Aquatic birds have been identified as valuable indicators of environmental change, including changes brought about by anthropogenic disturbances (e.g., McAuley & Longcore 1988; Blancher et al. 1992). Disturbances can affect abiotic attributes of habitats, such as water chemistry (Carignan et al. 2000) or biotic features, such as the abundance of food organisms (Jorgenson et al. 1992). The foraging behavior of aquatic birds can change in response to prey type, availability, and density (Parker 1988; Wanless & Harris 1992; Uttley et al. 1994). When disturbance affects the prey base of aquatic birds, birds may be able to compensate for changes in prey availability by altering their foraging behavior or the type of prey captured. Thus, changes in bird behavior or diet, as well as changes in bird numbers, can be indicators of water quality, and food web and habitat structure.

Forest harvesting is a disturbance that can affect aquatic as well as terrestrial habitats. One effect that commonly occurs in aquatic habitats is an increase in productivity due to nutrient influx (Rask et al. 1998; Carignan et al. 2000). Nutrient influx can increase primary production (Planas et al. 2000), which in turn may lead to increases in the abundance of invertebrates and fish, common prey of aquatic birds, as well as potentially change the structure of prey communities (e.g., Davies & Nelson 1994). At the same time, water clarity may decrease with increased productivity as phytoplankton becomes more dense, reducing the ability of aquatic birds that forage visually to detect invertebrate and fish prey (Eriksson 1985). Reduced prey intake could negatively affect the reproductive activity of birds (e.g., Hamer et al. 1993; Bukacinska et al. 1996), with the possibly of both short and long term population impacts. It is also possible that increased prey abundance may ameliorate any negative effects of reduced water clarity on prey detectability, resulting in little or no long-term changes in prey intake by aquatic birds following disturbances, and consequent reproductive output. Increases in productivity at higher trophic levels of lakes may occur within the same growing season as
increased nutrient influx (Grant & Tonn 2002), as well as 1–2 years afterwards (Mills 1985; Jorgenson et al. 1992).

We investigated the effects of forest-harvesting disturbance on foraging behavior of two species of visually foraging aquatic birds, the Bufflehead (Bucephala albeola Linnaeus) and the Common Loon (Gavia immer Brünnich), 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 & Paszkowski in press).

We compared the foraging behavior of Bufflehead and Common Loon on lakes with adjacent forest cut-blocks and on unharvested lakes to test the a priori hypothesis that lake characteristics altered by forest harvesting affect the duration of dives of aquatic birds. Dive duration is an appropriate component of foraging behavior to measure because it can be quantified unambiguously, and is affected by abiotic and biotic characteristics of lakes (Eriksson 1985; Gingras & Paszkowski in press). We formulated a series of predictions regarding diving patterns based on the changes to lake systems in response to forestry activities that had been reported by other studies (see Northcote & Hartman 2004 for several relevant reviews). Although changes in productivity of invertebrates and fish populations may be expected as a consequence of post-harvest nutrient influxes (see references above), we expected water clarity to decrease (due to increased algal growth post-harvest) before changes in higher trophic levels occurred. Therefore, we predicted that dive duration for both species would be greater on harvested lakes due to decreased water clarity and detectability of prey. Across all lakes, regardless of treatment, we expected dive duration to be negatively correlated with water clarity.

We also examined the relation between dive duration for the two bird species and fish biomass. Dive duration of birds is likely influenced by a number of attributes specific to each type of prey (e.g., body size of invertebrates, schooling tendencies of fish). Previous work in Alberta found that loons tend to make shorter, more frequent dives when foraging for macroinvertebrates than when foraging for fish (Gingras & Paszkowski in press). Thus we expected that dives by Common Loons foraging on lakes with higher fish biomass would be longer than those on lakes with fewer fish (i.e., where invertebrates would make up a higher proportion of the diet) because the greater size and motility of fish makes them more difficult to capture and manipulate (Ydenberg 1986; Barr 1996). Because fish may compete with Bufflehead for invertebrates and thus reduce prey densities, we expected dive duration to also be positively correlated with fish biomass for this species. This type of competitive interaction with fish has been well documented for the conspecific Common Goldeneye (B. clangula (L.), Eadie & Keast 1982).

