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Wetland Use and Selection by Breeding Waterbirds in the Boreal Forest of Quebec, Canada

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Abstract Wetlands of remote forested landscapes of Quebec support numerous species of breeding waterbirds yet species-habitat associations remain poorly quantified. From 1990 to 2005, we conducted systematic helicopter surveys of breeding waterfowl and common loons (*Gavia immer*) across a 540,000-km² forested region of Quebec. Data from this survey were used to investigate local habitat use and selection by waterbirds, based on a wetland classification system derived from digital forestry maps. Detailed indicated-breeding-pair (IBP) distributions were developed for broad aquatic, wetland, and shoreline habitat types. We

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Present Address: L.-V. Lemelin (⊠) Ministère des Ressources Naturelles et de la Faune du Québec, 880 chemin Sainte-Foy, 5e étage, Québec, QC, Canada G1S 4X4 e-mail: louis-vincent.lemelin@mrnf.gouv.qc.ca also estimated selection ratios within groups of similar habitat types. Small (\leq 8 ha), connected ponds were highly used and selected by five dabbling duck species and by wood duck (*Aix sponsa*), Canada goose (*Branta canadensis*), ring-necked duck (*Aythya collaris*), hooded merganser (*Lophodytes cucullatus*), common goldeneye (*Bucephala clangula*), and Barrow's goldeneye (*B. islandica*). Dabbling duck species, wood duck, and Canada goose made extensive use of streams (25–41% of all IBP). Community organization was mainly driven by openness of aquatic habitat and water movement, i.e., from lentic to lotic habitats. Failure to include streams in waterfowl surveys and habitat mapping could produce biased estimates of wetland habitat use and selection in the boreal forest.

Introduction

Waterfowl breed in a wide variety of environments in North America (Bellrose 1976), but the habitat requirements of waterfowl distributed at low densities in remote areas are often not well quantified. This is the case for waterbird populations that breed in forested landscapes of Quebec, forests that cover an area of more than 500,000 km² and support over 355,000 breeding pairs of ducks, geese and loons (Bordage et al. 2003). The vast forest landscapes of Quebec nevertheless harbor the core of the breeding ranges of the American black duck (*Anas rubripes*) (Longcore et al. 2000) and the eastern North American population of Barrow's goldeneye (Robert et al. 2000), a population currently designated as being of special concern by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC 2007). Overall, 18 species of waterfowl and the common loon (*Gavia immer*) breed regularly in Quebec forests.

Relating the distribution of breeding pairs across classes of wetland habitat is an effective way to analyze the importance of broad habitat types for waterfowl species. Such relationships have been investigated using various classification systems. For example, in the boreal Claybelt of Ontario, Rempel et al. (1997) analyzed the distribution of 14 waterfowl species according to a specifically designed habitat classification system based on aerial photography. In Maine and New York, Ringelman et al. (1982) and Dwyer and Baldassarre (1994) linked the distribution of American black duck and mallard (Anas platyrhynchos) to Cowardin et al.'s (1979) habitat classification system. In portions of Quebec's boreal forest, Bordage (1987, 1988) examined pair distribution of American black duck and common merganser (Mergus merganser), but only across open water classes. Furthermore, McNicol et al. (1987), in northern Ontario and Nummi and Pöysä (1995) in Finland, compared waterfowl pairs per kilometer of shoreline for the most abundant species present among several lake size classes. These studies revealed interesting relationships between waterfowl and habitat characteristics, such as waterbody size, water acidity, wetland fertility or wetland type. However these studies highlighted limitations for conducting a regionally comprehensive assessment of waterbird community patterns: small sample sizes for many species or samples for only the few, most abundant species; small geographical scales or narrow environmental gradients; a very coarse habitat classification; and stream habitats were not considered.

We attempted to overcome some of these challenges by evaluating habitat associations between wetland habitat types and 19 species of breeding waterbirds, in forested landscapes of Quebec, using two existing data sets. Specifically, 16 years of Black Duck Joint Venture (BDJV)-Canadian Wildlife Service (CWS) aerial survey data were examined in relation to an original wetland classification based on Quebec digital forestry maps. Our study aimed to quantify habitat use and selection by waterfowl species and the common loon across broad and ecologically meaningful habitat types at a large geographical scale, information that is lacking for this vast region. Unlike previous studies, our classification scheme specifically recognizes streams, and we hypothesize that they would be used and selected by several dabbling duck species. Results provide a benchmark for future work about environmental quality and impacts of wetland change. Our findings may also help to develop sound environmental management strategies because habitat types supporting both high densities and high numbers of breeding birds are identified.

Methods

Study Area

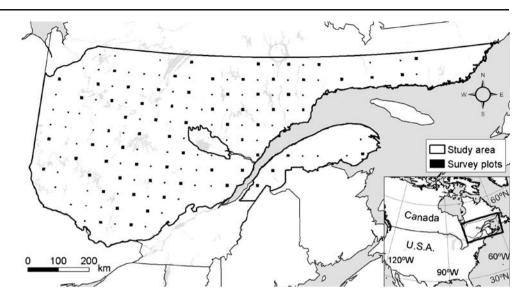
The study area was the region covered by the BDJV-CWS aerial survey in Quebec, corresponding to the forestdominated landscapes of the province (Fig. 1). It extends northwards from northern temperate deciduous forest to the boreal coniferous forest zone. The area contains numerous interconnected lakes, ponds, rivers, and streams. Open water and wetlands with tree cover <25% together encompass nearly 18% of the total area (Ménard et al. 2006). Beaver (*Castor canadensis*) were ubiquitous within the study area, although their abundance is higher in the western part of the region (Lafond and Pilon 2004).

Waterfowl Surveys

Data came from the first 16 years (1990–2005) of the BDJV-CWS waterfowl aerial survey for Quebec. The survey design has been modified over time. From 1990 to 1992, 82 square plots (10×10 km), which were systematically distributed at 100-km intervals, were surveyed. The number of plots was reduced to 43 in 1993–1994, and to 35 in 1995. From 1996 to 2005, plot size was reduced to $5 \times$ 5 km with 50-km spacing between plots, and the number of plots was increased to 156; half of the plots were surveyed once each year in a rotating scheme (Bordage et al. 2003).

