP (μgL^{-1})
Harvested lakes:											
Pre-harvest-1996 (9 lakes)											
Mean±SE	301±23	123±22	0	45±9	8±2	62±16	6.0±1.1	272±32	7.9±0.2	3.0±0.5	43±6
Range	208-417	31-244	0	14-92	1-21	14-157	1.4-11.2	112-416	7.0-9.4	1.2-6.1	21-58
Post-harvest-1997 (11 lakes)											
Mean±SE	215±22	106±14	76±15	42±7	8±2	53±14	5.4±0.9	274±33	7.7±0.2	1.7±0.2	123±36
Range	109-340	29-175	27-193	14-92	1-21	9-157	1.1-11.1	88-450	6.9-9.4	0.4-2.6	27-355
1998 (10 lakes)											
Mean±SE	207±23	102±15	80±15	45±7	9±2	53±15	4.6±0.8	285±35	7.9±0.3	1.6±0.4	68±24
Range	109-340	29-175	27-193	19-92	1-21	9-157	0.7-8.4	100-448	6.4-9.4	0.6-4.4	13-263
Unharvested lakes (3 lakes all years):											
1996											
Mean±SE	367±31	75±28	5±5	53±11	15±5	81±12	4.5±1.3	210±37	7.8±0.3	2.6±0.5	41±3
Range	329-428	46-130	0-15	35-74	5-20	65-104	2.8-7.1	151-279	7.4-8.4	1.6-3.3	36-47
1997											
Mean±SE	As in 1996						5.0±1.7	175±29	7.9±0.4	2.1±0.1	50±7
Range							3.8-8.3	136-232	7.3-8.8	2.0-2.3	36-59
1998											
Mean±SE	As in 1996						4.9±1.9	176±24	8.0±0.8	1.6±0.7	45±13
Range							2.5-8.6	165-221	6.4-8.9	0.9-3.1	24-67

Table 3.2. Densities (mean abundance per hectare±1 SE, range in parentheses) of selected species of aquatic birds on boreal lakes in Alberta. Data represent 12 lakes in 1996, 14 lakes in 1997, and 13 in 1998. COLO=common loon, RNGR=red-necked grebe, BUFF=bufflehead, COGO=common goldeneye, RNDU=ring-necked duck, SCAUP=greater and lesser scaup, AMWI=American wigeon, BWTE=blue-winged teal, and MALL=mallard.

Year	Species COLO	RNGR	BUFF	COGO	RNDU	SCAUP	AMWI	BWTE	MALL
1996	0.05±0.01 (0.02-0.11)	0.16±0.06 (0-0.73)	0.07±0.02 (0-0.29)	0.11±0.04 (0-0.41)	0.03±0.02 (0-0.22)	0.14±0.06 (0-0.58)	0.03±0.01 (0-0.11)	0.01±0.01 (0-0.09)	0.07±0.02 (0.01-0.22)
1997	0.08±0.02 (0.02-0.23)	0.14±0.04 (0-0.46)	0.05±0.02 (0-0.22)	0.06±0.01 (0-0.14)	0.15±0.05 (0-0.58)	0.07±0.04 (0-0.58)	0.01±0.01 (0-0.15)	0.01±0.01 (0-0.07)	0.04±0.03 (0-0.43)
1998	0.07±0.02 (0-0.23)	0.18±0.06 (0-0.62)	0.07±0.02 (0-0.24)	0.07±0.02 (0-0.31)	0.09±0.03 (0-0.34)	0.07±0.04 (0-0.46)	0.09±0.03 (0-0.41)	0.17±0.05 (0-0.58)	0.11±0.03 (0-0.29)

Table 3.3. Results of multiple linear regression analyses of the densities (abundance per hectare, multiplied by 100) of diving species of aquatic birds on 12-14 boreal lakes in Alberta. ab=abundance, ^{a}=Species that feed predominantly on fish and invertebrates, ^{b}=species that feed predominantly on invertebrates, ^{c}=species that feed predominantly on aquatic plants. Diet information from Ehrlich et al. (1988). α(entry)=0.20, α(elimination)=0.25. (1996=12 lakes, 1997=14 lakes, 1998=13 lakes). Lat=Latitude, Long=Longitude, Conif=Amount of conifer-dominated forest within 800 m of study lakes, Cut=Amount of land covered by cutblocks within 800 m of study lakes, Open=Amount of land covered by open water within 800 m of study lakes. Area=lake area, ZMax=maximum depth, Cond=conductivity, Secc=Secchi depth, TP=euphotic zone total phosphorus, LBF=Presence of large-bodied fish, SBF=Presence of small-bodied fish. L indicates log transformations, L1 identifies log (x+1) transformations.

Year	Model	R^2	P
Total divers (All species occurring on lakes that dive from the water surface, including focal and non-focal species):			
1996	L1(ab/ha*100)=2.05-0.40(LOpen)	0.52	0.08
1997	L1(ab/ha*100)=25.72-0.36(LSecc)-0.76(Long)-0.48(LZmax)-0.40(LBF)+0.48(LArea)	0.83	0.05
1998	L1(ab/ha*100)=18.63-0.83(LBF)-0.16(ZMax)-1.32(Long)+0.62(LArea)+1.65(Lat)-0.66(LTP)+0.22(LConif)+0.30(LOpen)	0.99	0.003
Common loon^{a}:			
1996	L1(ab/ha*100)=0.95-0.59(LArea)+0.41(LConif)	0.78	0.001
1997	L1(ab/ha*100)=1.90-0.72(LArea)+0.16(LConif)-0.12(L1Cut)	0.82	<0.001
1998	L1(ab/ha*100)=-0.84-0.87(LBF)-2.32(LTP)-0.25(ZMax)+1.05(LOpen)+2.27(Lat)-0.95(Long)+0.29(LConif)+0.07(L1Cut) +0.12(LArea)+0.06(pH)+0.04(SBF)	1.0	0.001
Red-necked grebe^{a}:			
1996	L1(ab/ha*100)=0.69-1.22(LOpen)+0.76(LArea)	0.40	0.06
1997	L1(ab/ha*100)=2.24-1.53(LZmax)-0.59(SBF)	0.40	0.06
1998	L1(ab/ha*100)=62.40-1.89(Long)-0.52(L1Cut)-1.58(LOpen)+0.57(LArea)	0.66	0.05
Bufflehead^{b}:			
1996	L1(ab/ha*100)=-2.25+2.20(LTP)-0.60(LOpen)-0.04(L1Cut)	0.74	0.01
1997	L1(ab/ha*100)=39.61-1.25(Long)+2.31(LSecc)-0.96(LZMax)-0.26(LBF)+0.59(LTP)-0.0015(Cond)+0.29(SBF)	0.98	<0.001
1998	L1(ab/ha*100)=0.47-0.50(LBF)+0.13(L1Cut)+0.85(LTP)-0.86(SBF)-0.84(LSecc)-0.31(LArea)-0.30(LOpen)	0.99	<0.001
Common goldeneye^{b}:			
1996	L1(ab/ha*100)=-56.34+3.68(Lat)	0.50	0.01
1997	L1(ab/ha*100)=15.21+1.19(LArea)+1.15(LTP)+0.90(LSecc)-1.21(Lat)	0.89	<0.001
1998	L1(ab/ha*100)=-0.11-0.14(ZMax)+0.62(LArea)+0.24(L1Cut)	0.57	0.05
Ring-necked duck^{c}:			
1996	No variables entered regressions with $P \leq 0.20$.		
1997	L1(ab/ha*100)=18.55+0.54 (SBF)+1.56(LOpen)-0.60(LBF)+0.32(pH)-0.68(Long)	0.78	0.02
1998	L1(ab/ha*100)=-3.24+1.00(LTP)+1.76(LOpen)-0.90(LBF)+0.55(LArea)	0.88	0.001
Scaup^{b}:			
1996	L1(ab/ha*100)=-3.28-0.79(LOpen)+0.005(Cond)+0.35(pH)-0.52(LBF)+0.58(LArea)	0.90	0.006
1997	L1(ab/ha*100)=0.77-1.53(LSecc)	0.38	0.02
1998	L1(ab/ha*100)=0.85+0.004(Cond)-0.16(ZMax)-0.45(L1Cut)-0.85(SBF)+0.33(LConif)-0.27(LBF)	0.90	0.008

Table 3.4. Results of multiple linear regression analyses of the densities (abundance per hectare, multiplied by 100) of dabbling species of aquatic birds on 12-14 boreal lakes in Alberta. ab=abundance, [a]=Species that feed predominantly on fish and invertebrates, [b]=species that feed predominantly on invertebrates, [c]=species that feed predominantly on aquatic plants. Diet information from Ehrlich et al. (1988). α(entry)=0.20, α(elimination)=0.25. (1996=12 lakes, 1997=14 lakes, 1998=13 lakes). Lat=Latitude, Long=Longitude, Conif=Amount of conifer-dominated forest within 800 m of study lakes, Cut=Amount land covered by of cutblocks within 800 m of study lakes, Open=Amount of land covered by open water within 800 m of study lakes. Area=lake area, ZMax=maximum depth, Cond=conductivity, Secc=Secchi depth, TP=euphotic zone total phosphorus, LBF=Presence of large-bodied fish, SBF=Presence of small-bodied fish. L indicates log transformations, L1 identifies log (x+1) transformations.

Year	Model	R^2	P
Total dabblers (All species occurring on lakes that dabble from the water surface, including focal and non-focal species):			
1996	L1(ab/ha*100)=2.27-0.23(Secc)-0.45(SBF)-0.001(Cond)	0.79	0.04
1997	L1(ab/ha*100)=0.14+0.76(LBF)	0.66	0.01
1998	L1(ab/ha*100)=-1.75+0.003(Cond)+0.19(pH)-0.85(SBF)-3.27(LSecc)+0.63(LArea)+0.12(ZMax)	0.98	<0.001
American wigeon:			
1998	L1(ab/ha*100)=-2.38+3.04(LTP)-0.80(LConif)	0.62	0.008
Blue-winged teal:			
1998	L1(ab/ha*100)=0.70-1.57(LSecc)-0.87(SBF)+0.004(Cond)+0.53(LBF)-0.16(ZMax)+0.21(LConif)	0.94	0.002
Mallard:			
1996	L1(ab/ha*100)=1.97-0.15(Secc)-0.38(LConif)	0.57	0.02
1997	L1(ab/ha*100)=-0.42+0.48(LBF)+0.42(LConif)-0.39(SBF)	0.57	0.03
1998	L1(ab/ha*100)=-2.22+0.18(pH)-0.30(LConif)+0.70(SBF)+0.0008(Cond)+0.38(LArea)+0.26(L1Cut)+0.82(LOpen)-0.31(LBF)	0.99	0.002

Table 3.5. Results of simple linear regressions of the amount of forest harvested within 800 m of lakes, and densities of selected species of aquatic birds on boreal lakes in Alberta. Twelve lakes were sampled in 1996, 14 lakes in 1997 and 13 in 1998. Regular type=positive relationship between bird densities and the amount of forest harvested, bold type=negative relationship between the amount of forest harvested and bird densities. COLO=common loon, RNGR=red-necked grebe, BUFF=bufflehead, COGO=common goldeneye, RNDU=ring-necked duck, SCAUP=greater and lesser scaup, AMWI=American wigeon, BWTE=blue-winged teal, and MALL=mallard.

Year	Species								
		COLO	RNGR	BUFF	COGO	RNDU	SCAUP	AMWI	BWTE	MALL
1996	R^2	**0.18**	**<0.001**	**0.15**	<0.001	0.04	**0.13**	Analysis not done		**0.05**
	P	0.17	0.95	0.21	0.96	0.53	0.25			0.50
1997	R^2	**0.04**	**0.003**	**0.06**	<0.001	**0.16**	**0.007**	Analysis not done		0.004
	P	0.51	0.84	0.40	0.99	0.15	0.78			0.82
1998	R^2	**0.006**	**0.14**	0.14	0.02	**0.04**	**0.06**	**0.003**	0.03	**0.02**
	P	0.80	0.21	0.21	0.64	0.53	0.42	0.87	0.58	0.68

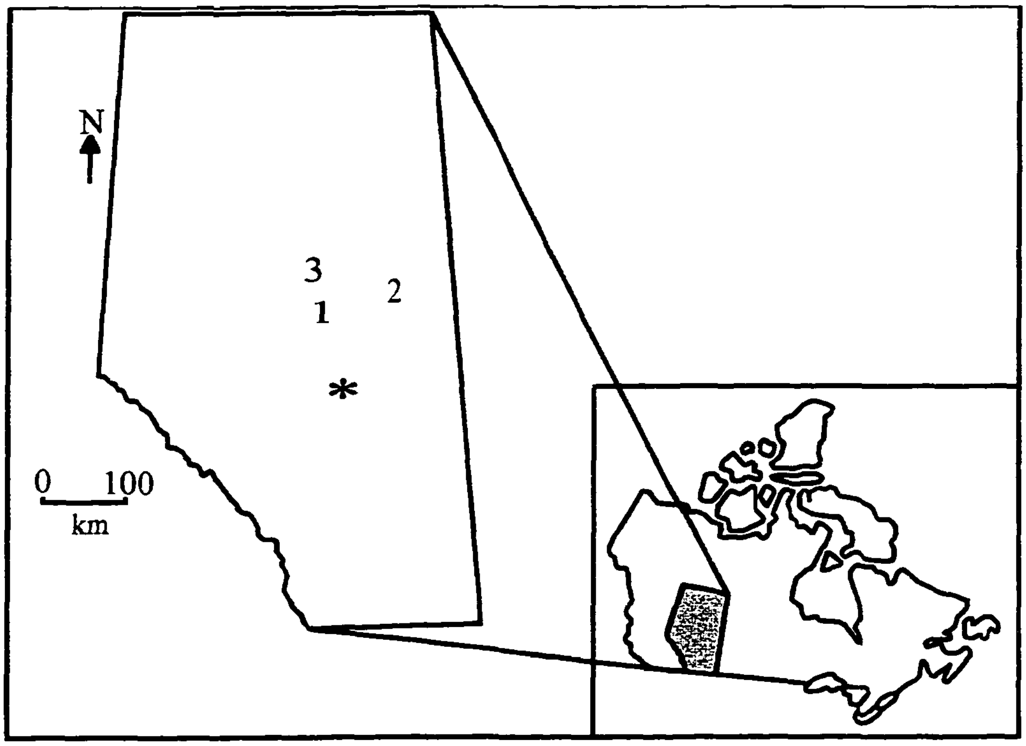

Figure 3.1. Location of study lakes in Alberta, Canada (inset). Numbers represent clusters of lakes. 1=SCL20, SCL100, SCL200, SCL800, 2=LLB20, LLB100, LLB200, LLB800, SHI100, OSP100, 3=SPH20, SPH100, SPH200, SPH800. The asterisk identifies Edmonton.