**METHODS**

1) Study sites

We documented Bufflehead and Common Loon foraging behavior 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′N, 111°40′W; 55°8′N, 113°43′W and 55°22′N, 113°40′W. Lakes ranged in size from 14–104 ha, and were meso- to hypereutrophic (Table 1). Six of the eight study lakes were part of the Terrestrial and Riparian Organisms, Lakes and Streams (TROLS) project, a large scale research program that used experimental forest harvesting regimes around 12 lakes to assess the effectiveness of buffer strips (Prepas et al. 2001; Hannon et al. 2002).

Forest surrounding the study lakes is dominated by trembling aspen (Populus tremuloides Michx), balsam poplar (Populus balsamifera L.), white spruce (Picea glauca (Moench) Voss), black spruce (Picea mariana (Miller)) and jack pine (Pinus banksiana Lamb). Forest harvesting in the region typically occurs in 2–3 passes, each 10 years apart, creating a heterogeneous landscape of harvested patches of various ages scattered amongst unharvested areas. Harvested cut-blocks are approximately 30 ha in size on average, and contain 5–20 residual trees per hectare. Forest was cut around three study lakes once between October 1996 and April 1997. Our study occurred one summer before (1996) and two summers after (1997, 1998) forest harvesting. Harvested areas were separated from riparian vegetation around lakes by a 100 m-wide treed buffer. Harvesting removed forest from ~10–40% (mean=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 greater than
or equal to 800 m of intact forest; 3% of the land area between 450–800 m of the fifth lake was harvested in 1994. We refer to these five lakes as ‘unharvested lakes’ hereafter. Around unharvested lakes, 0–11% (mean 3.1, SE 2.1) of the drainage basin was harvested. Lakes were named using a three-letter code to identify their location, followed by either 100, which identifies lakes that were eventually harvested, or 800 for lakes that remained unharvested.

2) Sampling bird behavior

We documented dive duration of adult female and post-fledge young-of-the-year Buffleheads, and adult male and female Common Loons. We were unable to reliably distinguish fledged young-of-the-year Buffleheads from adult female Buffleheads based on plumage (Gauthier 1993), nor could we reliably distinguish male and female loons.

We visited each lake for up to 5 days a year during June–August, 1996–1998, with 0–28 days between visits to a lake. We conducted observations on birds between 0700-2100 MST. Each focal bird was observed from a boat or the lakeshore and the duration of dives measured with a stopwatch. 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). In addition, Common Loons often peer underwater before diving for prey (McIntyre 1988). Dive durations were recorded for actively foraging birds and ceased when the focal bird stopped diving or disappeared. Each such session was termed an observation bout. Observation bouts were a maximum of 2 h long, but were typically much shorter (ca. 60 min). Each visitation day we recorded 1–3 observation bouts for Bufflehead, and 1–5 observation bouts for Common Loon. On a given day, we attempted to collect data from different individuals, however, the same bird was sometimes observed more than once. We separated observation bouts on the same individual by at least 1 h. Across all lakes and years, we recorded a total of 23 observation bouts for Bufflehead and 66 observation bouts for Common Loon.

Ducklings accompanied some focal female Buffleheads during the study. Because Buffleheads do not feed their young (Gauthier 1993), and females foraged in the same areas on lakes when accompanied

Table 1. Characteristics of study lakes. Z mean = mean depth; Z max = maximum depth; TP = euphotic zone total phosphorus concentration; Secchi = mean Secchi depth, and range in brackets. Annual mean for 1996 and mean of annual means for 1997–1998 presented for Z max, TP, and Secchi depth. Fish presence and biomass determined in 1996 and 1998. BRST = brook stickleback (*Culaea inconstans* (Kirtland)), FSDC = finescale dace (*Phoxinus neogaeus* Cope), FTMN = fathead minnow (*Pimephales promelas* (Rafinesque)), NRPK = northern pike (*Esox lucius* (L.)), YLPR = yellow perch (*Perca flavescens* (Mitchell)), WHSC = white sucker (*Catostomus commersoni* (Lacépède)).