Surveys were carried out by experienced observers in a helicopter (Bell 206 L with bubble side-windows) that flew over every water body, watercourse, and wetland within the plots. Depending on habitat type and topography, flight altitude was 15–50 m above ground level and speed varied from 60–100 km/h. Although the survey was primarily designed to estimate American black duck population size, all waterfowl species, as well as many other bird species (including common loon), were also noted. Greater and lesser scaups (*Aythya marila* and *A. affinis*) were grouped together because they cannot be reliably separated to species level during aerial surveys.

During the survey, observations were recorded onto topographic maps (1:50,000 scale) with a precision of c. 100 m. Surveys were timed to occur at the end of the egglaying and beginning of the incubation period of the American black duck, an early nesting species. Therefore, surveys took place on average from May 6–30. All analyses used breeding pair observations, which were determined following indicated-breeding-pair (IBP) criteria of the BDJV in eastern Canada (Bordage et al. 2003). Usually, indicated pairs are counts of pairs, lone drakes, or small groups of single drakes, based on the premise that females may be at the nest while males stay on waiting sites (Dzubin 1969). In this study, sightings of 1–3 Canada Fig. 1 Study area (540,000 km²) and design of the Black Duck Joint Venture-Canadian Wildlife Service aerial survey in Quebec. Only survey plots used in the analyses are shown. Larger squares represent 10×10 -km plots, which all overlap one 5×5 -km plot



goose individuals were recorded as 1 IBP. As American black ducks were not routinely sexed on the survey due to low sexual dimorphism, IBP was based on the number of individuals observed either as single (1 IBP), two-bird groups (1.5 IBP each), or flocks of 3 and 4 individuals (3 and 4 IBP, respectively). For other dabbling ducks and wood duck, IBP was calculated based on the number of males either singly or in groups of up to 4 individuals (including females and unsexed birds), with the exception of 3 males and 1 female which were recorded as 0 IBP. For diving species (diving ducks and sea ducks), except ringnecked duck, IBP was calculated based on the number of males in breeding plumage, observed either singly or in groups of up to 4 total individuals including females and unsexed birds. For ring-necked duck, IBP was calculated as the number of males observed either singly or in groups of up to 4 males, regardless of females and unsexed birds. Only sightings of 1 or 2 common loons were recorded as 1 IBP.

Habitat Classification

Habitat data were extracted from digital 1:20,000 forestry maps obtained from the Quebec Ministry of Natural Resources and Wildlife (Létourneau 1999). Maps were produced gradually from 1990 to 2004 and were available for 73 (out of 82) 10×10 -km waterfowl survey plots and 143 (out of 156) 5×5 -km plots, located in the portion of Quebec that is primarily managed for timber harvesting. Mapping was carried out using 1:15,000 and 1:40,000 aerial photographs and stereoscopic photo-interpretation. The minimum mapping area was 0.06 ha for open water bodies, 0.2 ha for watercourses, 1 ha for other non-treed wetland polygons, and 0.01 ha for islands (Létourneau 1999; MRNQ 1999). Streams, defined at the photo-interpretation stage as all watercourses <0.2 ha, including

intermittent streams, were recorded on forest maps as linear features and therefore measured based on their length (nearest m).

Four areal (polygon features) habitat classes were measured directly from maps: open water areas; open wetlands (vegetated wetlands with < 25% tree cover, for example, including meadow marshes, densely vegetated emergent marshes, riparian fens, and bogs); shrub swamps (mostly Alnus rugosa stands); and flooded swamps (dominated by standing dead trees, mostly following beaver flowage). Remaining areas were mostly upland forests and poorly drained merchantable coniferous stands. Within open water areas, lakes were further defined as all water bodies >8 ha and ponds as water bodies ≤ 8 ha, based on one of the criteria used by Cowardin et al. (1979) to separate lacustrine from palustrine waters. Near-shore waters of lakes were distinguished from offshore waters with a boundary set at 100 m in-water from shorelines, consistent with pair location precision. In the absence of available bathymetric data, this zone criterion yields classes that are akin to the lacustrine littoral and limnetic subclasses of the Cowardin et al. (1979) classification. Connected ponds were distinguished from isolated ponds based on the presence of a mapped, surface hydrological link (stream or river). This distinction is useful as the two habitats may be ecologically different and addressed differently by some legislations (Leibowitz 2003). Rivers, which corresponded to areal watercourses on the maps, were directly transferred into the classification.

Shoreline vegetation may also be a significant predictor of waterfowl use (Nummi et al. 1994). Based on the polygons adjacent to water on the maps, shorelines of open water and streams were classified into five types: open wetlands, shrub swamps, flooded swamps, small (<20 ha) islands, and forests (mainly upland forests, poorly drained forests, and islands >20 ha). The three components of the forest shoreline type were grouped because preliminary analyses showed similar selection by waterfowl species.

Pair-Habitat Association

Indicated-breeding-pair locations and habitat maps were superimposed in a geographic information system (ArcGIS 9.1; ESRI 2005). Given the level of precision for location mapping, the area within a 100-m radius from pairs was scanned for probable aquatic or wetland habitat types and, following a simple rule, IBPs were associated with these habitat types. Firstly, IBPs were assigned to the closest open water habitat type. When no such habitat was present, IBPs were alternatively assigned to the closest stream habitat, and, when no stream was present, to the closest open wetland habitat. All pairs that were previously associated with an open water habitat type or a stream were also assigned to the closest shoreline type. All pairs that were mapped further than 100 m from any open water. open wetland, or stream (2.6% of all pairs) were excluded from further analyses, as birds were probably moving between habitats when they were detected.

Statistical Analyses

Habitat use and selection were evaluated in a two-tiered approach by analyzing pair distributions (data from all years were pooled, enabling us to include less abundant species) across comparable habitat classes, i.e. among open water classes first, then among shoreline types of open water and streams. Habitat use was simply defined as the percent of observed pairs associated with a given habitat type over the total number of pairs detected in all habitats (Manly et al. 2002). For each observed value of habitat use, a confidence interval was computed with the large-sample 95% confidence interval formula (Manly et al. 2002).