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Chapter 4. Effects of forest harvesting on nest predation in cavity-nesting waterfowl: Experiments in a forest dominated landscape.

4.1 Introduction

Waterfowl populations in North America are threatened by habitat loss (Owen and Black 1990), however, the effects of habitat destruction and fragmentation on waterfowl nesting in forested landscapes are poorly known. Past studies investigating the effects of habitat fragmentation on waterfowl in North America have focussed on grassland-nesting species (Duebbert and Lokemoen 1976, Pasitchniak-Arts and Messier 1995, Larivière and Messier 1998, Pasitchniak-Arts et al. 1998). These studies have not demonstrated consistent positive or negative effects of habitat fragmentation on waterfowl; the effects of fragmentation, including edge effects, varied with habitat type. How habitat destruction and fragmentation affect waterfowl that nest in a forest-dominated landscape is poorly known. For cavity-nesting waterfowl, extensive loss of forest can severely reduce the availability of nest sites, by reducing both the area and age of forest stands. Forest harvesting also changes the distribution and abundance of terrestrial fauna, including avian nest predators (Kirkland 1977, Snyder and Bissonette 1987, Thompson et al. 1989).

Increased avian nest predation is an oft-cited result of habitat fragmentation and may be particularly evident in smaller habitat patches and at habitat edges (Paton 1994, Andrén 1995). Many nest predation studies demonstrating fragmentation effects, including edge effects, have been conducted in forest patches in agricultural matrices. However, relatively few studies conducted in forest-dominated landscapes show edge effects at either natural (bogs and lakes) or anthropogenic (clearcut) edges (Paton 1994, Andrén 1995, Pöysä et al. 1997). Lack of edge effects in forest-dominated landscapes may be due to relatively low predator species richness and abundance, and the lack of predator attraction to edges (Andrén 1995). However, predator abundance and nest predation may increase with increased deforestation of the landscape (Andrén 1995, Hartley and Hunter 1998).

Nest predation studies conducted in forest-dominated landscapes have focussed primarily on ground- and shrub-nesting birds (Andrén 1995), particularly galliforms and passerines (e.g. Ratti and Reese 1988, Rudnicky and Hunter 1993, Vander Haegen and DeGraaf 1996, Fenske-Crawford and Niemi 1997, Song and Hannon 1999, Tittler and Hannon 2000). Only two studies have documented nest predation in cavity-nesting birds in forest-dominated landscapes (Holt and Martin 1997, Pöysä et al. 1997), and one of these considered waterfowl (Pöysä et al. 1997). This study found no edge effects at natural (lake) edges in a forested landscape but did not investigate the effects of forest harvesting. Thus, the effects of habitat destruction and fragmentation on nest predation of cavity-nesting waterfowl remain unknown.

I used artificial cavity nests to experimentally determine relative levels of nest predation on cavity-nesting waterfowl in harvested areas and unharvested forest around lakes in the boreal mixedwood forest of western Canada, an important breeding and summering area for waterfowl (Bellrose 1980). In the past, fragmentation has proceeded relatively slowly in this region, however due to technological advances rendering boreal hardwoods usable for pulp and paper production (Peterson and Peterson 1992), large areas of the boreal forest of western Canada are now available for harvesting. Potential effects of forest harvesting on waterfowl are unknown. Cavity-nesting waterfowl in the western boreal mixedwood forest include bufflehead (*Bucephala albeola*), common goldeneye (*Bucephala clangula*), common merganser (*Mergus merganser*), and hooded merganser (*Lophodytes cucullatus*). Potential mammalian predators of waterfowl cavity nests in the region include short-tailed weasel (*Mustela erminea*), long-tailed weasel (*Mustela frenata*), mink (*Mustela vison*), marten (*Martes americana*), northern flying squirrel (*Glaucomys sabrinus*), and red squirrel (*Tamiasciurus hudsonicus*). Potential avian nest predators in the area include common raven (*Corvus corax*), and gray jay (*Perisoreus canadensis*), and although they are not true predators, northern flickers (*Colaptes auratus*) may also destroy eggs.

I used artificial waterfowl cavity nests to test the following hypotheses: (i) nest predation levels in cutblocks (clearcuts with 5-20 trees/ha remaining) are lower than predation levels in uncut forest, (ii) nest predation levels in riparian forest buffer strips differ from predation levels in uncut forest, (iii) nest predation levels in uncut forest vary with distance from the riparian forest edge, and (iv) nest predation is higher around lakes in harvested versus unharvested landscapes.

4.2 Methods

4.2.1 Study sites

I conducted research from May-July inclusive, in 1997 and 1998 in the boreal mixedwood forest surrounding 10 lakes in north-central Alberta, Canada. Six of the 10 study lakes were part of the TROLS (Terrestrial and Riparian Organisms, Lakes and

Streams) project, a large-scale multidisciplinary study using experimental forest harvesting protocols at 12 lakes and five streams to determine the effects of different buffer strip widths on aquatic and terrestrial boreal systems. Study lakes were in three clusters around 55°10'N, 111°40'W; 55°8'N, 113°43'W and 55°22'N, 113°40'W, and ranged in size from 8.6-103.6 ha. Forest surrounding study lakes is dominated by trembling aspen (*Populus tremuloides*), balsam poplar (*Populus balsamifera*), white spruce (*Picea glauca*), black spruce (*Picea mariana*) and jack pine (*Pinus banksiana*) (Silins 1994, Strong and Leggat 1992). Extensive commercial forest harvesting began in this region in 1993. Forest harvesting is carried out in two to three passes 10 years apart, creating a mosaic landscape of harvested patches of various ages and unharvested stands. Average cutblock size is approximately 30 ha, and cutblocks contain 5-20 residual trees/ha, as mentioned previously. When forest surrounding lakes is harvested, a forest buffer strip 100 m wide separates riparian vegetation and the adjacent lakeshore from harvesting activity. The purpose of buffer strips is to protect lake water quality. (Although riparian vegetation separated the forest from the lake edge around some study lakes, for clarity, I refer to the forest/riparian vegetation edge as the lakeshore hereafter). Forest blocks around five study lakes were harvested once between September 1995 and April 1997 (harvested lakes). Harvesting removed about 10-40% of forest from the drainage basins of harvested lakes. Forest within 800 m of four the remaining five study lakes was unharvested in both years of my study (unharvested lakes). Forest within 450 m of the fifth lake was harvested in 1994. However, less than 3% of the forest within 800 m of this lake was harvested, and 11% of the drainage basin. Thus, it remained in the unharvested category. The amount of forest harvesting in drainage basins of other unharvested lakes was 0-5%.

4.2.2 Artificial nests

I placed four transects of artificial cavity nests around 9/10 study lakes. Six transects were located around the tenth lake as space allowed. Each transect consisted of four nests approximately 30 m apart. Transects were ≥ 200 m apart. Around harvested lakes, I placed one nest transect in a cutblock at 50 m from the forest/cutblock edge, therefore approximately 150 m from the lakeshore, and one nest transect 50 m from the lakeshore edge of a 100 m wide forest buffer strip. I also located one nest transect in uncut forest 50 m from the lakeshore, and one nest transect in uncut forest 150 m from the lakeshore (Figure 4.1a). At the tenth harvested lake, I also placed one additional transect in both a buffer strip, and a cutblock. At unharvested lakes, I placed two nest transects 50 m from the lakeshore and two nest transects 150 m from the lakeshore (Figure 4.1b). Nest transects were in the same areas in both years of the study, although nests were not always on the same trees both years.

Artificial cavity nests were constructed with dimensions approximating the mean dimensions of natural bufflehead and common goldeneye nest cavities (Bellrose 1980, Gauthier 1993, Eadie et al. 1995). Nests consisted of two 4.6 L plastic buckets wired together to create a cylindrical cavity 18 cm in diameter and 39 cm long with a 10 cm diameter entrance hole. Cavities were covered with coarse light brown burlap fabric to reduce conspicuousness and ensure predators could grip the plastic surface. Also, a 3-5 cm wide strip of burlap was placed inside the nest cavity and attached to the lower edge of the entrance hole to allow predators to escape from cavities.

To facilitate predator identification in 1998, hair-catchers were attached at cavity entrances. Hair-catchers consisted of a flexible plastic strip (0.16 x 3 x 29 cm) fitted around the lip of the entrance hole and secured with double-sided indoor/outdoor carpet tape (Manco brand product 10-1) (Bears 1999). A strip of carpet tape (3 x 32 cm) adhered to the surface of the plastic strip to collect hairs and feathers of potential predators entering artificial nests. There was also a small piece of carpet tape at the top of the burlap tongue inside the nest boxes (Bears 1999). Carpet tape remained strongly adhesive throughout the experiment.

4.2.3 Experimental procedure

I nailed nest cavities to trees approximately 2 m above ground, and placed leaf litter on the bottom of cavities. One small wax-filled chicken egg (Pasitschniak-Arts and Messier 1995) and one plasticine egg of approximately the same size were placed into each cavity. Small chicken eggs approximated the size of real bufflehead and common goldeneye eggs (Gauthier 1993, Eadie et al. 1995). Before placing nests in cavities, each egg was scented with two to three drops of commercially produced duck scent to reduce bias against olfactory predators caused by the absence of adult birds and down nest lining from artificial nests (Willebrand and Marcström 1988, Pasitschniak-Arts and Messier 1995). Latex gloves were worn when handling nest contents to reduce human odour (Pasitschniak-Arts and Messier 1995, Yahner and Mahan 1996).

Nest predation trials were 30 days long, paralleling bufflehead and common goldeneye incubation periods (Gauthier 1993, Eadie et al. 1995). To help maintain olfactory stimuli at nests throughout the experiment, two to three drops of duck scent were added to each remaining egg or the empty nest 13-16 days after starting trials. At this time in 1998, carpet tape with hair adhering to it was removed, before a new piece of tape was added. If there were no hairs on the tape, another layer of tape was placed on top of the first, to maintain consistent adhesiveness among nests (Bears 1999).

At the conclusion of artificial nest trials, I examined eggs for predation and in 1998, hair-catchers were checked for hair samples. I considered a nest depredated if one or both eggs were pecked, bitten, broken or removed. When possible, I identified mammalian nest predators by comparing tooth marks left in eggs to impressions made in plasticine using museum specimens. I could not identify avian predators to species level from egg damage. Hair samples were removed from carpet tape using carbon tetrachloride (CCl_4) (Bears 1999). After removal, hairs were cleaned by soaking them in CCl_4 (Pasitschniak-Arts and Messier 1995) for 15-30 min.. Hair lengths were measured, and diameter, stricture location, colour pattern and shield appearance determined. Confocal laser scanning microscopy was used to examine medulla structure and scanning electron microscopy to examine scale patterns. Hairs were identified to species level by using identification keys based on these characteristics (Mathiak 1938, Williams 1938, Mayer 1952, Adorjan and Kolenosky 1969, Moore et al. 1974, Wallis 1992) and samples taken from museum specimens (Bears 1999).

4.2.4 Statistical analysis

I analysed predation data in S-Plus 4.5 (MathSoft Inc. 1998) using generalised linear models (GLIM) with quasi-likelihood functions. The procedure I used was similar to nested logistic regression. The differences between null and residual deviances provide an indication of the amount of variation in the data that is accounted for by the models. I used quasi-likelihood functions in GLIM because these functions do not assume that errors conform to a particular distribution (McCullagh and Nelder 1989). To compensate for the potential lack of biological and statistical independence between transects around lakes, and between nests within transects, I nested nests on transects within lakes in GLIMs. I also included year (first or second summer of the study) in models, and examined interactions between transect type and year. I rejected null hypotheses at $P \leq 0.01$, rather than $P \leq 0.05$ because I conducted multiple comparisons with components of the data set (Miller 1981). I excluded nests destroyed by black bears (*Ursus americanus*) from analyses (54 in 1997, 56 in 1998, Table 4.1). Black bears depredate nests of cavity-nesting waterfowl (Erskine 1972, Eadie et al. 1995), including those in nest boxes (J.E. Thompson, pers. comm.). However, the artificial nest cavities I used were much more accessible and easier for black bears to destroy than natural cavities, and therefore did not provide a useful relative measure of black bear depredation of real cavity nests.

To investigate the effects of forest harvesting on cavity nest predation, I compared predation at harvested lakes between (i) cutblocks and uncut forest 150 m from the lakeshore, (ii) buffer strips and uncut forest 50 m from the lakeshore, and, to investigate edge effects, (iii) uncut forest 50 m and 150 m from the lakeshore. At unharvested lakes, I compared artificial nest predation in forest at 50 m versus 150 m from the lakeshore, again, to investigate edge effects. I also compared predation in uncut forest between harvested and unharvested lakes (i) at 50 m from the lakeshore, and (ii) at 150 m from the lakeshore. Finally, I compared overall predation at harvested versus unharvested lakes, without separating transect types. Comparing predation in buffer strips with uncut forest 50 m from the lakeshore, and predation in cutblocks with uncut forest 150 m from the lakeshore, controlled for the possibility of different levels of predation at different distances from the lakeshore.