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

*TP determined by persulphate oxidation (Menzel & Corwin 1965, as modified by Prepas & Rigler 1982). Euphotic zone depth (i.e., the depth at 1% light penetration) determined using LiCor Li 1000 light meter or Secchi depth.

b 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).

*: data not collected, **: No fish captured, but fish presence detected with depth sounder.
by young as they did when foraging alone, we included dives performed by female Buffleheads accompanied by young in analyses. We excluded Common Loon dives that resulted in chick provisioning from analyses, to ensure that foraging by adult Common Loons was not influenced by the food requirements of dependent chicks.

3) Sampling environmental parameters

We measured selected environmental parameters as follows. Secchi depth was measured at the deepest point of each lake approximately two times per month throughout the summer, in accordance with the sampling schedules of the TROLS project (see Table 1 for range of values). For correlation analysis (see Statistical analysis section below), we used Secchi values from the sampling period closest to when foraging observations were done. Mean depth was determined once in 1993 by Silins (1994). Fish were sampled using overnight sets of multi-mesh gill nets (mesh size: 6.25–75.0 mm, net size: 42×1.5 m). Net locations were determined according to a stratified random design; fishing effort (6–18 net-nights) was adjusted for lake area and depth and was concentrated in shallower depths (<3 m) (W. Tonn & A. Danylchuk, unpublished data). Captured fish were identified to species, measured (total length), and weighed (up to 200 individuals/species/sample; wet mass, g), and data subsequently converted to biomass per unit effort. For fish that were measured but not weighed, lake-specific mass-length regressions were used to estimate biomass. The biomass estimates were then summed over all species in a lake for a single value of total fish biomass per unit effort per lake. All lakes contained fish, except LLB100 (Table 1).

4) Statistical analysis

To test for differences in dive duration for each focal species on harvested versus unharvested lakes, we conducted nested analyses of variance with unequal sample sizes in SPSS 8.0 (SPSS Inc. 1997), nesting lake within harvesting treatment. We used observation bouts composed of sequences of five or more dives to calculate mean dive duration per bout. Mean dive duration of observation bouts was then used as the dependent variable in analyses. We acknowledge that different observation bouts occurring on the same lake, in both the same year and in different years of the study, were not strictly independent and the robustness of conclusions must be tempered accordingly. The unharvested category consisted of two lakes in 1996 (LLB100 and SCL100, pre-harvest) and five lakes in 1997–1998 (LLB800, SCL800, SPH800, BEA800, CAB800) and the harvested category of three lakes in 1997–1998 (LLB100, SCL100, SPH100, post-harvest). Data from 1997 and 1998 were pooled for each lake because there were insufficient degrees of freedom to analyze years individually. Also, our data set did not allow for lakes with pre- and post-harvest data to be treated as repeated measures. Instead, LLB100 and SCL100 were essentially treated as different lakes in the pre- (unharvested) and post (harvested) years. Although we could not confirm normality of the data set, we 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). We confirmed homogeneity of variances using Levene’s test. We followed significant nested ANOVA with post-hoc comparisons (Student-Newman-Keul’s tests; Day & Quinn 1989; Underwood 1997), using the Kramer modification for unequal sample sizes (Day & Quinn 1989).

To examine potential mechanisms by which forest harvesting affects foraging behavior, we correlated mean Bufflehead and Common Loon dive duration with environmental factors (water clarity represented by Secchi depth, and fish biomass), using Spearman rank correlations conducted in SPSS 8.0 (SPSS Inc. 1997). Mean dive duration was calculated for each lake in each year and correlated with environmental data collected on lakes in the same year. We also correlated duration of Common Loon dives and mean lake depth. Although water depth is unlikely to be affected by forest harvesting, it can be positively correlated with dive duration for some species (e.g., Wannless et al. 1997) and therefore contribute to differences in dive duration among lakes which are unrelated to forest harvesting. Dive data from LLB100, 1997, were used in this analysis by assigning fish biomass to 0, based on gill netting results from 1996 and 1998. We did not correlate duration of Bufflehead dives with lake depth because Bufflehead foraging on all lakes occurred in water ≤2 m deep. To compensate for conducting more than one comparison with some elements of the data set, we 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.
RESULTS