To estimate patterns and strength of habitat selection, expected percentages of habitat use were derived based on the relative availability distribution of habitat types following Neu et al. (1974). Availability was determined based on areal coverage for open water habitat types and on length for streams and shoreline types. However, habitat availability assessment had to account for the breeding range of species within the study area. Because the aim was to study selection of site-scale habitat features within a species' geographic range, only survey plots for which ≥ 1 pair of a given species had been observed at least once over the years were considered available. Areas of plots available to each species were added up for the total number of years that the plots were surveyed. Habitat selection was then expressed with a simple estimator corresponding to the ratio of observed:expected use for a given habitat type (selection ratios according to Manly et al. 2002). This selection ratio is a measure of relative density, and reflects the number of times a habitat is used compared to its availability. A ratio value <1 (or >1) indicates a weaker (or stronger) selection. Unlike chi-square values, selection ratios vary on a fixed-scale and are largely independent of sample size.

Unlike the habitat use analysis described above, habitat selection had to be analyzed separately for habitat types measured in the same units (i.e., as an area or a length). Thus, habitat use was analyzed for open water habitat types, open wetlands, and streams, whereas habitat use and selection were analyzed within open water habitat types. Shoreline type use and selection were analyzed within open water habitat types and streams separately because streams remained largely unused by many species, which would have unduly inflated selection ratios of open water habitats. For each species, expected use was compared with the observed use confidence interval to infer statistical significance of habitat selection.

A test for selective use of water bodies ≤ 8 ha versus >8 ha was performed by comparing observed pair numbers. However, because differences in shoreline type availability alone could lead to an apparent selection for one class of water body size over the other (an effect known as Simpson's paradox [Agresti 1996]), shoreline type availability was controlled by computing Mantel-Haenszel (MH) odds ratios (SAS Institute 2002). Thus, this test estimated the strength of selection (with 95% confidence intervals) for shorelines of either class of water body size, after controlling for the effects of shoreline length and shoreline type.

To synthesize community structure and identify ecological relationships between species and habitat types, a correspondence analysis was performed (CANOCO 4.5, ter Braak and Smilauer 2002) on the two-way contingency table of pair frequencies computed for species by all combinations of aquatic versus shoreline habitat types (Legendre and Legendre 1998). This multivariate analysis differs from species by species analyses in that it considers all species simultaneously and uses all possible combinations of aquatic and shoreline habitat types.

Results

From 1990 to 2005, we used 31,508 IBP locations for 18 waterfowl species (17 after pooling greater scaup [*Aythya marila*] and lesser scaup [*A. affinis*]) and the common loon in habitat association analyses. Most pairs of all species were associated with open water areas (54.3–100.0%). The five species of dabbling ducks (American wigeon [*Anas americana*], blue-winged teal [*A. discors*], green-winged teal [*A. crecca*], American black duck, and mallard), wood duck, and the Canada goose all used streams in higher

proportions than the 10 species of diving ducks and common loon, with 24.6–41.4% versus 0.0–21.0% of pairs located in streams (Table 1). In the latter group of diving species, the lowest use of open water areas was observed in hooded merganser (77.8%), followed by ring-necked duck (87.0%).

Among open water areas, all species used lake offshore waters less than expected based on areal coverage with estimated selection ratios $(\hat{S}) \le 0.2$ for 15 of the 18 species (Table 1). Connected ponds received the highest use from all dabbling duck species, wood duck, Canada goose, ringnecked duck, hooded merganser, common goldeneve, and Barrow's goldeneye. This was followed by lake shore zones. However, waterfowl species made higher selection of ponds over lake near-shore waters, as shown by estimated selection ratios \geq 1.5. The common loon was the only species to select lake near-shore waters first ($\hat{S} = 1.5$). Isolated ponds were primarily selected by many species, but the maximum use of these habitats only reached 3.8% pairs for Canada goose. Rivers were chosen over lakes near-shore waters by the Canada goose and all duck species except scaup and scoters, but to a lesser extent than connected ponds.

Among open water shoreline types, forest shorelines were used most frequently by most species, except for Canada goose, blue-winged teal, and green-winged teal, which made comparable use of open wetland shorelines, and scaup, which mainly used open wetland shorelines (Table 2). Open wetland shorelines were used more than expected by the highest number of species (17/18). Flooded swamp shorelines were used in a higher proportion than available by all species of dabbling ducks, wood duck, ring-necked duck, and hooded merganser, with selection ratios consistently > 2.2. Small island shorelines were used more than expected by six species (common loon, Barrow's goldeneye, black scoter [*Melanitta nigra*], Canada goose, and surf scoter [*M. perspicillata*]).

For stream shorelines, some diving species were observed too infrequently to be included in analyses (Table 3). Among the more abundant species, highest use was shared between forest (common merganser, wood duck, hooded merganser, blue-winged teal, mallard, common goldeneye, and bufflehead [*Bucephala albeola*]) and open wetland shorelines (Canada goose, ring-necked duck, and American black duck). Duck species frequenting streams generally chose flooded swamp over shrub swamp, and shrub swamp over open wetland shorelines except for ring-necked duck, and common and hooded mergansers.

In controlling for shoreline type availability in water bodies, we found that nine species selected shorelines of water bodies ≤ 8 ha versus > 8 ha (Table 4). The common loon, red-breasted merganser (*Mergus serrator*), and common merganser, which are the three main fish-eating species, selected shorelines of larger water bodies. The two first axes of the correspondence analysis explained 56% and 20% of the variance in species–habitat relationships, totalling 76% (Fig. 2). Observed patterns were only marginally influenced by rare species as ordination excluding the five least common species (Table 1) yielded qualitatively similar results.

Discussion

Importance of Small Water Bodies and Streams for Waterbirds

The BDJV-CWS aerial survey provided a large dataset with spatially recorded observations that enabled us to explore waterfowl-habitat associations, which substantially improved current knowledge (cf. Gauthier and Aubry 1995; Poole 2008). Our study quantified habitat use and selection for all waterfowl species and the common loon simultaneously, clarifying community-level patterns, especially the importance of small water bodies and streams for several waterbird species.