4.3 Results

In 1997, I recorded 21 nest predation events. At harvested lakes, 11/48 nests (22.9%) were depredated and at unharvested lakes, 10/58 nests (17.2%) were depredated (Table 4.1). (As described above, other nests were destroyed by bears). Seven predation events were mammalian; tooth marks in eggs indicated that red squirrels were responsible for these. I identified one avian predation event based on egg damage. In the remaining 13 predation events, predators removed eggs and carried them away from nest sites, thus, I could not identify predators.

In 1998 I recorded 39 nest predation events. At harvested lakes, 13/38 nests (34.2%) were depredated, compared to 26/66 nests (39.4%) at unharvested lakes (Table 4.1). Tooth marks in eggs demonstrated that red squirrels were responsible for 14 predation events. The results of hair analyses suggested red squirrels were responsible for six additional predation events in which eggs were removed from artificial nests. There were two avian predation events in 1998, identified by egg damage. Hair analyses suggested that two of the remaining 17 predation events were due to red squirrel or northern flying squirrel, one was due to short-tailed weasel or long-tailed weasel and one was due to red squirrel or marten. (Collection of multiple hair types at these nests, and difficulty distinguishing some hairs, precluded more precise identification (Bears 1999)). Identities of predators in 13 events were unknown, due to egg removal and lack of hair samples.

The numbers of wax-filled chicken eggs versus plasticine eggs depredated did not differ significantly (1997: 15 wax-filled and 15 plasticine eggs taken, 1998: 39 wax-filled and 30 plasticine eggs taken; $G_1 = 0.36$, $P>0.05$). Both eggs were removed from most nests (only plasticine egg removed: 7 nests, only wax-filled egg removed: 16 nests, both eggs removed: 38 nests).

At harvested lakes, in both 1997 and 1998, nest predation was lower in cutblocks than on any other transect type. Only one nest in a cutblock was depredated during my study. This nest was depredated by a red squirrel. Nest predation was significantly lower in cutblocks than in uncut forest 150 m from the lakeshore; year did not significantly affect predation (Table 4.2, Figure 4.2). (Extremely low predation in cutblocks precluded examination of an interaction between year and transect type using GLIMs). Levels of nest predation in riparian buffer strips did not differ significantly from uncut forest 50 m from the lakeshore; again, the effect of year was not significant, and there was no significant interaction between year and transect type, although standard errors were relatively large (Table 4.2, Figure 4.2).

At both harvested and unharvested lakes, predation did not differ significantly in uncut forest at 50 m versus 150 m from the lakeshore, and at harvested lakes, predation levels were not significantly different between years; the deviance values show that the model fitted the data very poorly (Table 4.2, Figure 4.2). However, at unharvested lakes, there was a highly significant year effect (Table 4.2, Figure 4. 2); in 1998 predation increased 13% at transects 50 m from the lakeshore and 32% at transects 150 m from the lakeshore, compared to 1997. At both harvested and unharvested lakes, there was no significant interaction between year and transect type (Table 4.2).

Nest predation in uncut forest around harvested lakes, versus unharvested lakes, did not differ significantly at either 50 m or 150 m from the lakeshore (Table 4.2, Figure 4.2). Also, there were no significant year effects on nest predation at either distance from the lakeshore (Table 4.2, Figure 4.2), and there were no significant year by transect type interactions (Table 4.2). Although not a statistically significant difference, in 1997, nest predation in uncut forest 150 m from the lakeshore was almost 40% higher at harvested lakes than unharvested lakes. In 1998 however, the difference was only 2%, due to increased predation at unharvested lakes.

When results for all nest transects were combined, lake treatment (harvested versus unharvested) did not affect nest predation levels, however year did. Overall, predation was higher in 1998. The effect of year did not differ significantly between lake treatments (Table 4.2).

4.4 Discussion

Almost all nest predators identified in my study were mammalian and almost all mammalian predation events were unambiguously attributed to red squirrels. Although some authors report that birds can be important predators of open nests (Angelstam 1986, Andrén 1992, Hannon and Cotterill 1998), Pöysä et al. (1997) corroborate my findings by suggesting that waterfowl cavity nests are more frequently depredated by mammals than birds. However, I may have underestimated the importance of avian predation if avian predators were removing eggs from artificial cavity nests (Haskell 1995). Previous studies have identified marten, mink and red squirrels as predators of cavity nests in North America and northern flickers may also destroy eggs of cavity-nesting birds (Eadie et al. 1995). In Sweden and Finland, the pine marten (*Martes martes*) is a major nest predator (Eriksson 1979, Fredga and Dow 1984, Pöysä et al. 1997).

The number of plasticine and wax-filled chicken eggs attacked by predators did not differ significantly in my experiment, and in most nests, both eggs were depredated, removing potential analytical problems associated with differential depredation of plasticine and real eggs in nest predation experiments (Bayne et al. 1997).

In my experiment, artificial nest cavities were depredated significantly less in cutblocks than in comparable unharvested forest. Similarly, Ratti and Reese (1988) and Rudnicky and Hunter (1993) found predation of artificial ground and shrub nests was lower in clearcuts in a forest-dominated landscape. Red squirrels and marten, both potential nest predators, tend to avoid clearcuts for at least six years after harvesting (Kirkland 1977, Snyder and Bissonette 1987, Thompson et al. 1989, Whitfield and Hall 1997). As most identified mammalian nest predators in my study were red squirrels, lack of predation in cutblocks concurs with squirrel avoidance of harvested areas. Short-tailed weasel and long-tailed weasel do not exhibit clear responses to clearcutting, although data are sparse (Simms 1979, Thompson et al. 1989, Hansson 1994). Although there are few records of cavity-nesting waterfowl nesting in clearcuts (R.G. Anderson and S.Woodley pers. comm.), if birds are able to nest in residual trees in cutblocks, they may experience lower nest predation and potentially higher nest success for up to six years after forest harvesting.

Artificial cavity nest predation levels in riparian forest buffer strips did not differ significantly from unharvested riparian forest in my study. Red squirrel abundance in riparian forest buffer strips is not known to differ from unharvested forest, however, data are sparse (Whitfield and Hall 1997). Contrasting my results, Vander Haegen and DeGraaf (1996) found higher predation of open cup nests in 20-80 m wide riparian buffer strips than in intact riparian sub-boreal Acadian forest. They identified red squirrels and blue jays (*Cyanocitta cristata*) as important nest predators. They did not determine red squirrel abundance in buffer strips and intact riparian forest, but blue jays were more abundant in buffer strips than intact forest (Meiklejohn 1994, cited in Vander Haegen and DeGraaf 1996). In contrast, avian predators did not depredate nests in buffer strips in my study unless they were completely removing eggs from nests and thus could not be identified. Vander Haegen and DeGraaf (1996) suggested predation in buffer strips may be higher than in intact forest due to mammals using buffers as corridors to travel between larger habitat patches. The results of my study, and Whitfield and Hall (1997), do not support this conclusion.

Paton (1994), drawing heavily on studies conducted in habitats abutting farms and fields, concluded that nest predation was most likely to increase within 50 m of habitat edges. However, studies of forest-clearcut edges in forest-dominated landscapes have failed to find edge effects (Andrén 1995, Cotterill and Hannon 1999, Song and Hannon 1999). Similarly, predation on real and artificial waterfowl cavity nests in forests is not known to increase with increasing proximity of nests to lakeshores (Pöysä et al. 1997). My study concurs with these conclusions. Nest transects in buffer strips were 50 m from both the lakeshore and cutblock edge, and predation levels in buffer strips did not differ from intact riparian forest. Predation on artificial cavity nests also did not differ in intact forest at 50 m versus 150 m from the lakeshore, around either harvested or unharvested lakes. Mean nest predation levels found in artificial nests in my study are slightly lower than levels recorded by Pöysä et al. (1997). Pöysä et al. (1997) found mean artificial cavity nest predation was 40% over three years at three study areas, compared to 30% over two years for 10 lakes in my study. Mean nest predation levels in uncut forest patches in my study were close to ranges found in real common goldeneye nests in nest boxes near lake shorelines in Sweden and Finland. Predation of cavity nests in these locales can range from 10-88% (Eriksson 1979, Fredga and Dow 1984, Pöysä et al. 1997).

At relatively small spatial scales, increased nest predation, including negative edge effects, has not been linked to clearcutting (Andrén 1995, Tittler and Hannon 2000). However, depredation of artificial ground nests can increase with increasing amounts of clearcutting at the landscape level (Hartley and Hunter 1998). At the lake level, my results for artificial cavity nests showed that predation levels did not differ around harvested and unharvested lakes. This may be due to the currently low level of forest harvesting in the landscape around my study sites.

The effect of year was significant in my study in analyses comparing nest predation at 50 m versus 150 m from the lakeshore at unharvested lakes, reflecting the very low nest predation levels at 150 m from the lakeshore around unharvested lakes in 1997. Predation levels in buffer strips also differed greatly between years, however, the low number of nest transects and high variability in predation prevented this difference being statistically significant. These patterns contributed to a significant year effect when I compared total predation at harvested versus unharvested lakes. Changes in nest predation between years of my study may be due to changes in the abundance, distribution, and movement patterns of nest predators. For example, red squirrel abundance can more than double in response to changes in food supply and weather conditions (Kemp and Keith 1970, Rusch and Reeder 1978, Gurnell 1983). Although I have no data on squirrel abundances or food availability, weather conditions did differ between years of my study. Winter temperatures preceding the summer of 1997 tended to be colder than in the winter preceding summer of 1998. Also, precipitation was higher in winter of 1996-1997, through summer 1997, compared to winter of 1997-1998 through summer 1998 (Environment Canada unpubl.). The milder temperatures in winter of 1997-1998 may have facilitated red squirrel survival over winter, and therefore contributed to the increased levels of nest predation recorded in my study in 1998.

My results show that 1-30 months after low level forest harvesting, depredation of waterfowl artificial cavity nests did not increase, and predation was not higher at 50 m compared to 150 m from the forest edge adjacent to lakeshores. However, predation levels may change with increasing deforestation in the landscape, and increasing time since forest harvesting, especially if habitat changes induced by forest harvesting affect red squirrel abundance and distribution. The loss of nest cavities may negatively affect waterfowl more strongly than changes in nest predation due to harvesting, particularly at higher levels of forest harvesting. Also, when harvesting is extensive in the landscape, older trees, which are more likely to harbour nest cavities, may become concentrated into buffer strips adjacent to lakes. This may increase the risk of nest predation for cavity-nesting waterfowl by creating highly rewarding foraging patches for nest predators. Studies of real waterfowl cavity nests are required to determine the importance of these processes in the boreal forest of western North America. Determining the effects of habitat loss due to forest harvesting on cavity-nesting waterfowl, before large scale habitat loss occurs, increases the likelihood that pre-harvest waterfowl populations and assemblages will be retained in post-harvest landscapes.

Note: A version of this chapter has been accepted for publication in The Auk.

Table 4.1. Predators identified at artificial nests located in riparian forest buffer strips (BS) and cutblocks (CB) adjacent to harvested lakes, and in uncut forest 50 m and 150 m from the forest edge adjacent to harvested and unharvested lakes (H 50, H 150, and U 50, U 150, respectively). Nests destroyed by black bears were not included in statistical analyses (see text), but numbers of nests destroyed are presented here.

Year	Predator	BS	CB	H 50	H 150	U 50	U 150
1997	Red Squirrel	1	1		1	3	1
	Avian predator			1			
	Unidentified			3	4	4	2
	Black bear	12	10	11	7	15	7
1998	Red Squirrel	3		3	1	5	8
	Red Squirrel or Northern Flying Squirrel					1	1
	Red Squirrel or Marten						1
	Short-tailed or Long-tailed Weasel	1					
	Avian predator					1	1
	Unidentified	2			3	5	3
	Black bear	14	12	14	10	7	7

Table 4.2. Results of generalised linear model analyses of predation at artificial cavity nests. Results significant at P≤0.01 (see text).