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 (LLB100 and SCL100; Fig. 1, 2). However, overall dive duration on unharvested lakes did not differ significantly from harvested lakes for either species (nested ANOVA: Bufflehead: $F_{1,3} = 0.85, P = 0.58$; Common Loon: $F_{1,8} = 0.56, P = 0.52$, Fig. 1, 2). Unrelated to disturbance status, mean duration of dives differed significantly among lakes for Buffleheads (nested ANOVA: Bufflehead: $F_{3,23} = 3.21, P = 0.04$), and differed at the $P < 0.1$ level for Common Loons ($F_{8,66} = 1.93, P = 0.07$). Post-hoc comparisons failed to identify lakes on which Bufflehead dive duration differed significantly. Given the significant ANOVA result, we conclude that mean Bufflehead dive duration differed significantly between LLB100 and SPH100, the lake pair with the most divergent values.

2) Correlations of dive duration with environmental factors

For Buffleheads, dive duration was negatively correlated with Secchi depth (Spearman rank correlation, $r = -0.81, P = 0.01, N = 8$, Fig. 3). Although there was a trend for Bufflehead dive duration to increase with fish biomass, the relationship was not significant (Spearman rank correlation, $r = 0.74, P = 0.26, N = 4$).

For Common Loons, dive duration was not significantly correlated with Secchi depth or fish biomass (Spearman rank correlations, Secchi depth, $r = 0.22, P = 0.36, N = 18$; fish biomass, $r = -0.29, P = 0.48, N = 8$). The duration of Common Loon dives was also not correlated with mean lake depth (Spearman rank correlation: $r = 0.34, P = 0.26, N = 14$).

DISCUSSION

Our study found no evidence that forest harvesting influences the behavior of aquatic birds as measured...
by dive duration for Bufflehead and Common Loon. We did, however, document behavioral differences across lakes independent of forestry activity. For example, mean duration of dives by Buffleheads differed between two of the eight study lakes, LLB100 and SPH100. Dives on LLB100 were shorter than on SPH100, possibly because LLB100 was fishless. Further, although not statistically significant, the duration of Bufflehead dives on fishless LLB100 was also shorter than on the other two lakes, both of which contained fish. This fact, combined with a trend for dive length to increase with fish biomass, supports the possibility that competition for food occurred between Buffleheads and fish. The absence of data on invertebrate biomass, however, limits our ability to draw firm conclusions. Nonetheless, resident fish species all consume aquatic invertebrates (Nelson & Paetz 1992; Beaudoin et al. 2001), as does Bufflehead (Gauthier 1993), and the presence of both large- and small-bodied fish can negatively affect macroinvertebrate abundance (Mallory et al. 1994; Tonn et al. 2004). Other studies have inferred that competition for invertebrate prey can occur between diving ducks and larger-bodied fish species (e.g., Eadie & Keast 1982; Winfield & Winfield 1994).

Diet composition and prey characteristics can also affect Common Loon foraging behavior, and therefore cause dive duration to differ between foraging bouts within and among lakes (Barr 1996; Gingras & Paszkowski in press). For example, fast moving, larger prey, such as fish, may demand longer chases and more manipulation time than smaller, slower prey (e.g., leeches), thereby increasing the length of time birds spend underwater (Ydenberg 1986; Ulenaers et al. 1992; Barr 1996). Supporting this possibility, Gingras and Paszkowski (in press) documented that Common Loon dives were shorter on average on fishless lakes than on lakes occupied by small-bodied fish. In an opposite pattern, 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). In our study, dive duration on the one fishless lake we examined did not differ from duration on the seven lakes containing fish. In addition, the duration of Common Loon dives was not correlated with fish biomass, in agreement with Nocera and Burgess (2002). Large-bodied fish, such as northern pike, are major contributors to biomass values in two study lakes, but may not represent a common source of prey for Common Loons as these birds seldom consume fish over 300 g (McIntyre & Barr 1997). Larger fish may even compete with loons for smaller fish. For some species of diving birds, dive duration increases with water depth (e.g., Wanless et al. 1997). However, mean lake depth and Common Loon dive duration were not correlated in our study. Loons tended to forage over most of the lakes’ surfaces, which suggests that they were foraging primarily in the upper portions of the water column.