There have been few attempts to relate breeding waterfowl density to water body size in forested areas. From the data presented by Bordage (1987, 1988), the densities of both American black duck and common merganser pairs were higher in lakes <10 ha and decreased with increasing lake size (classes 11-100 ha, 101-500 ha, and >500 ha). This trend is confirmed by our study and it applies to other waterfowl species as well since zones located >100-m offshore proved to be largely unused by any species. Shoreline length, which is also a routinely used denominator for reporting waterfowl densities (e.g. Haapanen and Nilsson 1979; Toft et al. 1982; Gauthier and Smith 1987; Elmberg et al. 2003), is thus susceptible to be a better predictor of pair number than lake size. This approach has been used in Finland by Nummi and Pöysä (1995), who compared pair densities per km of shoreline among several lake size classes; for all abundant species (mallard, greenwinged teal, and common goldeneye), they reported that density decreased in lakes >10 ha. In a similar analysis of northern Ontario lakes, McNicol et al. (1987) observed that this relationship held for insectivores (hooded merganser and common goldeneye) and generalist feeders (mallard, American black duck, and ring-necked duck) but was reversed in species that are mostly piscivorous (common merganser and common loon). However, our results show that small island shorelines are strongly selected by several species, perhaps as predator-free nesting sites, and that this shoreline type should be considered differently than other shorelines for these species. More generally, our results add to the body of evidence suggesting that larger water bodies may be preferred by piscivores (DesGranges and Darveau

| Open water Lake—offshore water Use ^b x 1.7 \hat{S} 0.7 \hat{S} 0.0 Lake—near-shore water Use x 30.1 \hat{a} 2.6 \hat{S} 0.7 Pond—connected | | | | | | IVIGII | nnin | nocau | | המכוס | IIInd | ocne | DIJC | CUME | HOIME | KDIME | COLO |
|--|-------|------|------|-------|-------|--------|-------|-------|-------|-------|-------|------|-------|-------|-------|-------|-------|
| offishore wat x a -near-shore w x a -connected | | | | | | | | | | | | | | | | | |
| x a -near-shore w x a -connected | | | | | | | | | | | | | | | | | |
| a -near-shore w x a -connected | 0.0 | 13.4 | 0.0 | 2.9 | 2.0 | 2.9 | 1.0 | 4.2 | 2.8 | 0.9 | 6.2 | 6.1 | 13.0 | 5.1 | 0.6 | 12.3 | 21.9 |
| -near-shore w x a -connected | 0.0 | 8.2 | 0.0 | 1.0 | 0.3 | 1.3 | 0.3 | 2.4 | 0.5 | 1.8 | 2.9 | 2.4 | 7.5 | 0.7 | 0.5 | 7.2 | 2.1 |
| -near-shore v x a -connected | 0.0 | 0.3 | 0.0 | 0.I | 0.1 | 0.1 | 0.0 | 0.1 | 0.1 | 0.0 | 0.2 | 0.2 | 0.4 | 0.1 | 0.0 | 0.2 | 0.6 |
| x a -connected | | | | | | | | | | | | | | | | | |
| <i>a</i> -connected | 25.2 | 32.8 | 21.1 | 23.3 | 33.7 | 30.7 | 27.7 | 47.1 | 35.5 | 32.1 | 43.2 | 55.7 | 61.0 | 58.3 | 26.5 | 61.7 | 67.2 |
| -connected | 6.7 | 11.2 | 13.0 | 2.7 | 1.1 | 3.6 | 1.3 | 6.0 | 1.5 | 8.9 | 6.0 | 5.0 | 10.9 | 1.7 | 2.7 | 10.6 | 2.4 |
| | 0.6 | 0.9 | 0.5 | 0.5 | 0.7 | 0.6 | 0.6 | 1.0 | 0.8 | 0.6 | 0.9 | 1.2 | 1.3 | 1.3 | 0.6 | 1.9 | 1.5 |
| | | | | | | | | | | | | | | | | | |
| Use <i>x</i> 54.9 | 67.5 | 43.3 | 52.6 | 59.2 | 53.6 | 50.2 | 65.5 | 40.3 | 54.5 | 64.2 | 41.3 | 33.2 | 13.0 | 23.9 | 65.5 | 13.6 | 7.5 |
| <i>a</i> 2.8 | 7.2 | 11.9 | 15.9 | 3.1 | 1.2 | 3.9 | 1.4 | 5.9 | 1.6 | 9.1 | 6.0 | 4.8 | 7.5 | 1.4 | 2.9 | 7.5 | 1.3 |
| Ŝ 5.9 | 7.5 | 8.8 | 5.0 | 6.1 | 5.5 | 5.2 | 6.8 | 4.3 | 5.6 | 4.2 | 4.9 | 3.3 | 1.5 | 2.5 | 6.4 | 2.4 | 0.8 |
| Pond-isolated | | | | | | | | | | | | | | | | | |
| Use x 3.8 | 1.2 | 0.0 | 2.6 | 1.6 | 1.7 | 1.0 | 1.7 | 3.4 | 0.9 | 0.0 | 2.7 | 1.1 | 1.3 | 0.4 | 2.6 | 0.0 | 0.1 |
| a 1.1 | 1.7 | 0.0 | 5.1 | 0.8 | 0.3 | 0.8 | 0.4 | 2.2 | 0.3 | 0.0 | 2.0 | 1.0 | 2.5 | 0.2 | 1.0 | 0.0 | 0.2 |
| Ŝ 19.2 | 5.4 | 0.0 | 11.8 | 8.6 | 9.0 | 4.4 | 0.0 | 10.8 | 4.6 | 0.0 | 11.3 | 4.0 | 2.7 | 2.2 | 13.1 | 0.0 | 0.7 |
| River | | | | | | | | | | | | | | | | | |
| Use <i>x</i> 9.5 | 6.1 | 10.4 | 23.7 | 13.0 | 9.0 | 15.3 | 4.1 | 4.9 | 6.4 | 2.8 | 9.9 | 4.0 | 11.7 | 12.3 | 4.8 | 12.3 | 3.3 |
| a 1.7 | 3.7 | 7.3 | 13.5 | 2.1 | 0.7 | 2.8 | 0.6 | 2.6 | 0.8 | 3.2 | 3.0 | 2.0 | 7.2 | 1.1 | 1.3 | 7.2 | 0.9 |
| Ŝ 1.7 | 1.4 | 1.6 | 3.0 | 2.2 | 1.6 | 2.4 | 0.7 | 0.5 | 1.1 | 1.1 | 1.1 | 0.9 | 1.3 | 2.2 | 0.7 | 2.2 | 0.6 |
| Total open water | | | | | | | | | | | | | | | | | |
| Use <i>x</i> 62.6 | 67.4 | 64.4 | 54.3 | 59.9 | 74.1 | 57.1 | 87.0 | 93.9 | 91.7 | 93.0 | 91.2 | 98.4 | 100.0 | 89.6 | 77.5 | 98.8 | 98.9 |
| a 2.2 | 5.9 | 9.2 | 11.7 | 2.4 | 0.9 | 2.9 | 0.9 | 2.8 | 0.8 | 4.7 | 3.3 | 1.2 | 0.0 | 1.0 | 2.2 | 2.4 | 0.5 |
| Pairs 1,209 | 9 163 | 67 | 38 | 777 | 6,883 | 629 | 4,456 | 263 | 3,759 | 106 | 259 | 377 | 77 | 3,387 | 1,060 | 81 | 1,524 |
| Stream | | | | | | | | | | | | | | | | | |
| Use <i>x</i> 32.9 | 31.8 | 33.7 | 41.4 | 37.7 | 24.6 | 39.9 | 11.7 | 5.4 | 7.8 | 5.3 | 7.0 | 1.6 | 0.0 | 9.9 | 21.0 | 1.2 | 1.0 |
| a 2.1 | 5.9 | 9.1 | 11.5 | 2.4 | 0.9 | 2.9 | 0.9 | 2.6 | 0.8 | 4.1 | 3.0 | 1.2 | 0.0 | 1.0 | 2.2 | 2.4 | 0.5 |
| Pairs 635 | 77 | 35 | 29 | 615 | 2,283 | 439 | 601 | 15 | 321 | 9 | 20 | 9 | 0 | 376 | 287 | 1 | 15 |
| Open wetland | | | | | | | | | | | | | | | | | |
| Use <i>x</i> 4.6 | 0.8 | 1.9 | 4.3 | 2.5 | 1.4 | 3.0 | 1.3 | 0.7 | 0.5 | 1.8 | 1.8 | 0.0 | 0.0 | 0.4 | 1.5 | 0.0 | 0.1 |
| a 0.9 | 1.1 | 2.6 | 4.7 | 0.8 | 0.2 | 1.0 | 0.3 | 1.0 | 0.2 | 2.4 | 1.5 | 0.0 | 0.0 | 0.2 | 0.7 | 0.0 | 0.2 |
| Pairs 88 | 2 | 2 | 3 | 40 | 129 | 33 | 65 | 2 | 21 | 2 | 5 | 0 | 0 | 17 | 21 | 0 | 2 |
| <i>n</i> Pairs 1,932 | 2 242 | 104 | 70 | 1,632 | 9,295 | 1,101 | 5,122 | 280 | 4,101 | 114 | 284 | 383 | LT | 3,780 | 1,368 | 82 | 1,541 |