	Null deviance	Residual deviance	Variables	SE	df	F	P
Cutblocks vs. uncut forest 150 m from the lakeshore, at harvested lakes:							
	49.59	38.69	Transect type	1.76	1, 46	10.55	0.002
			Year	0.42	1, 47	0.13	0.72
Buffer strips vs. uncut forest 50 m from the lakeshore, at harvested lakes:							
	49.08	33.47	Transect type	2.63	1, 34	1.30	0.26
			Year	2.29	1, 35	4.47	0.04
			Year x Transect type interaction	1.23	1, 32	2.74	0.11
Uncut forest 50 m vs. 150 m from the lakeshore, at harvested lakes:							
	51.73	50.25	Transect type	1.27	1, 35	0.18	0.67
			Year	1.29	1, 36	0.03	0.87
			Year x Transect type interaction	0.77	1, 33	0.05	0.82
Uncut forest 50 m vs. 150 m from the lakeshore, at unharvested lakes:							
	145.67	128.02	Transect type	2.21	1, 121	0.05	0.82
			Year	0.75	1, 122	9.87	0.002
			Year x Transect type interaction	0.49	1, 119	1.70	0.19
Uncut forest 50 m from the lakeshore at harvested vs. unharvested lakes:							
	92.46	86.25	Transect type	1.85	1, 70	1.83	0.18
			Year	1.21	1, 71	1.06	0.31
			Year x Transect type interaction	0.67	1, 68	0.22	0.64
Uncut forest 150 m from the lakeshore at harvested vs. unharvested lakes:							
	107.52	92.03	Transect type	1.75	1, 86	1.83	0.18
			Year	1.00	1, 87	6.08	0.02
			Year x Transect type interaction	0.60	1, 84	2.33	0.13
Harvested lakes vs. unharvested lakes:							
	247.51	230.59	Transect type	1.15	1, 207	0.13	0.72
			Year	0.55	1, 208	9.60	0.002
			Year x transect type interaction	0.35	1, 205	1.36	0.25

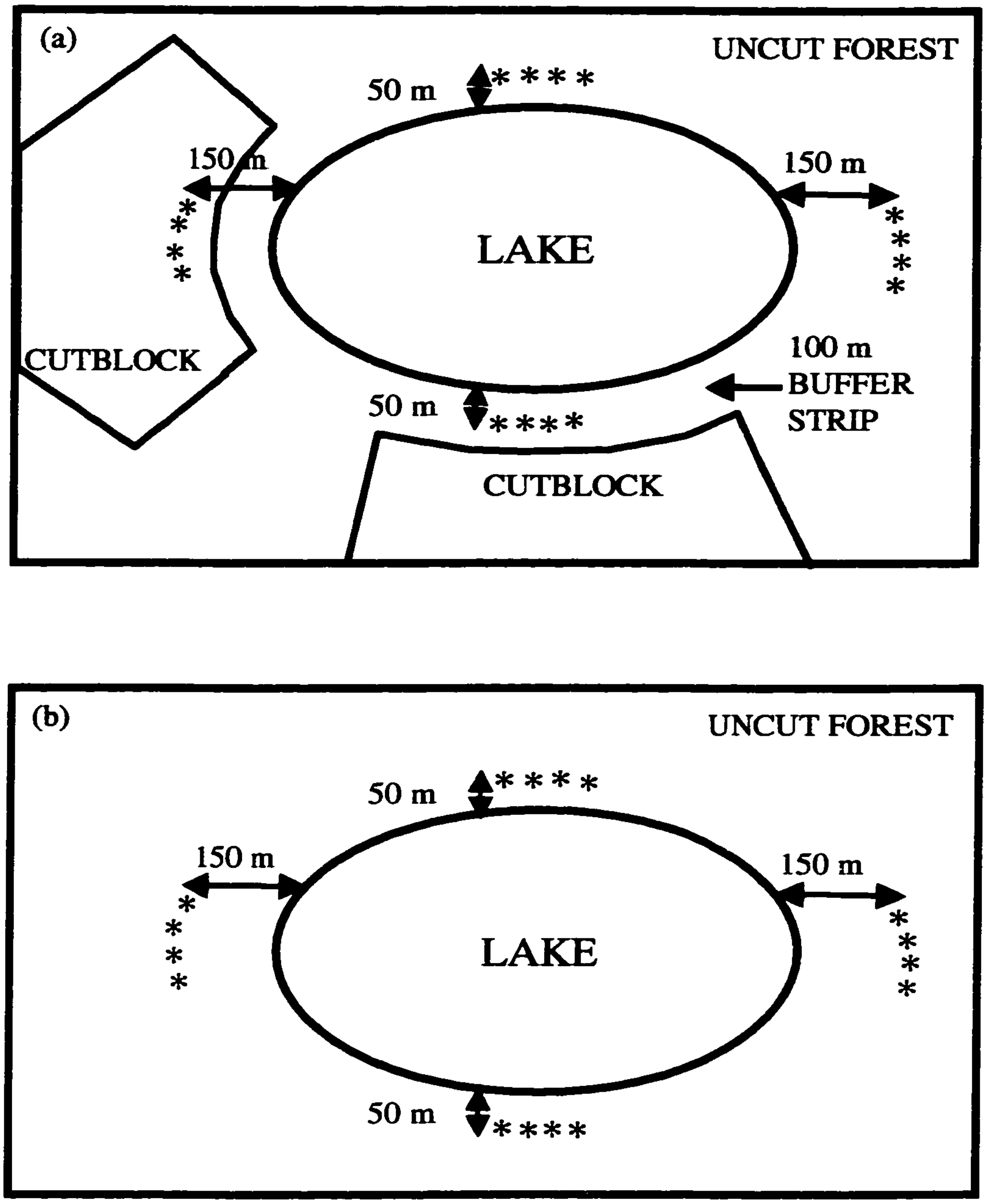

Figure 4.1. Layout of artificial cavity nest transects around (a) harvested and (b) unharvested lakes. (Each asterisk represents one artificial cavity nest).

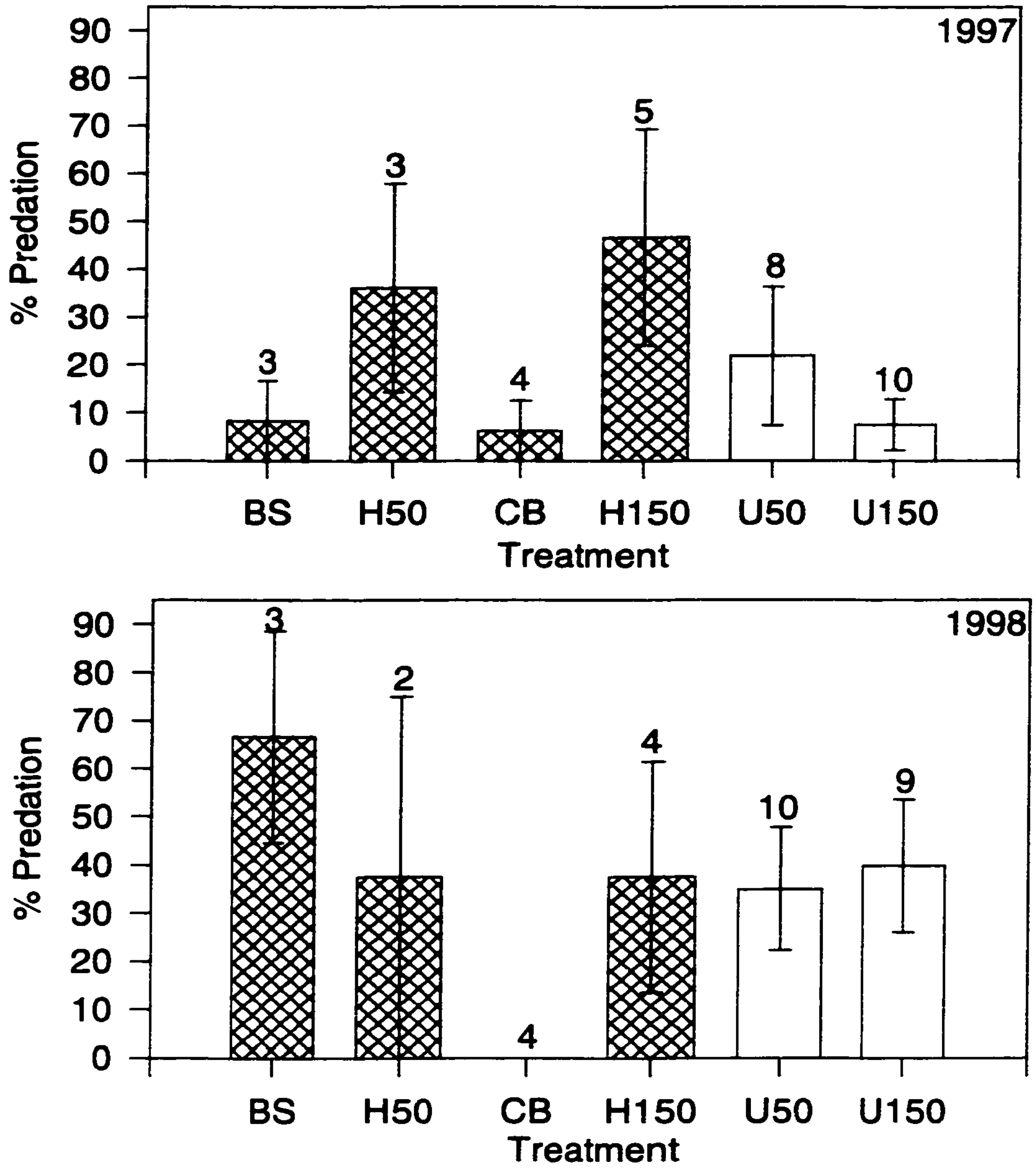

Figure 4.2. Nest predation levels (mean percent per transect±1SE) in 1997 and 1998 in riparian buffer strips abutting cutblocks (BS), 50 m from the lakeside forest edge at harvested lakes (H50), cutblocks (CB), 150 m from the lakeside forest edge at harvested lakes (H150), and 50 m and 150 m from the lakeside forest edge at unharvested lakes (U50 and U150 respectively). Numbers above bars are number of transects included. Hatched bars=transects at harvested lakes, open bars=transects at unharvested lakes.

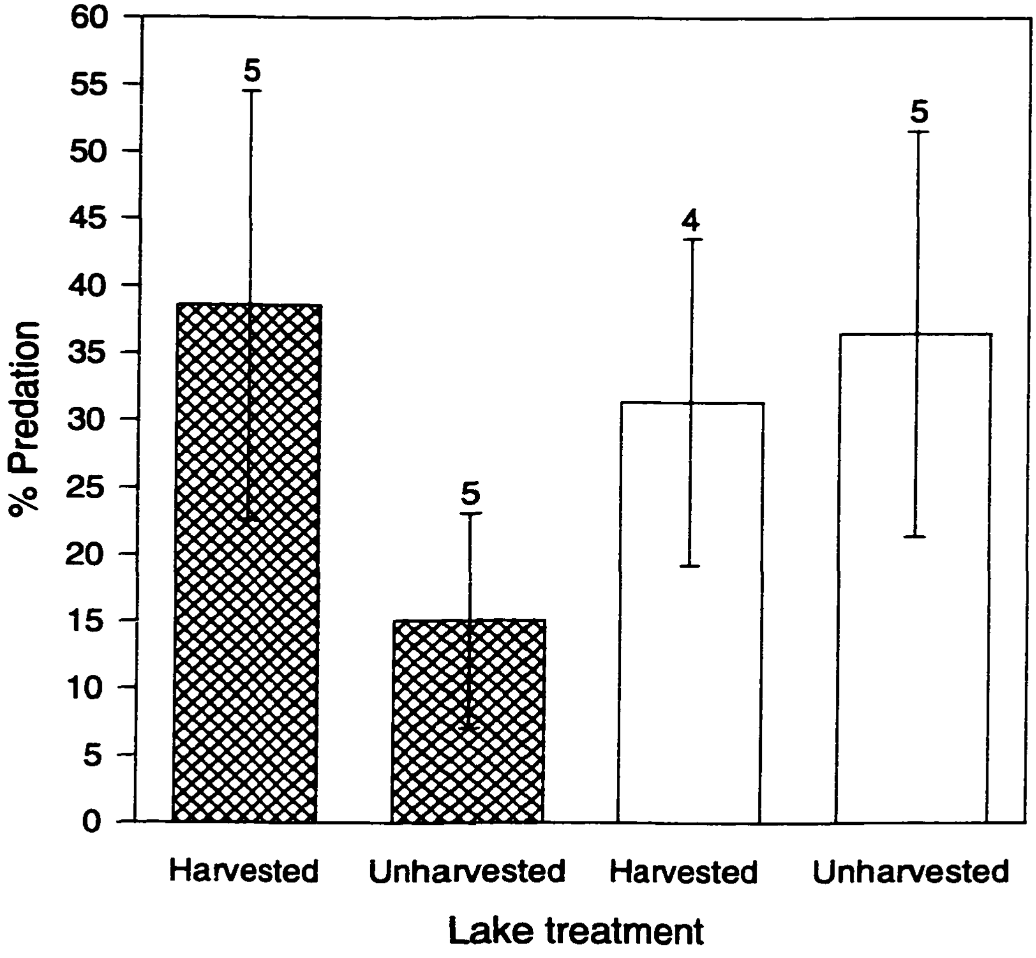

Figure 4.3. Nest predation levels (mean of percent predation per lake, for each lake type±1SE) in 1997 (hatched bars) and 1998 (open bars) at harvested and unharvested lakes. (Predation at all transects combined for each lake). Numbers above bars are number of lakes included. (In 1998, all nests at one harvested lake were destroyed by bears, therefore four lakes were included in analyses).

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Chapter 5. Effects of low-level forest harvesting around boreal Alberta lakes on bufflehead and common loon foraging behaviour.

5.1 Introduction

The most important determinant of the distribution and abundance of organisms is the availability of appropriate habitat. Habitat characteristics affecting aquatic bird distribution and abundance include lake nutrient status, pH, lake morphometry, and the nature of vegetation surrounding lakes (Blancher et al. 1992, Kauppinen 1993, Hanson and Butler 1994, Newton 1994, Paszkowski and Tonn 2000). Disturbance changes habitat characteristics, and can directly and indirectly affect organisms resident in disturbed and adjacent areas. Because aquatic birds are sensitive to the environmental characteristics of their habitats, they have been identified as valuable indicators of habitat changes, including those brought about by anthropogenic disturbances. For example, reproduction of aquatic birds can be negatively affected by acidification, through changes in abundance and nutritional value of aquatic prey, and changes in prey community composition (Rattner et al. 1987, McAuley and Longcore 1988, Blancher et al. 1992).

When disturbance affects the prey base of aquatic birds, they may be able to compensate for changes in prey availability by altering their feeding strategies, in terms of foraging behaviour, the type of prey captured, or both. Behavioural plasticity can allow birds to maintain normal activities, including reproduction (Uttley et al. 1994), despite changes in prey base. Aquatic bird foraging behaviour is known to change in response to prey type, prey availability, and prey density (Parker 1988, Wanless and Harris 1992, Uttley et al. 1994). Thus, it follows that bird foraging behaviour will differ between habitats offering different prey bases.