Although we could not attribute patterns in dive duration to forest harvesting, Bufflehead dive duration increased significantly with decreasing water clarity. If this represents a cause and effect relationship, versus an outgrowth of other attributes of clear versus murky lakes, decreased water clarity may force Buffleheads to increase search times while foraging visually, and thus increase the duration of dives to maintain prey intake. We expected a similar relation between water clarity and dive duration for Common Loons but this was not apparent. Buffleheads focus much more intensively on invertebrate prey than Common Loons, which appear to feed on both invertebrates and fish on many lakes (McIntyre 1988; Gauthier 1993; Gingras & Paszkowski 1999). Therefore, relationships between Bufflehead dive duration and environmental factors may be simpler and consequently easier to detect than for Common Loons. It is also possible that loons are less flexible in their foraging behaviors than buffleheads (Nocera & Burgess 2002).

There may have been a lack of detectable effects of forest harvesting on Bufflehead and Common Loon foraging behavior in our study for a number of reasons. Firstly, post-harvest increases in euphotic zone total phosphorus and Secchi depth proved to be not significant in our study lakes (Table 1, Prepas et al. 2001). If nutrient influx does not increase post-harvest, primary production will not increase, thus, expected post-harvest changes in prey base will not occur. Whereas mean Secchi depth on lakes sampled before and after harvesting did decrease slightly, decreases were not statistically significant, and cannot be assumed to be a result of forestry (Prepas et al. 2001). Secondly, to reduce pseudoreplication, we focused 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 (Langlois PW, unpublished) and fish prey bases among study
lakes probably increased the complexity of relationships between bird behavior and lake characteristics, reducing the detectability of harvesting effects.

Quantifying foraging behavior 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 all represent strategies to clarify whether forest harvesting affects aquatic bird foraging patterns on boreal lakes in western Canada. The fact that Bufflehead dive duration and Secchi depth were correlated in this study suggests that foraging behavior may be used as an indicator of at least some environmental conditions. Further assessment will determine whether changes in aquatic bird foraging patterns are reliable indicators of environmental changes in lakes, which could ultimately translate into more dramatic post-harvest changes in bird populations and communities.

ACKNOWLEDGMENTS

This work was conducted as part of J.P.P.’s Ph.D. research. Thanks to A. Danylikchuk, E.E. Prepas, and W.M. Tonn for sharing data, and H. Bears and T. Morcos for their exceptional assistance in the field. This work was conducted, in part, within the TROLS project, which was funded by Ainsworth Lumber Co. Ltd., Alberta Economic Development and Tourism, Alberta Environmental Protection, Alberta-Pacific Forest Industries Ltd., C.S. Resources, Employment Canada, Manning Diversified Forest Products, National Research Council of Canada Industrial Research Assistancehip Program, Natural Sciences and Engineering Research Council of Canada (Collaborative Special Projects Grant, and University-Industry Co-operative Research and Development Grant), National Water Research Institute, R.L. & L. Environmental Services Ltd., Syncrude Canada, University of Alberta, and Weyerhaeuser Canada Ltd. The Institute for Wetland and Waterfowl Research, Canadian Circumpolar Institute, North American Loon Fund, and the Edmonton Bird Club provided additional funding.

REFERENCES

Gingras BA & Paszkowski CA (in press) Feeding behavior and modelled energetic intake of Common Loon adults and chicks on small boreal lakes with and without fish. Hydrobiologia.