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Wetlands

^b Values and confidence intervals of habitat use percentages are given in the form $x \pm a$ (%)

| Table 2 Habitat use (%) and estimated selection ratios (\hat{S}) of breeding pairs of 18 waterfowl species and the common loon across shoreline types of open water habitat types in forest landscapes of Quebec, Canada, 1990–2005. Significant estimated selection ratios (with 95% CI excluding 1) are italicized (use lower than availability, $\hat{S} < 1$) or highlighted in bold (use higher than availability, $\hat{S} > 1$) | it use (%) , 1990–2(|) and estim 005. Signif | ated select icant estim | ion ratios (ated select | Ŝ) of bree ion ratios (| ding pairs with 95% | of 18 wate CI excludi | rfowl sp ng 1) are | ecies and italicized | the comi (use low | mon loon er than av | across sh ailability, | oreline ty $\hat{S} < 1$) or | pes of o | pen wate ted in bo | r habitat ty ld (use hig | ypes in foi gher than a | est landsc vailability | apes of $\hat{S} > 1$) |
|---|-------------------------|----------------------------|----------------------------|-----------------------------|----------------------------|------------------------|--------------------------|-----------------------|-------------------------|----------------------|------------------------|--------------------------|-------------------------------|----------|-----------------------|-----------------------------|----------------------------|---------------------------|-------------------------|
| Shoreline type | | CaGo ^a | WoDu | AmWi | BwTe | GwTe | ABDu | Mall | RnDu | Scau | CoGo | BaGo | Buff | SuSc | BlSc | CoMe | HoMe | RbMe | CoLo |
| Open wetland | | | | | | | | | | | | | | | | | | | |
| Use ^b | x | 42.8 | 21.5 | 20.7 | 34.2 | 40.8 | 31.9 | 30.3 | 36.2 | 52.0 | 20.7 | 13.3 | 31.8 | 16.4 | 17.9 | 15.0 | 27.4 | 31.4 | 10.5 |
| | а | 2.8 | 6.3 | 9.7 | 15.1 | 3.1 | 1.1 | 3.6 | 1.4 | 6.0 | 1.3 | 6.5 | 5.7 | 3.7 | 8.6 | 1.2 | 2.7 | 10.1 | 1.5 |
| Ŝ | | 3.1 | 1.4 | 1.3 | 1.8 | 3.0 | 2.4 | 2.1 | 2.7 | 3.1 | 1.5 | 1.2 | 2.1 | 1.2 | 1.0 | 1.1 | 2.0 | 2.0 | 0.8 |
| Shrub swamp | | | | | | | | | | | | | | | | | | | |
| Use | x | 6.2 | 8.6 | 12.1 | 18.4 | 13.3 | 6.9 | 16.2 | 4.7 | 5.2 | 2.8 | 1.0 | 5.9 | 2.8 | 4.5 | 4.2 | 4.8 | 2.9 | 1.7 |
| | а | 1.4 | 4.3 | 7.8 | 12.3 | 2.1 | 0.6 | 2.9 | 0.6 | 2.7 | 0.5 | 1.8 | 2.9 | 1.7 | 4.6 | 0.7 | 1.3 | 3.6 | 0.6 |
| Ŝ | | 1.4 | 1.5 | 1.6 | 2.3 | 3.0 | 1.5 | 3.3 | 1.0 | 0.8 | 0.7 | 0.6 | 1.1 | 0.8 | 1.0 | 0.9 | 0.9 | 0.6 | 0.4 |
| Flooded swamp | ~ | | | | | | | | | | | | | | | | | | |
| Use | x | 1.9 | 14.7 | 34.5 | 15.8 | 5.2 | 4.4 | 12.1 | 6.8 | 0.0 | 1.3 | 0.0 | 5.4 | 0.0 | 0.0 | 1.3 | 8.3 | 2.9 | 1.0 |
| | а | 0.8 | 5.4 | 11.4 | 11.6 | 1.4 | 0.5 | 2.6 | 0.7 | 0.0 | 0.4 | 0.0 | 2.8 | 0.0 | 0.0 | 0.4 | 1.7 | 3.6 | 0.5 |
| Ŝ | | 1.1 | 4.8 | 13.4 | 3.9 | 2.6 | 2.2 | 4.9 | 3.4 | 0.0 | 0.7 | 0.0 | 1.9 | 0.0 | 0.0 | 0.6 | 3.5 | 3.1 | 0.5 |
| Small island | | | | | | | | | | | | | | | | | | | |
| Use | x | 6.2 | 3.1 | 1.7 | 0.0 | 3.6 | 3.3 | 3.8 | 2.9 | 4.8 | 4.5 | 9.5 | 2.9 | 5.4 | 14.9 | 7.6 | 2.4 | 4.3 | 13.9 |
| | а | 1.4 | 2.6 | 3.1 | 0.0 | 1.2 | 0.4 | 1.5 | 0.5 | 2.6 | 0.7 | 5.6 | 2.1 | 2.3 | 8.0 | 0.9 | 0.9 | 4.4 | 1.7 |