Forest harvesting can disturb aquatic as well as terrestrial habitats. Effects on aquatic habitats may include increased nutrient influx (Campbell and Doeg 1989, Prepas et al. in press), which may increase primary production by phytoplankton and macrophytes. Water clarity may decrease with increased phytoplankton abundance, reducing detectability of invertebrate and fish prey for aquatic birds foraging visually (Eriksson 1984, Eriksson 1985), rendering prey less available to them. Reduced availability of prey can reduce prey intake, and consequently reproductive activity (Anderson et al. 1982, Hamer et al. 1993, Bukacinska et al. 1996), possibly negatively affecting aquatic bird populations in both the short and long term. However, increased primary production may lead to increases in prey availability by increasing invertebrate and fish abundance and biomass, as well as changing the structure of prey communities (Campbell and Doeg 1989, Growns and Davis 1991, Davies and Nelson 1994). These changes in higher trophic levels of lakes may occur within the same growing season as increased nutrient influx (Kiesling 1999), but appear more frequently reported 1-2 years afterwards (Mills 1985, Jorgenson et al. 1992). Increased prey availability may ameliorate potential negative effects of reduced water clarity on prey detectability, resulting in little or no long-term post-harvest changes in prey intake by aquatic birds, and consequent reproductive activity. From these changes in lakes caused by nutrient influxes resulting from forest harvesting, it follows that both biotic and abiotic characteristics of lakes situated in harvested and unharvested drainage basins could differ.

I investigated the effects of forest harvesting disturbance on foraging behaviour of two aquatic birds, the bufflehead (*Bucephala albeola*) and the common loon (*Gavia immer*), on boreal lakes in north-central Alberta, Canada. The bufflehead is a diving duck that forages predominantly on aquatic invertebrates including odonates, chironomids, and corixids (Gauthier 1993). The common loon forages by diving for fish (McIntyre 1988), as well as aquatic macroinvertebrates, including leeches, amphipods, and larval odonates and coleopterans (Gingras 1997). I selected the bufflehead and common loon as focal species because their modes of foraging are similar, and both species commonly occur on lakes in boreal Alberta. I observed bufflehead and common loon foraging behaviour to test the hypothesis that differences between disturbed and undisturbed lake characteristics resulting from forest harvesting affect the duration of aquatic bird dives. Thus, I expected dive duration to differ on disturbed versus undisturbed lakes, and investigated whether this behaviour could be used to indicate differences between lakes that may be due to forest harvesting disturbance, in the absence of more direct monitoring of lake environments. Dive duration is an appropriate component of foraging behaviour for study because it can be quantified unambiguously, and is affected by abiotic and biotic characteristics of lakes (Eriksson 1985, Gingras 1997). Although changes in higher trophic levels are expected as a consequence of post-harvest nutrient influxes (see references above), I expected water clarity to decrease (due to increased algal growth post-harvest) before changes in higher trophic levels occurred. Therefore, I predicted that bufflehead and common loon dive duration would be greater post-harvest compared to before forest harvesting around lakes, due to decreased water clarity reducing the detectability, and consequently, the availability of prey. For the same reason, I expected dive duration to be greater on disturbed versus undisturbed lakes. In addition, I expected that dives executed by common loons foraging for fish would be longer than when they foraged for invertebrates, due to the greater size and motility of fish, rendering fish more difficult to capture and manipulate (Ydenberg 1986, Ulenaers et al. 1992, Barr 1996, Gingras 1997).

5.2 Methods

5.2.1 Study sites

I documented bufflehead and common loon foraging behaviour from June-August, on two lakes in 1996, and eight lakes in 1997 and 1998, in the boreal mixedwood forest of north-central Alberta, Canada. Study lakes were in three groups, clustered around 55°10’, 111°40’; 55°8’, 113°43’ and 55°22’, 113°40’. Lakes ranged in size from 14 - 104 ha, and were meso- to hypereutrophic (Table 5.1). Six of the eight study lakes were part of the TROLS (Terrestrial and Riparian Organisms, Lakes and Streams) project, a large scale research program using experimental forest harvesting regimes around 12 lakes and five streams to determine the effectiveness of buffer strips in protecting boreal systems from ecological change resulting from forest harvesting. Forest surrounding the study lakes is dominated by trembling aspen (*Populus tremuloides*), balsam poplar (*Populus balsamifera*), white spruce (*Picea glauca*), black spruce (*Picea mariana*) and jack pine (*Pinus banksiana*) (Silins 1994, Strong and Leggat 1992). Forest around study lakes, and in the region in general, is harvested in 2-3 passes 10 years apart, creating a heterogeneous landscape of harvested patches of various ages and unharvested areas. Harvested areas are approximately 30 ha in size, on average, and contain 5-20 residual trees per hectare. Forest blocks were removed from around three study lakes once between October 1996 and April 1997, thus, my study occurred one summer before (1996) and two summers after (1997, 1998) forest harvesting around these lakes. Harvested areas were separated from riparian vegetation around lakes by a 100 m-wide buffer of forest vegetation. Harvesting removed forest from ~10-40% ($\bar{x}$=21.6, SE=8.4) of the drainage basins of the three 100 m-buffered study lakes (harvested lakes hereafter). Four of the remaining five study lakes were surrounded by ≥800 m of intact forest; 3% of the land area between 450-800 m of the fifth lake was harvested in 1994. I refer to these five lakes as 'unharvested lakes' hereafter. Around unharvested lakes, 0-11% ($\bar{x}$=3.1, SE=2.1) of the lake drainage basins were harvested.

5.2.2 Sampling bird behaviour

I documented foraging behaviour, specifically dive duration, of female and post-fledge young-of-the-year buffleheads, and male and female common loons. (I was unable to reliably distinguish fledged young-of-the-year buffleheads from adult female buffleheads based on plumage (Gauthier 1993). Also, I could not reliably distinguish male and female loons, however no consistent intersexual differences in common loon dive duration have been found on other lakes in a prairie parkland-boreal transition region of Alberta (Gingras 1997)). I visited lakes over 1-5 days from June-August, in 1996-1998, and collected data from 1-3 observation bouts of bufflehead, and 1-5 observation bouts of common loons each day. I observed from 1-18 female and young-of-the-year buffleheads, and 1-8 common loons across all lakes during my study. The number of days between data collection episodes at any site ranged from 0-28. I conducted observations between 06:00 and 20:00. I observed each focal bird from a boat or the lake shore, measuring the duration of dives executed with a stopwatch. Observation bouts were a maximum of 2 hr long. I separated observation bouts (foraging bouts hereafter) on the same bird by at least 1 hr. Some focal female buffleheads were accompanied by ducklings during the study, however buffleheads do not feed their young (Gauthier 1993), and females foraged in the same areas on lakes when accompanied by young as they did when foraging alone. Therefore, I included dives performed by female buffleheads accompanied by young in analyses. I excluded common loon dives that resulted in chick provisioning from analyses, to ensure that prey selections by adult common loons were not influenced by the food requirements of dependent chicks. Both buffleheads and common loons dive in non-foraging situations, however, foraging dives tend to occur together in bouts, with bouts separated by other activities such as preening and sleeping (McIntyre 1988, Gauthier 1993, Gingras 1997). In addition, common loons sometimes 'peer' underwater before diving for prey (McIntyre 1988).

5.2.3 Statistical analysis

To test for differences in dive duration for each focal species on harvested versus unharvested lakes, I conducted nested analyses of variance in SPSS 8.0 (SPSS Inc. 1997), nesting lake within harvesting treatment. I used foraging bouts composed of sequences of five or more dives to determine mean dive duration per bout. Mean dive duration of foraging bouts was then used as the dependent variable in analyses. I pooled data into the categories of unharvested (two lakes in 1996, and five lakes in 1997-1998) and harvested (three lakes in 1997-1998) lakes because the data set did not produce sufficient degrees of freedom to analyse years individually. However, I recognise that different foraging bouts occurring on the same lake, in both the same year, and in different years of the study, were not strictly independent (Hurlbert 1984). Although I could not confirm normality of the data set, I conducted parametric ANOVA on the premise that this analysis is robust to departures from normality, and it is more important that sample variances are homogeneous, than that data are from normal distributions (Underwood 1997). I confirmed homogeneity of variances using Levene's test. I followed significant nested ANOVA with post-hoc comparisons (Student-Newman-Keul's (SNK) tests (Day and Quinn 1989, Underwood 1997)), using the Kramer modification for unequal sample sizes (Day and Quinn 1989).

To examine potential mechanisms by which forest harvesting may affect foraging behaviour, I correlated mean bufflehead and common loon dive duration with environmental factors (water clarity represented by Secchi depth, and fish biomass, Table 5.1), using Spearman rank correlations conducted in SPSS 8.0 (SPSS Inc. 1997). I also correlated duration of common loon dives and mean lake depth. Although mean lake depth is unlikely to be significantly affected by forest harvesting, lake depth may affect dive duration (Erskine 1972) and therefore contribute to differences in dive duration between lakes which are unrelated to forest harvesting. I did not correlate mean duration of bufflehead dives with mean lake depth because bufflehead foraging on all lakes occurred in water $\leq$2 m deep, and I did not record finer scale variation in depth of foraging sites. I used yearly data from lakes, collected between 30 May and 31 August, across all years of the study in correlation analyses, despite the lack of complete independence of foraging bouts on the same lake in different years, noted previously. I correlated dive duration each year with environmental data collected on lakes in the same year, except for mean lake depth which was determined once in 1993 (Silins 1994). To compensate for conducting more than one comparison with some elements of the data set, I used Bonferroni α adjustments. Thus, correlations between buffleheads and environmental variables were significant at the 5% level when $P<0.025$. The corresponding value for common loons was $P<0.017$.

Secchi depth was measured at the deepest point of each lake on 1-3 days within 23 days of foraging behaviour data collection, in accordance with the sampling schedules of the TROLS project. I used the mean of these measurements in correlation analyses. (The ranges of lake Secchi depths are displayed in Table 5.1). Mean depth was determined by Silins (1994). Fish biomass was recorded as biomass caught per unit effort, determined using overnight sets of multi-mesh gill nets (mesh size: 6.25 - 75.0 mm, net size: 42 m x 1.5 m). Net locations were determined according to a stratified random design; lake area and depth determined the number and general location of net sets (Tonn and Danylchuk unpubl.). The time gill nets were set and retrieved was recorded, and on retrieval, the weights of fish captured were determined using Acculab LCD V-200 and V-3000 electronic balances. Biomass per unit effort was calculated using the weight of each species of fish caught per net, divided by the length of time each net was set. This catch per unit effort for each net was then averaged over all nets, in each lake, for each species. These average values for each species were then summed over all species, within each lake. All lakes contained fish, except LLB100 (Table 5.1).

Thus, I determined (i) whether mean dive duration of buffleheads and common loons differed between harvested lakes after forest removal, and unharvested lakes, (ii) whether bufflehead dive length was correlated with water clarity, and fish biomass, and (iii) whether common loon dive length was correlated with water clarity, fish biomass, and mean lake depth.

5.3 Results

5.3.1 Dive duration on harvested versus unharvested lakes

The duration of both bufflehead and common loon dives increased slightly on harvested lakes that were sampled before and after forest removal (Figures 5.1, 5.2). However overall, dive duration on unharvested lakes did not differ significantly from harvested lakes for either species (nested ANOVA: bufflehead: $F_{1,3}=0.85$, $P>0.5$; common loon: $F_{1,8}=0.56$, $P>0.5$, Figure 5.1), although statistical power was low ($1-\beta<0.5$ for both study species). Unrelated to disturbance status, mean duration of dives differed significantly between lakes for buffleheads (nested ANOVA: bufflehead: $F_{3,23}=3.21$, $P=0.04$), and differences between lakes approached significance for common loons ($F_{8,66}=1.93$, $P=0.07$). Post-hoc comparisons failed to identify lakes on which bufflehead dive length differed significantly (SNK test comparing LLB100 and SPH100, the lakes with the greatest difference between mean dive duration: $Q_{4,23}=6.60$, $P>0.05$), due to the low statistical power of these tests (Underwood 1997).

Thus, based on the significant ANOVA result, I could conclude only that mean bufflehead dive duration differed significantly between LLB100 and SPH100.

5.3.2 Correlations of dive duration with environmental factors

For buffleheads, dive duration was significantly negatively correlated with Secchi depth (Spearman rank correlation, r=-0.81, P=0.01, n=8, Figure 5.3). Bufflehead dive duration increased with fish biomass, but the relationship was not significant (Spearman rank correlation, r=0.74, P=0.26, n=4). For common loons, correlations between dive duration and Secchi depth, and fish biomass, were not strong or significant (Spearman rank correlations, dive duration correlated with Secchi depth, r=0.22, P=0.36, n=18; dive duration correlated with fish biomass, r=-0.29, P=0.48, n=8). Duration of common loon dives was positively, but non-significantly, correlated with mean lake depth (Spearman rank correlation: r=0.34, P=0.26, n=14).

5.4 Discussion

The duration of bufflehead and common loon dives did not differ significantly on harvested versus unharvested lakes. However, mean duration of bufflehead dives was significantly different between LLB100 and SPH100, possibly because LLB100 is fishless. The duration of bufflehead dives was in fact (non-significantly) shorter on LLB100 than on all lakes containing fish, and dive length increased (non-significantly) with fish biomass overall, which may suggest competition for food is occurring between buffleheads and fish. Resident fish species all consume aquatic invertebrates (Beaudoin 1998, Nelson and Paetz 1992, Turner and Tonn unpubl.), as the bufflehead does (Erskine 1972, Gauthier 1993), and the presence of both large- and small-bodied fish can negatively affect macroinvertebrate abundance (Hanson and Butler 1994, Mallory et al. 1994, Cox et al. 1998). Also, inferential evidence suggests competition can occur between diving ducks and larger-bodied fish (e.g. perch *Perca flavescens*, and roach *Rutilus rutilus*) for invertebrate prey (Eriksson 1979, Eadie and Keast 1982, Winfield and Winfield 1994). Reduced prey abundance due to fish, and competition with fish, may increase the duration of bufflehead dives as birds must remain underwater longer to encounter prey.