| Ŝ | | 1.2 | 0.6 | 0.2 | 0.0 | 0.7 | 0.7 | 0.7 | 0.6 | 0.8 | 0.9 | 2.8 | 0.5 | 1.1 | 2.7 | 1.5 | 0.5 | 0.8 | 2.8 |
| $\operatorname{Forest}^{\mathrm{c}}$ | | | | | | | | | | | | | | | | | | | |
| Use | x | 42.8 | 52.1 | 31.0 | 31.6 | 37.2 | 53.4 | 37.5 | 49.4 | 38.1 | 70.5 | 76.2 | 54.0 | 75.4 | 62.7 | 71.9 | 57.1 | 58.6 | 72.8 |
| | а | 2.8 | 7.7 | 11.1 | 14.8 | 3.0 | 1.2 | 3.8 | 1.5 | 5.9 | 1.5 | 8.1 | 6.1 | 4.3 | 10.8 | 1.5 | 3.0 | 10.7 | 2.2 |
| Ŝ | | 0.6 | 0.7 | 0.5 | 0.5 | 0.5 | 0.7 | 0.5 | 0.7 | 0.6 | 0.9 | 0.9 | 0.8 | 1.0 | 6.0 | 1.0 | 0.8 | 0.8 | 1.0 |
| и | Pairs | 1,185 | 163 | 58 | 38 | 947 | 6,733 | 610 | 4,403 | 252 | 3,650 | 105 | 239 | 354 | 67 | 3,210 | 1,052 | 70 | 1,185 |
| ^a For species codes see Table 1 footnote | les see T | able 1 foot | note | | | | | | | | | | | | | | | | |
| ^b Values and confidence intervals of habitat use percentages are given in the form $x \pm a$ (%) | nfidence | intervals o | f habitat u | ise percent | ages are g | iven in th | e form x^{\pm} . | a (%) | | | | | | | | | | | |
| ^c Forest shoreline type mainly includes upland forest, forest swamps, and islands >20 ha | le type m | ainly inclu | ides uplan | d forest, fo | rest swan | ips, and is | slands >20 | ha | | | | | | | | | | | |
| | | ` | 4 | ~ | | - | | | | | | | | | | | | | |
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| Table 3 | Habitat use (%) and estimated selection ratios (\hat{S}) of breeding |
|-----------|--|
| pairs of | 11ª waterfowl species across shoreline types of streams in |
| forest la | ndscapes of Quebec, Canada, 1990-2005. Significant estimat- |

ed selection ratios (with 95% CI excluding 1) are italicized (use lower than availability, $\hat{S} < 1$) or highlighted in bold (use higher than availability, $\hat{S} > 1$)

| Shoreli | ne type | CaGo ^b | WoDu | AmWi | BwTe | GwTe | ABDu | Mall | RnDu | CoGo | Buff | CoMe | НоМе |
|---------------------|---------|-------------------|------|------|------|------|-------|------|------|------|------|------|------|
| Open v | wetland | | | | | | | | | | | | |
| Use ^c | x | 58.1 | 24.7 | 20.0 | 31.0 | 35.8 | 37.3 | 24.8 | 46.1 | 30.2 | 30.0 | 33.5 | 30.0 |
| | а | 3.8 | 9.6 | 13.3 | 16.8 | 3.8 | 2.0 | 4.0 | 4.0 | 5.0 | 20.1 | 4.8 | 5.3 |
| Ŝ | | 4.3 | 2.0 | 1.0 | 2.1 | 2.8 | 3.0 | 1.8 | 3.6 | 2.4 | 2.1 | 2.6 | 2.4 |
| Shrub | swamp | | | | | | | | | | | | |
| Use | x | 19.5 | 15.6 | 37.1 | 24.1 | 23.9 | 22.6 | 26.2 | 15.6 | 25.9 | 25.0 | 15.7 | 16.4 |
| | а | 3.1 | 8.1 | 16.0 | 15.6 | 3.4 | 1.7 | 4.1 | 2.9 | 4.8 | 19.0 | 3.7 | 4.3 |
| Ŝ | | 3.2 | 2.2 | 4.2 | 2.4 | 3.8 | 3.7 | 3.5 | 2.5 | 4.3 | 3.1 | 2.6 | 2.4 |
| Floode | d swamp | | | | | | | | | | | | |
| Use | x | 0.9 | 14.3 | 8.6 | 3.4 | 4.7 | 5.8 | 9.3 | 12.8 | 4.0 | 10.0 | 4.8 | 11.5 |
| | а | 0.8 | 7.8 | 9.3 | 6.6 | 1.7 | 1.0 | 2.7 | 2.7 | 2.2 | 13.1 | 2.2 | 3.7 |
| Ŝ | | 1.3 | 9.5 | 8.7 | 3.0 | 5.9 | 7.0 | 8.9 | 15.3 | 4.9 | 8.0 | 5.7 | 12.0 |
| Forest ^d | | | | | | | | | | | | | |
| Use | x | 21.4 | 45.5 | 34.3 | 41.4 | 35.6 | 34.3 | 39.6 | 25.5 | 39.9 | 35.0 | 46.0 | 42.2 |
| | а | 3.2 | 11.1 | 15.7 | 17.9 | 3.8 | 1.9 | 4.6 | 3.5 | 5.4 | 20.9 | 5.0 | 5.7 |
| Ŝ | | 0.3 | 0.6 | 0.5 | 0.6 | 0.4 | 0.4 | 0.5 | 0.3 | 0.5 | 0.5 | 0.6 | 0.5 |
| п | Pairs | 635 | 77 | 35 | 29 | 615 | 2,283 | 439 | 601 | 321 | 20 | 376 | 287 |

^a Species with number of observations <20 were omitted (Scau, BaGo, SuSc, BlSc, RbMe, and CoLo)

^b For species codes see Table 1 footnote

^c Values and confidence intervals of habitat use percentages are given in the form $x \pm a$ (%)

^d Forest shoreline type mainly includes upland forest and forest swamps

| Table 4 Selective use of water |
|------------------------------------|
| bodies ≤ 8 ha vs. > 8 ha by |
| breeding pairs of 18 waterfowl |
| species and the common loon in |
| forest landscapes of Quebec, |
| Canada, 1990–2005. Expected |
| values were derived from |
| shoreline length distribution |
| with shoreline type as control |
| variable. Mantel-Haenszel (MH) |
| odds ratio estimate is a measure |
| of the strength of selection. P |
| values are associated with the |
| Cochran-Mantel-Haenszel sta- |
| tistic (1 df). |
| |

| Water body size selection | Species | n (Pairs) | MH | | Р |
|---------------------------|------------------------|-----------|------------|---------|---------|
| | | | Odds ratio | 95% CI | |
| ≤8 ha | Wood duck | 153 | 3.3 | 2.0-5.5 | < 0.001 |
| | Hooded merganser | 1,002 | 3.1 | 2.5-3.7 | < 0.001 |
| | Barrow's goldeneye | 102 | 2.9 | 1.6-5.2 | < 0.001 |
| | Ring-necked duck | 4,223 | 2.8 | 2.5-3.0 | < 0.001 |
| | Green-winged teal | 822 | 2.7 | 2.1-3.3 | < 0.001 |
| | Common goldeneye | 3,414 | 2.5 | 2.3-2.8 | < 0.001 |
| | Canada goose | 1,073 | 2.4 | 2.0-2.8 | < 0.001 |
| | American black duck | 6,122 | 2.0 | 1.9-2.2 | < 0.001 |
| | Mallard | 514 | 1.6 | 1.2-2.1 | < 0.001 |
| | Blue-winged teal | 29 | 1.6 | 0.5-4.6 | 0.402 |
| | Bufflehead | 223 | 1.3 | 0.9-1.9 | 0.148 |
| | American wigeon | 51 | 1.3 | 0.5-3.1 | 0.574 |
| | Scaup spp. | 239 | 1.1 | 0.7-1.5 | 0.696 |
| | Surf scoter | 339 | 1.0 | 0.7-1.4 | 0.913 |
| >8 ha | Common loon | 1,139 | 4.8 | 3.8-6.1 | < 0.001 |
| | Red-breasted merganser | 61 | 3.3 | 1.4-7.6 | 0.006 |
| | Black scoter | 58 | 2.3 | 0.9–5.6 | 0.069 |
| | Common merganser | 2,795 | 1.5 | 1.3-1.6 | < 0.001 |

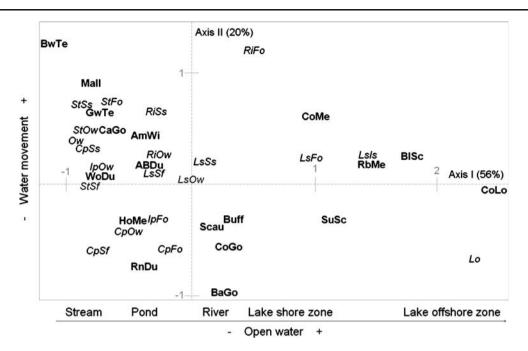


Fig. 2 Correspondence analysis ordination diagram (*bi-plot*) of waterfowl and common loon habitat associations in forest landscapes of Quebec, Canada, 1990–2005. We interpreted the first axis in the ordination as a gradient (*from left to right*) of increasing openness and associated depth of aquatic habitat. The second axis likely represents a gradient (*from bottom to top*) of increasing water movement, i.e., from lentic to lotic habitats. The two first character positions of the habitat

classes are aquatic and wetland habitat types and the two last, where applicable, are shoreline habitat types. Habitat codes: Lo=lake offshore water, Ls=lake near-shore water, Ri=river, Cp=connected pond, Ip=isolated pond, St=stream, Ow=open wetland, Ss=shrub swamp, Sf=flooded swamp, Is=island, and Fo=forest. For species codes see Table 1 footnote

1985). We also highlight the importance of ponds for most other species. Indeed, many species not only showed a stronger selection for water bodies ≤ 8 ha on the basis of both water surface area and shoreline length, but they also used these wetlands in higher absolute numbers. Smaller wetland size reduces exposure to wind and wave action (Cowardin et al. 1979). Influence of beaver, presence of macrophytes (Longcore et al. 2006), and absence of fish (Mallory et al. 1994; Marklund et al. 2002), which are conditions most likely to be found in wetlands of limited extent, are other positive factors that may also contribute in explaining the importance of small wetlands for nonpiscivorous waterfowl species.