Diet composition and prey characteristics can also affect common loon foraging behaviour, and therefore cause dive duration to differ in different foraging bouts within and among lakes (Barr 1996, Gingras 1997). For example, fast moving, larger prey, such as fish or large macroinvertebrates (e.g. larval odonates), may demand longer chases and more manipulation time than smaller, slower prey (e.g. smaller leeches), thereby increasing the length of time birds spend underwater (Ydenberg 1986, Ulenaers et al. 1992, Barr 1996). Supporting this speculation, Gingras (1997) concluded that common loon dives were shorter on average on fishless lakes than lakes occupied by small-bodied fish in Alberta. Also, increases in the duration of common loon dives have been attributed to decreased fish availability in lakes in other geographic areas (Parker 1985, cited in McIntyre 1988). However, in my study, loon dive duration was not shorter on the one fishless lake I examined, compared to lakes containing fish. Also, the duration of common loon dives did not correlate positively, or significantly with fish biomass, instead displaying a weak negative relationship. These results may be due to the invertebrate component of common loon diets. Also, large-bodied fish could affect common loons as prey or competitors, and loons seldom consume fish over 300 g in weight (McIntyre and Barr 1997). Thus, not all the biomass of large-bodied fish recorded may be accessible as prey, and larger fish may represent the strongest competitors for common loon prey. Lake depth was also expected to affect the duration of common loon dives (Erskine 1972). However, correlations of mean depth with common loon dive duration were not significant on my study lakes, and loons tended to forage over most of lake surfaces. This suggests that study lakes did not contain extensive areas that were prohibitively deep for foraging loons, in agreement with McIntyre and Barr (1997).

Although I could not attribute patterns in dive duration to forest harvesting, bufflehead dive duration increased significantly with decreasing water clarity. Decreased water clarity may force buffleheads foraging visually to increase the duration of their dives to maintain prey intake. The relationship of water clarity with the duration of common loon dives was weaker than for bufflehead. I expected decreasing water clarity would also lead to increases in common loon dive duration, due to decreased detectability of prey. However, the duration of common loon dives showed a non-significant increase with increasing water clarity. This may be due to interactions between water clarity and prey base (Eriksson 1985), and diet composition. Buffleheads focus much more exclusively on invertebrate prey than common loons, which appear to feed on both invertebrates and fish frequently (McIntyre 1988, Gauthier 1993, Gingras and Paszkowski 1999). Therefore, relationships between bufflehead dive duration and environmental factors may be simpler and consequently easier to detect than for common loons.

There may have been no detectable effects of forest harvesting on bufflehead and common loon dive duration in my study for a number of reasons. Firstly, post-harvest increases in euphotic zone total phosphorus and Secchi depth were not significant in my study lakes (Table 5.1, Prepas et al. in press). If nutrient influx does not increase post-harvest, primary production will not increase, thus, expected post-harvest changes in prey base will not occur. Secondly, to reduce pseudoreplication, I focussed on the lake as the experimental unit in analyses, e.g. by correlating mean dive duration per lake, per year, with environmental variables. Consequently, statistical power to detect differences between foraging patterns on harvested and unharvested lakes was low. Thirdly, differing macroinvertebrate and fish prey bases in study lakes (Langlois 1999, Tonn and Danylchuk unpubl.) probably increased the complexity of relationships between bird foraging behaviour and lake characteristics, reducing the detectability of harvesting effects on aquatic bird foraging behaviour.

Quantifying foraging behaviour and prey base more completely, increasing the number of study lakes, lengthening studies to encompass more years before and after harvesting, and examining lakes with larger amounts of forest harvesting in their drainage basins, may clarify whether forest harvesting affects aquatic bird foraging patterns on boreal lakes in western Canada. This clarification will help determine whether changes in aquatic bird foraging patterns are indicative of environmental changes in lakes which could lead to post-harvest changes in bird populations and communities.

Table 5.1. Characteristics of study lakes. (TP=euphotic zone total phosphorus concentration[1]; Secchi=mean Secchi depth, and range in brackets[2], determined as described in the text). Mean of yearly means of Z_{max}, TP, and Secchi depth presented for 1997-1998. Values calculated from data collected May 30-August 31 for all lakes, except area and Z_{mean} which were determined once only, prior to my study. Fish presence and biomass determined in 1996 and 1998 as described in the text. BRST=brook stickleback (*Culaea inconstans*), FSDC=finescale dace (*Phoxinus neogaeus*), FTMN=fathead minnow (*Pimephales promelas*), NRPK=northern pike (*Esox lucius*), YLPR=yellow perch (*Perca flavescens*), WHSC=white sucker (*Catostomus commersoni*)).

Lake	Area (ha)	Z_{mean} (m)	Z_{max} (m)	TP (µg/L)	Secchi (m)	Fish present	Fish biomass (g caught per unit effort)
1996 (One year pre-harvest)							
LLB100	14	2.5	5.3	62.0	2.9 (1.3-4.3)	Fishless	0
SCL100	19	3.0	7.5	24.1	1.7 (1.4-2.2)	BRST, FSDC, FTMN	**
1997-1998 (One and two years post-harvest)							
Unharvested lakes:							
LLB800	104	3.0	7.9	42.8	2.2 (0.9-3.6)	NRPK, YLPR*	52.7
SCL800	74	1.4	2.6	66.4	1.6 (0.65-2.8)	BRST, FSDC, FTMN	40.3
SPH800	65	2.3	3.6	60.2	2.0 (0.7-3.7)	BRST, NRPK, WHSC*	5.5
BEA800	42	**	1.8	214.2	1.0 (0.8-1.2)	***	**
CAB800	28	**	1.8	175.2	0.7 (0.7)	BRST	**
Harvested lakes:							
LLB100	14	2.5	5.4	59.8	2.5 (1.4-3.0)	Fishless*	0
SCL100	19	3.0	6.9	22.2	1.6 (1.0-2.0)	BRST, FSDC, FTMN	7.6
SPH100	56	1.3	2.4	162.3	1.1 (0.5-3.0)	BRST*	14.9

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[1] TP determined by persulphate oxidation (Menzel and Corwin (1965), as modified by Prepas and Rigler (1982)). Euphotic zone depth determined using LiCor Li 1000 light meter or Secchi depth (Wetzel 1983).

[2] TP and Secchi depth did not differ between 1996, 1997 and 1998 (repeated measures ANOVA, TP: $F_{2,2}$=9.9, P=0.1; Secchi depth: $F_{2,2}$=3.3, P=0.2).

*=Fish not sampled in 1997, **=data not collected, ***=No fish captured, but fish located with depth sounder.

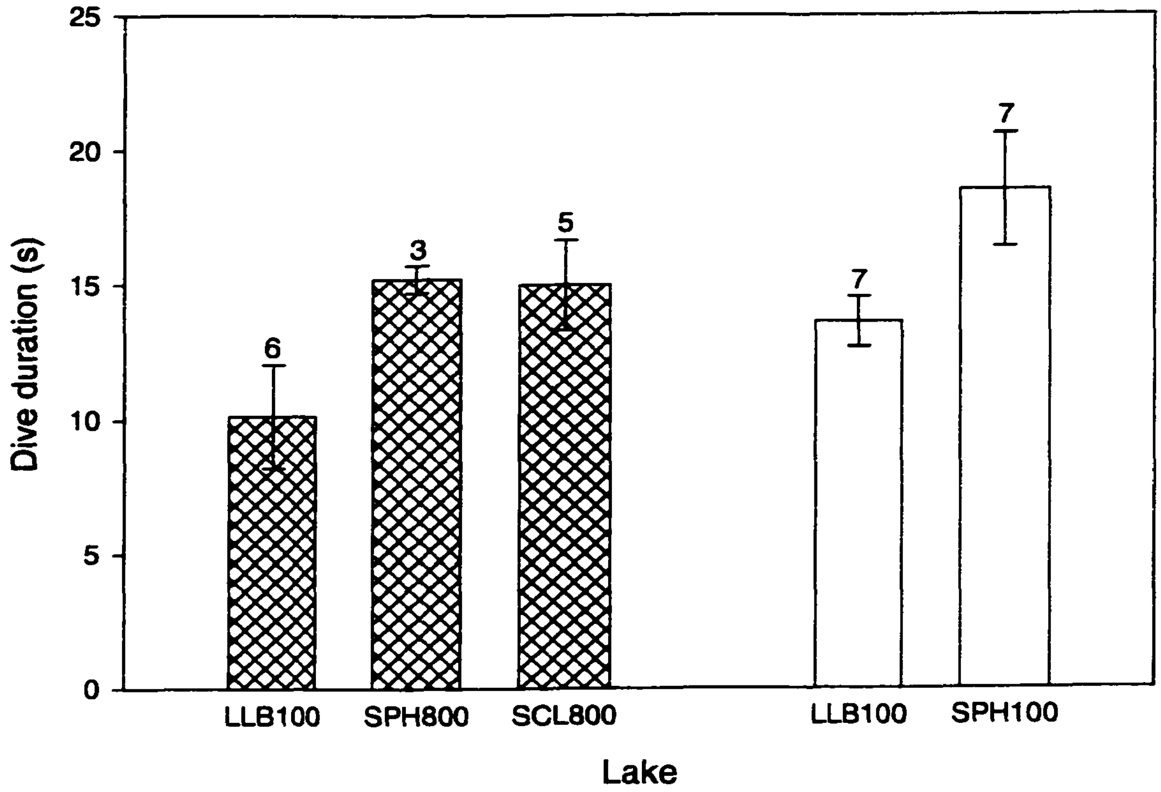

Figure 5.1. Duration of bufflehead dives (mean±1 SE) on unharvested lakes (hatched bars), and harvested lakes (open bars). Numbers above bars are the number of foraging bouts recorded. (LLB100 appears twice due to pre- and post-harvest sampling).

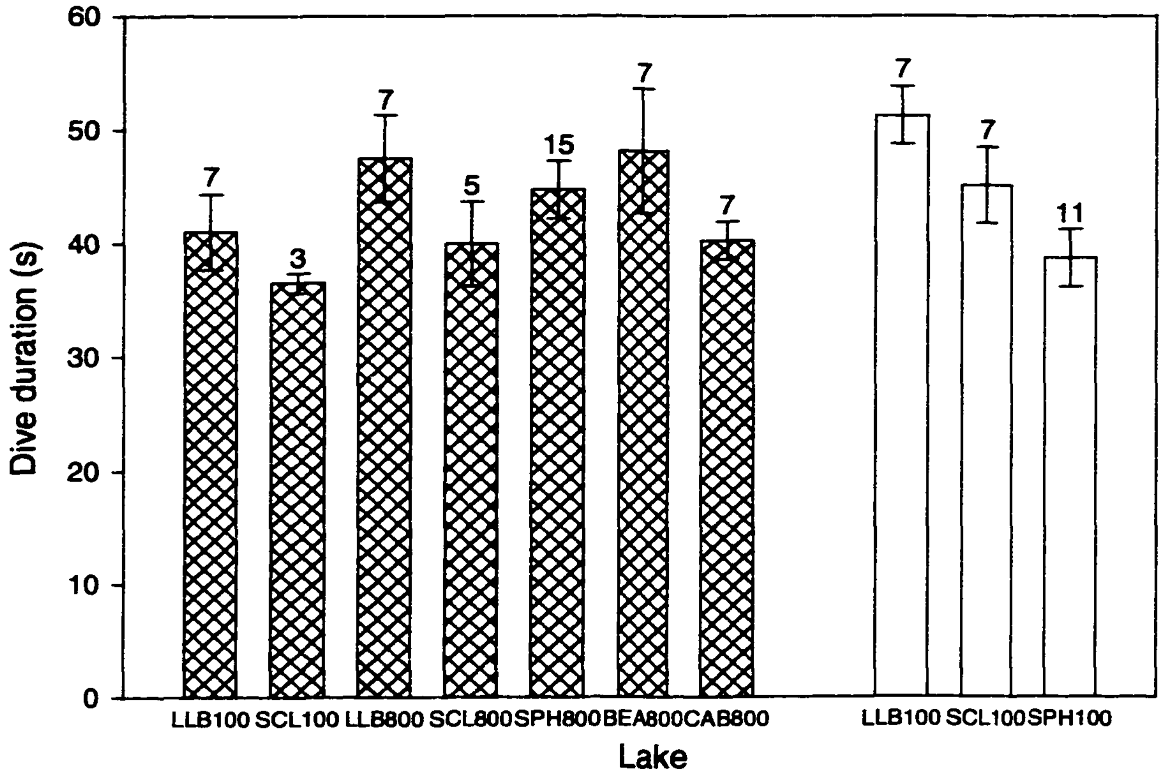

Figure 5.2. Duration of common loon dives (mean±1 SE) on unharvested lakes (hatched bars), and harvested lakes (open bars). Numbers above bars are the number of foraging bouts recorded. (LLB100 and SCL100 appear twice due to pre- and post-harvest sampling).