Studies of habitat use and selection by breeding waterfowl often relate pair distribution to pond or lake descriptors, leaving stream habitats unaddressed (e.g. Nummi et al. 1994; Paquette and Ankney 1996; Gabor et al. 2002). Whereas this approach may be appropriate for many regions and species, ignoring small streams when evaluating habitat importance could be a costly oversight in regions comparable to the forests of Quebec. We found that streams, mapped as linear features, were used consistently by all dabbling duck species (25–41% of pair observations), Canada goose (33%), wood duck (32%), and hooded merganser (21%), clearly demonstrating the significance of small streams in our study area. Therefore, ignoring the

contribution of streams to overall habitat supply may have a negative impact on applications such as predictive distribution models, as well as on the general understanding of waterfowl breeding ecology. In addition, stream characterization may help in refining species-stream relationships. In our study, streams with forested shorelines included numerous high-declivity and intermittent streams. This explains why all stream types running through wetland polygons were highly selected on a segment-length availability basis.

In other forested regions of North America, beaver ponds have been recognized as important waterfowl breeding habitats, because they are used by all dabbling ducks, wood duck, hooded merganser, and ring-necked duck (Renouf 1972; Brown and Parsons 1979; Brown et al. 1996; McCall et al. 1996; Rempel et al. 1997; Longcore et al. 2006). This species assemblage would fit our results perfectly if we rely on flooded swamps as indicators of beaver ponds. Indeed, the same species selected flooded swamps as open water shorelines. Moreover, even though flooded swamps only bordered a fraction of all beaver ponds present in our survey plots, flooded swamp shorelines supported considerable proportions of the total pairs of American wigeon (22%), wood duck (14%), mallard (10%), and blue-winged teal (10%). This confirms that beaver management practices and trapping efforts (often related to fur value) have the potential to impact waterfowl populations that breed in Quebec's forest wetlands.

From the waterfowl community organization standpoint, interpretation of our ordination bi-plot highlights water openness as the most significant gradient and water movement as the best complementary gradient to explain species variation in breeding pair habitat use. Although we cannot isolate water openness from water depth as explanatory factors, these habitat gradients are similar to those found in the study by Rempel et al. (1997), who also based their wetland habitat classification scheme on remotely sensed data.

Study Limitations and Potential Biases

The use of digital forestry maps provided a straightforward scheme for analyzing patterns of habitat use and selection of waterfowl over a large forest region. Even though wetland coverage can now be derived from satellite imagery, the detection of linear streams, which are important waterfowl habitats in Quebec forests, still necessitates the use of air photo interpretation (Ozesmi and Bauer 2002). However, other important habitats such as narrow fringes of emergent plants along shorelines, emergent rocks, or small bog ponds, could have been overlooked due to our minimum mapping area conventions. Probably more important are wetland dynamics that were induced by beaver activity, producing changes in the landscape between when the aerial photos were taken and when the waterfowl surveys were conducted. At frequencies and in locations that we could not record, impoundments appeared where small streams ran through open wetlands, streams became river-wide, and water body shorelines were redefined. This could explain why a species like the green-winged teal, which is known to use beaver flowages immediately after dam building (Nummi and Pöysä 1997), was not more closely associated to flooded swamps. Another potential weakness of our habitat classification lies in the definition of the open wetland class, which did not allow us to distinguish shorelines of floating riparian fens from marshes with emergent plant cover. Although it could be considered somewhat coarse, our wetland habitat classification relied on existing numerical data, which made it cost-effective. Forestry maps are also widely used by forestry stakeholders, and therefore, constitute an excellent planning tool upon which habitat management decisions can be based.

Errors undoubtedly occurred in the different steps of this species-habitat analysis. Apart from wetland identification and mapping, uncertainty could stem from survey timing, breeding pair detection and location. To survey all species within the appropriate survey window—after migrants have left and before mate desertion occurs—in a single survey is impossible. Our results, therefore, must be interpreted with caution, especially those for late breeding species such as scaup, scoters, and red-breasted merganser (Bordage et al. 2003) because these species may not have yet become established in their nesting habitat. Furthermore, detection probability was expected to be lower in small and structurally complex wetlands, and for small or secretive species. However, regarding differential detectability rates among habitats, breeding pair surveys occurred before leafing-out. Unlike other aerial survey methods, birds do not tend to hide upon the approach of helicopter (Ross 1985). Also, according to IBP criteria, females that were concealed or sitting on nests could be inferred by the presence of lone males. With respect to pair location, a potential bias may have occurred when employing the pairhabitat association rules, due to mapping precision $(\pm 100 \text{ m})$. However, we developed the algorithm to reduce bias as much as possible, thus ordering habitat association according to likely habitat preferences in waterfowl (open water areas > streams > open wetlands), and within areas likely included within pair home ranges. Despite the sequence used, our estimates of stream use (18.3% of all IBPs) relative to open water areas is amongst the highest reported, and would have been greater (22.7% of IBPs) if each pair had been assigned to the closest aquatic habitat. Finally, we consider that assigning each pair to the closest habitat would create an even greater bias than the one introduced by our algorithm. Therefore, despite these potential weaknesses, we suspect that our habitat association measurements are not strongly biased.

Wetland Conservation Implications

Within the scope of environmental changes in wetlands, whether from climate change or human activity, results of waterbird habitat use presented here may act as a benchmark for future environmental monitoring. We also suggest that habitat use could be considered a basis for broad-scale management decisions while habitat selection should be a basis for population or habitat restoration. Wetlands that were most selected by breeding pairs are likely to be more appropriate for local conservation or restoration efforts, whereas most utilized wetlands deserve consideration when planning at broad regional scales. For example, in the case of cavity-nesting duck species, state/ provincial forest management guidelines could include conservation measures such as cavity tree retention when harvesting stands located in the vicinity of the wetland types that are highly used by these species. At a broader scale, our results could aid decision-making by improving predictions about likely impacts of development activities (e.g., loss of wetlands to hydro-electric or other developments) or conservation actions (wetland restoration or

protection); however, actual impacts should be evaluated objectively using follow-up monitoring.

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