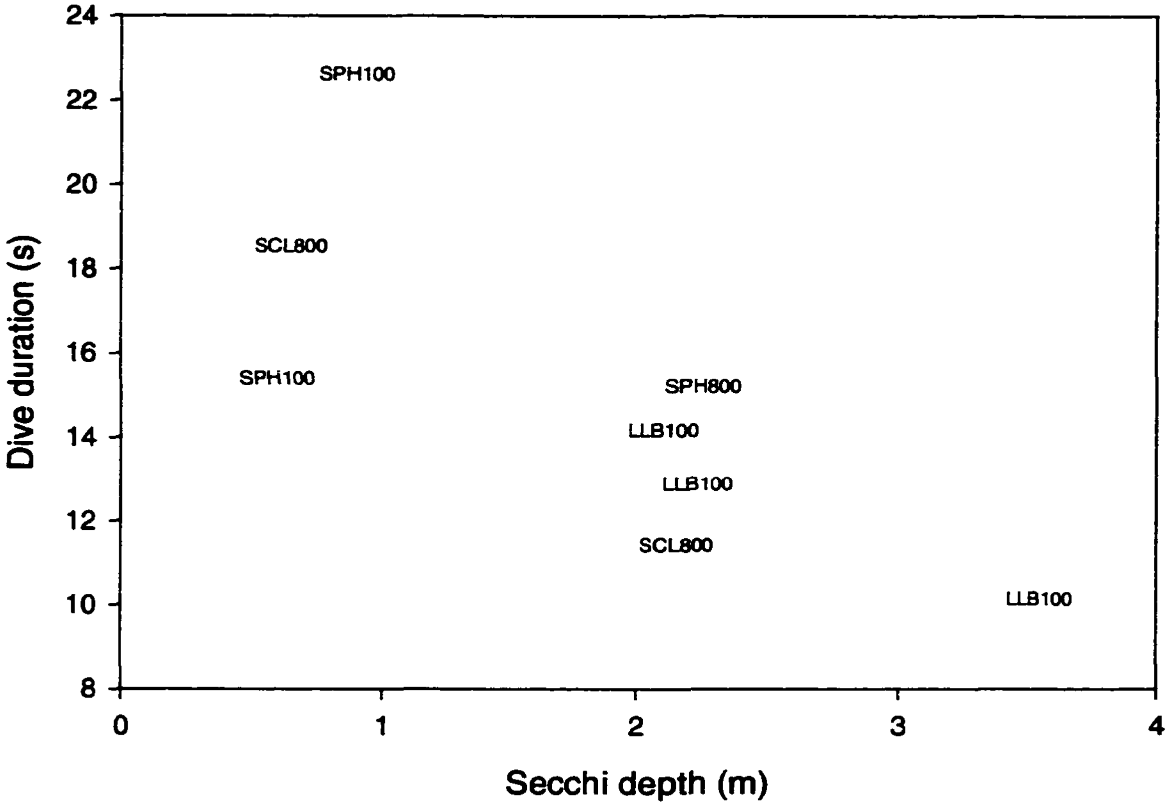

Figure 5.3. Yearly mean duration of bufflehead dives versus mean Secchi depth.

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Chapter 6. Conclusions

6.1 Summary of research findings

My results demonstrate that disturbance resulting from forest harvesting affected the composition of aquatic bird communities. Birds did not form distinct assemblages with respect to harvesting patterns, and the distribution of widespread species did not differ between disturbed and undisturbed lakes. Instead, species that occurred sporadically were more likely to be found on disturbed lakes, causing disturbed lakes to have higher species richness than their undisturbed counterparts. At current levels of forest harvesting, differences in environmental characteristics between harvested and undisturbed lakes appeared not to threaten pre-harvest aquatic bird assemblages. Changes in landscape characteristics caused by harvesting seemed more important, and may modify pre-harvest assemblages by facilitating percolation of birds from more open habitats into formerly relatively intact boreal forest environments. The invasion of fragmented areas, by species that did not penetrate the original intact habitats, occurs widely (Saunders et al. 1991).

Environmental gradients accounting for variation in community composition were complex, rather than being dominated by one or two environmental variables. Variation in the composition of aquatic bird communities was most effectively captured by lake morphometry, and water quality captured only very slightly less variation. The composition of fish communities followed water quality, in terms of explanatory power, and whether lakes were disturbed or undisturbed captured less variation than all these suites of variables. At the species level, lake morphometry entered the most multiple regression models, followed by fish community composition and landscape characteristics. However, water quality entered relatively few multiple regression models accounting for the densities of aquatic birds. This may have been due to variables that entered stepwise models before water quality capturing some of the same variation that was represented by water quality. Variables that entered regression models often differed between years, demonstrating the importance of conducting habitat association studies over multiple years, and interpreting the results of short-term studies cautiously.

The densities of five widespread species of aquatic birds differed before and after forest harvesting, however changes in densities of two of these species (American wigeon *Anas americana* and blue-winged teal *Anas discors*) were probably mediated by interannual variability in climate. Densities of ring-necked duck (*Aythya collaris*) and bufflehead (*Bucephala albeola*) differed significantly before and after harvesting, but consistent differences in densities were not observed in both post-harvest years of my study. However, densities of scaup (*Aythya affinis*, *Aythya marina*) were significantly lower in both post-harvest years, compared to before harvesting. Thus, scaup densities are most likely to be an effective indicator of forest harvesting disturbances, of the densities of nine focal species I examined. However, before scaup, or any species of aquatic bird, is employed to indicate disturbance, it is essential that the mechanisms causing their responses to disturbance are determined. Also, when any aquatic bird species are used as indicators, interannual variability in densities of populations occupying habitats not subject to anthropogenic disturbance should be established. These caveats also apply when aquatic bird communities are considered as potential indicators of disturbance; mechanisms causing changes in community composition, and interannual variability in community composition that is unrelated to disturbance, must be considered.

Forest harvesting did not increase predation of artificial cavity nests. In fact, nest predation was lower in cutblocks than in uncut forest. Predation did not differ significantly in buffer strips of riparian forest, versus intact riparian forest. At a larger spatial scale, nest predation did not differ around lakes with harvesting within 450 m of the shore, compared to lakes without harvesting within this distance of the shore. Also, there were no detectable edge effects on artificial cavity-nest predation. These results suggest that cavity-nest predation is not elevated at current levels of harvesting. In fact, predation may be lower in harvested, compared to unharvested landscapes, due to the near complete absence of predation in cutblocks. Ideally, studies of real nests should be conducted to corroborate my results from artificial nests. Also, monitoring predator movements would yield valuable additional information for assessments of the threat of post-harvest changes in nest predation, for both ground-nesting, and cavity-nesting birds.

Foraging behaviour of common loons (*Gavia immer*) and buffleheads did not differ significantly between lakes in harvested landscapes, versus lakes in undisturbed landscapes. However, the duration of bufflehead dives increased significantly with decreased water clarity. Also, the duration of bufflehead dives differed significantly on two lakes, demonstrating that bufflehead foraging behaviour is flexible, and suggesting that it is responsive to lake conditions. Bufflehead dives were non-significantly longer on lakes with fish compared to the fishless lake in my study, and dive duration was negatively (though non-significantly) related to fish biomass, both of which may suggest that buffleheads are competing with fish for invertebrate food. The duration of common loon dives was not strongly related to water clarity or fish biomass in my study. Despite the apparent flexibility in bufflehead foraging behaviour, changes in dive duration could not be used to indicate disturbance, at least not at the levels of disturbance that occurred around my study lakes. This is probably due to the lack of significant differences in environmental characteristics relevant to foraging patterns, on harvested versus unharvested lakes. Future foraging studies would benefit from increasing the number of study lakes, which would allow decreased pseudoreplication in statistical analysis, and documenting the prey base available to aquatic birds as extensively as possible. Quantifying prey bases would also facilitate interpretation of community- and population-level patterns.

6.2 Aquatic birds as indicators of disturbance

The differences in aquatic bird community composition and densities of focal species between disturbed and undisturbed lakes suggest that aquatic birds may be useful as indicators of harvesting disturbance. In my study, the hypothesised utility of aquatic birds as indicators of disturbances was partly based on their responses to disturbance-induced changes in prey base. However, the mechanism that appears most likely to be driving changes in aquatic bird communities is percolation of invading species through a newly disturbed landscape, rather than the expected post-harvest changes in aquatic bird prey base resulting from elevated post-harvest nutrient influxes. At the species level, mechanisms accounting for post-harvest changes in densities were ambiguous also, except for the two species that were probably affected by climate. The two mechanisms I examined, i.e. cavity-nest predation, and changes in foraging patterns, were less important than expected, based on other studies (Paton 1994, Andrén 1995, Parker 1988, Wanless and Harris 1992, Uttley et al. 1994). Increases in nest predation, and changes in prey base could become apparent as more forest is harvested around lakes. However, as previously suggested, it seems harvesting is more likely to decrease nest predation, at least while harvested areas are sparsely occupied by red squirrels (Kirkland 1977, Thompson et al. 1989). Also, the short duration of post-harvest nutrient influxes (Prepas et al. in press) casts doubt on whether harvesting will cause biologically significant changes in prey bases in lakes, except perhaps at very high levels of protracted disturbance. Thus, as previously mentioned, determining mechanisms that are responsible for changes in aquatic bird community composition and densities due to harvesting must be a priority for future research. Determining the temporal duration of differences in community composition and bird densities is also important, and confirming my results by examining other boreal systems exposed to harvesting disturbance would be valuable.

6.3 Disturbance theory and constraints on responses to disturbance

The results of my community-level research are more compatible with the intermediate disturbance hypothesis of Connell (1978), than Odum's (1985) prediction that diversity decreases in disturbed systems. Further research is necessary to determine the levels of disturbance at which the species richness of aquatic bird communities decreases, thereby concurring with other aspects of Connell's hypothesis. Currently, the intermediate disturbance hypothesis is the paradigm most frequently invoked to explain the results of disturbance studies. However, by no means all research produces results conforming to this hypothesis (Collins 1992, Tanner et al. 1994), or the set of predictions put forward by Odum (1985). Alternative hypotheses predicting disturbance-induced changes in communities include, for example, that species richness should be maintained in systems when the time intervals between disturbances are shorter than the length of time required for competitive exclusion to occur (Huston 1979). However, although various hypotheses have been proposed, there is no strong theoretical framework that can be employed to focus research on disturbance and its effects (Pickett and White 1985). Pickett and White (1985) emphasised that to advance disturbance theory, and allow sound mechanistic predictions of disturbance effects to be made, investigators must more explicitly identify the context of disturbances, including variables determining disturbance impacts, and parameters responding to disturbances. Although desirable, this may not be straightforward; in my study, variables predicted to mediate disturbance impacts on birds were themselves not affected by disturbance as I expected, and consequently mechanistic predictions were not upheld.

Inherent in the contexts within which disturbance occurs, are constraints on possible effects of disturbances. In my study, constraints that may affect whether or not communities change after disturbances, and the trajectories that these changes follow, could include habitat characteristics, as well as which species are already present on lakes. Trajectories of change will also be affected by stochasticity, which is involved in the assembly of any community (Weiher and Keddy 1999). Relevant habitat characteristics constraining disturbance effects on communities include the availability of appropriate resources, e.g. food, to incoming organisms. Effects of species already present in the community can include interspecific territoriality, or other forms of dominance, which could prevent incoming species from becoming established on lakes. The common loon is one species present in communities on my study lakes that aggressively repels both intra- and interspecifics (McIntyre and Barr 1997). The ring-necked duck (*Aythya collaris*) is an example of a species that can be dominated by other species of aquatic birds (Hohman and Eberhardt 1998).

Currently, birds causing higher species richness to be recorded on boreal lakes disturbed by harvesting do not appear to be displacing previously resident species, which could occur, for example, by interspecific dominance described above, or competition. Thus, whether the addition of species to aquatic bird communities as a result of harvesting is viewed as positive, negative, or a non-issue, is subjective. However, in terms of retaining pre-harvest communities in post-harvest boreal landscapes, post-harvest changes in community composition must be viewed as negative. Differences in aquatic bird communities and populations on harvested and undisturbed lakes that result from increased occurrences of birds more typical of prairie-parkland habitats, may have similar effects on lake biota (e.g. prey organisms and other aquatic birds) to the more natural phenomenon of drought-induced displacement of birds from prairie habitats. Determining the impacts of these invading species on other biota, and abiotic aspects of lake systems would be a prudent area for future research.

Spatial location of habitat patches may also affect the trajectories of community assembly (Weiher and Keddy 1999), and thus the likelihood that aquatic bird communities and densities will display disturbance effects. For example, I suspect that harvested and undisturbed southern lakes in my study area showed different community composition because of the relatively close proximity of these lakes to a colonising source of typically 'non-boreal forest' species. Disturbed lakes in more northerly locations are more removed from this source, and consequently less prone to invasion. Therefore, aquatic bird communities and densities on lakes more removed from sources of more typically 'non-boreal forest' colonists may be less likely to display disturbance effects.

6.4 Other disturbances in the boreal forest

In addition to forest harvesting, the boreal ecoregion experiences anthropogenic disturbance from oil and gas exploitation, and recreation (e.g. use of all-terrain vehicles, hunting, and fishing). Although the effect of these activities on aquatic birds have not been investigated, I expect the impact of recreational activities to be lower than the impacts of forest harvesting, because recreation is currently occurring on a fairly small scale in most of the boreal region. However, oil and gas exploration could affect aquatic birds due to the extensive landscape modification, including forest clearance, resulting from these activities. For example, coincident with oil and gas development is the creation and maintenance of roads, well sites, pipelines, compressor stations, and seismic exploration lines.

Natural disturbances that occur in the boreal ecoregion include both destructive events and environmental fluctuations (Pickett and White 1985), e.g. climatic variations, windthrow, and insect outbreaks. Also, winterkill of fish may be an important within-lake disturbance for aquatic birds, due to removal of fish as a prey source, and possible corresponding increases in prey populations (Langlois, Tonn, Prepas, and Danylchuk unpubl.). However, wildfire is the dominant natural disturbance in the boreal region (Rowe and Scotter 1973, Larsen 1980). The effects of fire on aquatic birds, and how these effects compare to forest harvesting, are not well known. Like forest harvesting, fire removes vegetation from the landscape. Fire can also cause nutrient influxes into aquatic habitats (Hauer and Spencer 1998), and changes in macroinvertebrate communities (Minshall et al. 1997, Scrimgeour et al. 2000). Thus, it appears that fire could affect aquatic birds in similar ways to harvesting. However, preliminary data suggest that although the composition of aquatic bird communities did not differ significantly between lakes exposed to fire, lakes exposed to harvesting, and undisturbed lakes, harvested and burnt lakes were more different from each other than burnt and undisturbed lakes. Due to concerns about the ecological damage and non-sustainability of more traditional high-yield, short-rotation logging, forestry practices in North America, including Alberta, are becoming more holistic and ecologically based (Maser 1994). When natural disturbance regimes are a part of harvest-planning considerations, knowing the ecological effects of natural disturbance is critical, as is knowing how the effects of forest fire, and forest harvesting, compare.

6.5 Challenges and recommendations for the future

Aquatic bird research in the western boreal forest of Canada is in its infancy. Only in the last six years have the results of community-level investigations in prairie parkland-boreal transition areas been reported (Paszkowski 1994, Paszkowski and Tonn 2000). Aerial population censuses in some western boreal zones have a longer history (J. B. Pollard, pers. comm.), however prior to my study, work conducted from the ground is almost nonexistent. Because of the fledgling nature of aquatic bird research in the western boreal forest, continuing investigations at both the community and population levels is very important, both to identify species that may be sensitive to habitat changes, and because habitat associations of community members are only beginning to be defined. Once habitat associations and limitations are known, mechanisms responsible for post-harvest changes in communities and populations may be more effectively predicted. One of the biggest challenges of conducting research on aquatic birds in the boreal region may be separating variation that is the result of forest harvesting disturbance, from that caused by other factors. For example, in my study, climate appeared important in determining interannual differences in both aquatic bird community composition, and bird densities. Although the effects of climate may reduce the detectability of disturbance effects on community composition and populations, the potential importance of the boreal forest to aquatic birds displaced from other parts of their range by drought should not be ignored. The refuge the boreal forest represents to these species may allow them to achieve higher reproductive output than would occur otherwise in dry years. Finally, as well as variation from external sources such as climate, variation between lakes in their characteristics such as morphometry and water quality, can be high. Minimising the differences between study lakes in these types of characteristics will help maximise the likelihood that investigators can detect disturbance effects, rather than having changes induced by disturbance be overwhelmed by background variation. Focusing disturbance studies on less productive lakes may enhance the likelihood that post-harvest changes in nutrient influxes will have detectable effects on aquatic biota, if these influxes occur. Similarly, if harvesting is responsible for increasing the species richness of aquatic bird communities, effects of harvesting disturbance may be more detectable on lakes occupied by less speciose communities, because more species can be added to these from source pools, compared to communities of higher initial richness.

My study examined the responses of aquatic birds to forest harvesting for up to four years after forest was removed. Thus, my results are only indicative of the short-term effects of harvesting disturbances. A profitable, and necessary, avenue of further research would be to build on my study by examining aquatic birds on the same study lakes that I used at longer intervals after harvesting. Ten years after the first pass of harvesting that I investigated in this study, the second pass of harvesting will remove more forest from the landscape. Examining the aquatic bird communities and populations at this point, and at the third pass of harvesting, would shed light on the longer term responses of birds to harvesting disturbances, and an increased amount of disturbance in the landscape around lakes. Thus, an individual short-term study, such as mine, has the most value as part of a coordinated longer term research initiative. If landscape changes are affecting the composition of aquatic bird communities and bird densities post-harvest, differences between communities and densities should become more pronounced with further harvesting, although rapid regeneration of deciduous vegetation in harvested areas may mitigate harvesting effects.

The boreal ecoregion of Alberta is currently forest-dominated. Due to the near complete lack of constraints imposed by previous forest exploitation regimes, this landscape represents an excellent opportunity for the development of harvesting practices that are minimally damaging to pre-existing ecosystems. Ongoing research is a vital part of reducing the ecological damage caused by continued forest extraction, as are continually incorporating both the results of research, and lower-impact harvesting technologies, into extraction practices. Also, properties of biological systems, and abiotic characteristics of the region, must be considered in the development of harvesting regimes. The lack of knowledge of ecosystems in the western boreal region means that these systems are more vulnerable to mismanagement than better known natural environments. If this region must be exploited for resources, enlightened and adaptive management practices are required to minimise the effects of resource extraction.

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Appendix 2.1. Patterns of occurrence, and life history characteristics of aquatic birds mentioned in the text. Harv=number of harvested lakes birds found on, Unharv=number of unharvested lakes birds found on, Foraging=foraging method, Diet=dominant food consumed (all aquatic organisms, unless otherwise stated). See Appendix 2.2 for species codes. Sources: Ehrlich et al. (1988), Semenchuk (1992).

Species	Harv	Unharv	Foraging	Diet	Nest site
Species occurring on >50% of lakes					
BUFF	10	8	Dives	Invertebrates	Cavity
COGO	10	6	Dives	Invertebrates	Cavity
COLO	16	14	Dives	Invertebrates, fish	Ground near water
MALL	12	10	Dabbles	Seeds, plants	Ground
RNDUSC	13	12	Dives	Plants, invertebrates	Ground
RNGR	11	9	Dives	Invertebrates, fish	Over water
Species occurring on 25-50% of lakes					
AWPE	6	2	Surface dips	Fish	Ground
BEKI	7	1	High dives	Fish	Burrow
BOFRGU	5	10	Surface dips	Terrestrial invertebrates	Tree, over water
BWTE	6	2	Dabbles	Seeds, plants	Ground
DCCO	7	1	Dives	Fish	Tree, ground
GLBH	4	4	Stalks and strikes	Fish	Tree
SDSA	5	4	Ground gleans	Terrestrial invertebrates	Ground
Species occurring on <25% of lakes					
AMBI	1	0	Stalks and strikes	Any live animal caught	Tree, ground
AMWI	3	1	Dabbles	Plants	Ground
BAEA	4	2	High patrols	Fish	Tree
BLTE	4	0	Hawks	Terrestrial invertebrates	Vegetation over water
CAGO	1	0	Surface dips	Plants, seeds	Ground
CANV	1	1	Dives	Plants	Vegetation over water
CARBHG	2	3	Ground gleans, Low dives	Omnivore	Ground
COFOTE	0	1	High dives	Fish	Ground, over water
COSN	2	0	Probes	Terrestrial invertebrates	Ground
EAGR	0	1	Dives	Invertebrates	Over water
GADW	2	0	Dabbles	Plants	Ground
GWTE	2	0	Dabbles	Plants, seeds	Ground
HOGR	1	1	Dives	Invertebrates	Over water
KILL	1	0	Ground gleans	Terrestrial invertebrates	Ground
MERG	1	1	Dives	Fish	Cavity, ground
NOPI	2	0	Dabbles	Seeds, plants	Ground
OSPR	0	1	High dives	Fish	Tree over/near water
REDH	0	1	Dives	Plants	Over water
RUDU	1	0	Dives	Invertebrates	Ground
SBDO	2	0	Probes	Invertebrates	Ground
SCOTER	1	3	Dives	Invertebrates	Ground
SOSA	3	1	Ground gleans	Terrestrial invertebrates	Tree
WIPH	1	0	Surface dips	Invertebrate	Ground
YELLOW	5	2	Probes	Fish, terrestrial invertebrates	Ground

Appendix 2.2. Species codes used in tables and ordination diagrams.

Species code	Common name	Scientific name
AMBI	American bittern	*Ardea herodias*
AMWI	American wigeon	*Anas americana*
AWPE	American white pelican	*Pelecanus erythrorhynchos*
BAEA	Bald eagle	*Haliaeetus leucocephalus*
BEKI	Belted kingfisher	*Ceryle alcyon*
BLTE	Black tern	*Chlidonias niger*
BOFRGU	Bonaparte's and Franklin's gull	*Larus philadelphia, Larus pipixcan*
BUFF	Bufflehead	*Bucephala albeola*
BWTE	Blue-winged teal	*Anas discors*
CAGO	Canada goose	*Branta canadensis*
CANV	Canvasback	*Aythya valisineria*
CARBHG	California, Ring-billed or Herring gull	*Larus californicus, Larus argentatus, Larus delawarensis*
COFOTE	Common and/or Forster's tern	*Sterna hirundo, Sterna forsteri*
COGO	Common goldeneye	*Bucephala clangula*
COLO	Common loon	*Gavia immer*
COSN	Common snipe	*Gallinago gallinago*
DCCO	Double-crested cormorant	*Phalacrocorax auritus*
EAGR	Eared grebe	*Podiceps nigricollis*
GADW	Gadwall	*Anas strepera*
GBLH	Great blue heron	*Ardea herodias*
GWTE	Green-winged teal	*Anas crecca*
HOGR	Horned grebe	*Podiceps auritus*
KILL	Killdeer	*Charadrius vociferus*
MALL	Mallard	*Anas platyrhynchos*
MERG	Common, Red-breasted and Hooded merganser	*Mergus mergus, Mergus serrator, Lophodytes cucullatus*
NOPI	Northern pintail	*Anas acuta*
OSPR	Osprey	*Pandion haliaetus*
REDH	Redhead	*Aythya americana*
RNDUSC*	Ring-necked duck and Lesser and Greater scaup	*Aythya collaris, Aythya affinis, Aythya marila*
RNGR	Red-necked grebe	*Podiceps grisegena*
RUDU	Ruddy duck	*Oxyura jamaicensis*
SBDO	Short-billed dowitcher	*Limnodromus griseus,*
SCOTER	White-winged and Surf scoter	*Melanitta fusca, Melanitta perspicillata*
SDSA	Spotted sandpiper	*Actitis macularia*
SOSA	Solitary sandpiper	*Tringa solitaria*
WIPH	Wilson's phalarope	*Phalaropus tricolor*
YELLOW	Lesser and Greater yellowlegs	*Tringa flavipes, Tringa melanoleuca*

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* Identification problems on some NCE lakes in 1997 precluded use of separate categories for scaup and ring-necked duck in some, but not all, analyses.

Appendix 2.3. Aquatic birds seen on the 30 study lakes in boreal Alberta.

Common name	Scientific name
American bittern	*Ardea herodias*
American coot	*Fulica americana*
American white pelican	*Pelecanus erythrorhynchos*
American wigeon	*Anas americana*
Bald eagle	*Haliaeetus leucocephalus*
Belted kingfisher	*Ceryle alcyon*
Black-bellied plover	*Pluvialis squatarola*
Black tern	*Chlidonias niger*
Bonaparte's gull	*Larus philadelphia*
Blue-winged teal	*Anas discors*
Bufflehead	*Bucephala albeola*
California, Ring-billed and/ or Herring gull	*Larus californicus, Larus delawarensis, Larus argentatus*
Canada goose	*Branta canadensis*
Canvasback	*Aythya valisineria*
Cinnamon teal	*Anas cyanoptera*
Common goldeneye	*Bucephala clangula*
Common loon	*Gavia immer*
Common merganser	*Mergus merganser*
Common snipe	*Gallinago gallinago*
Common and/or Forster's tern	*Sterna hirundo, Sterna forsteri*
Double-crested cormorant	*Phalacrocorax auritus*
Eared grebe	*Podiceps nigricollis*
Franklin's gull	*Larus pipixcan*
Gadwall	*Anas strepera*
Great blue heron	*Ardea herodias*
Green-winged teal	*Anas crecca*
Hooded merganser	*Lophodytes cucullatus*
Horned grebe	*Podiceps auritus*
Killdeer	*Charadrius vociferus*
Lesser and/or Greater scaup	*Aythya affinis, Aythya marila*
Lesser and/or Greater yellowlegs	*Tringa flavipes, Tringa melanoleuca*
Mallard	*Anas platyrhynchos*
Northern pintail	*Anas acuta*
Northern shoveler	*Anas clypeata*
Osprey	*Pandion haliaetus*
Pectoral sandpiper	*Calidris melanotos*
Pied-billed grebe	*Podilymbus podiceps*
Red-breasted merganser	*Mergus serrator*

Redhead	*Aythya americana*
Red-necked grebe	*Podiceps grisegena*
Ring-necked duck	*Aythya collaris*
Ruddy duck	*Oxyura jamaicensis*
Sanderling	*Calidris alba*
Semipalmated plover	*Charadrius semipalmatus*
Semipalmated sandpiper	*Calidris pusilla*
Short-billed dowitcher	*Limnodromus griseus,*
Solitary sandpiper	*Tringa solitaria*
Sora	*Porzana carolina*
Spotted sandpiper	*Actitis macularia*
Surf scoter	*Melanitta perspicillata*
White-winged scoter	*Melanitta fusca*
Wilson's phalarope	*Phalaropus tricolor*

Appendix 3.1. Scientific names and life history characteristics of aquatic birds mentioned in the text. Diet=dominant food consumed (all aquatic organisms, unless otherwise stated). Sources: Ehrlich et al. (1988), Semenchuk (1992).

Species	Scientific name	Diet	Nest site
Divers:			
Bufflehead	*Bucephala albeola*	Invertebrates	Cavity
Canvasback	*Aythya valisineria*	Plants	Vegetation over water
Common goldeneye	*Bucephala clangula*	Invertebrates	Cavity
Common loon	*Gavia immer*	Invertebrates, fish	Ground near water
Double-crested cormorant	*Phalacrocorax auritus*	Fish	Tree, ground
Eared grebe	*Podiceps nigricollis*	Invertebrates	Over water
Common merganser	*Mergus merganser*	Fish	Cavity
Hooded merganser	*Lophodytes cucullatus*	Fish	Cavity
Red-breasted merganser	*Mergus serrator*	Fish	Ground
Horned grebe	*Podiceps auritus*	Invertebrates	Over water
Lesser and/or Greater scaup	*Aythya affinis*, *Aythya marila*	Invertebrates	Ground
Pied-billed grebe	*Podilymbus podiceps*	Invertebrates	Over water
Red-necked grebe	*Podiceps grisegena*	Invertebrates, fish	Over water
Ring-necked duck	*Aythya collaris*	Plants	Ground
Ruddy duck	*Oxyura jamaicensis*	Invertebrates	Ground
White-winged scoter	*Melanitta fusca*	Invertebrates	Ground
Dabblers:			
American wigeon	*Anas americana*	Plants	Ground
Blue-winged teal	*Anas discors*	Seeds, plants	Ground
Canada goose	*Branta canadensis*	Plants, seeds	Ground
Cinnamon teal	*Anas cyanoptera*	Seeds	Ground
Green-winged teal	*Anas crecca*	Plants, seeds	Ground
Mallard	*Anas platyrhynchos*	Seeds, plants	Ground
Northern pintail	*Anas acuta*	Seeds, plants	Ground
Northern shoveler	*Anas clypeata*	Plants	Ground