Unequal summer use of beaver ponds by river otters: influence of beaver activity, pond size, and vegetation cover

F.A. LeBlanc, D. Gallant, L. Vasseur, and L. Léger

Abstract: River otters (*Lontra canadensis* (Schreber, 1777)) and beavers (*Castor canadensis* Kuhl, 1820) are semi-aquatic mammals that can occur sympatrically in freshwater ecosystems of North America, including beaver ponds. Although little research has been done on the relationship between these species, it has been described as commensal. Relatively little is known about what pond characteristics potentially influence otter use. During the summer of 2004, we documented otter activity signs (i.e., feces) at 56 beaver ponds located in Kouchibouguac National Park of Canada, along the east coast of New Brunswick. We sought to identify which of 16 variables describing pond attributes were related to otter use. Otter activity at beaver ponds was positively associated with beaver presence, pond size, and vegetation cover. We discuss how these pond characteristics can benefit otters in terms of two key habitat needs, availability of prey and shelter. Our results are a first indication that the source–sink dynamic of beavers, whereby ponds are created, expanded, and abandoned, will create a mosaic of ponds that ultimately influences the river otter's own pattern of habitat use and distribution.

Résumé : La loutre de rivière (*Lontra canadensis* (Schreber, 1777)) et le castor (*Castor canadensis* Kuhl, 1820) sont deux mammifères semi-aquatiques d'eau douce dont les distributions géographiques se chevauchent largement sur le continent nord-américain. Il est souvent évoqué que les loutres utilisent les étangs de castors, à titre de commensales. Très peu d'études ont été consacrées à la relation entre ces deux espèces. Nous connaissons peu les caractéristiques des étangs que les loutres sélectionnent. Au cours de l'été 2004, nous avons observé les signes d'activité (c.-à-d., fèces) de loutres autour de 56 étangs de castors dans le Parc national du Canada Kouchibouguac, sur la côte Est du Nouveau-Brunswick. L'objectif était d'identifier lesquelles de 16 variables descriptives des étangs influencent l'utilisation par les loutres. L'activité des loutres aux étangs est liée positivement à la présence de castors, à la taille des étangs et au couvert végétal. Nous discutons comment ces caractéristiques sont bénéfiques pour la loutre en ce qui a trait à deux besoins fondamentaux, soit la disponibilité de proies potentielles et de refuges. Nos résultats constituent une première indication que la dynamique spatio-temporelle des castors (c.-à-d., création, développement et abandon d'étangs) produit une mosaïque d'étangs aux caractéristiques différentes qui peuvent influencer la loutre au niveau de sa sélection de l'habitat et sa distribution spatiale.

Introduction

The river otter (*Lontra canadensis* (Schreber, 1777)) is a semi-aquatic mammal that has a continent-wide distribution in North America (Larivière and Walton 1998). This top-level predator in freshwater ecosystems has two basic habitat needs, accessibility to prey and shelter (Melquist and Hornocker 1983; Melquist and Dronkert 1987). They have a diverse diet, of aquatic preys consisting principally of fish (Greer 1955; Bowyer et al. 1994). River otters do not dig their own burrows but will depend mostly on those created by other animals (Melquist and Hornocker 1983).

The beaver (*Castor canadensis* Kuhl, 1820) is another semi-aquatic mammal with a continent-wide distribution (Jenkins and Busher 1979) and occurs sympatrically with river otters in most of its range. It is a species that exerts diverse and profound influence on freshwater ecosystems, as well as on the aquatic–terrestrial interface of terrestrial ecosystems. So much so, that it is considered an ecosystem engineer (Wright et al. 2002, 2004; Bailey et al. 2004). For example, by their creation of ponds by means of dam building, they modify the abundance and diversity of animal species in terrestrial and aquatic communities (Naiman et al. 1988; France 1997; Edwards and Otis 1999; Russell et al. 1999; Schlosser and Kallemeyn 2000). For a thorough review of the ecological impact of beavers, see Rosell et al. (2005).

For decades, researchers have reported that river otters use beaver ponds (Green 1932; Greer 1955; Melquist and Hornocker 1983; Dubuc et al. 1990; Newman and Griffin 1994; Reid et al. 1994*a*; Swimley et al. 1998) as a source of prey and shelter (i.e., lodges and burrows created by beavers). However, little else is known about the relationship

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between the beaver and the river otter. In one of the rare researches dedicated to the study of this relationship, Reid (1984) documented the effect of the river otter's dam-rifting behaviour on winter water levels in ponds and also determined that river otters more frequently used inactive rather than active beaver lodges and burrows for shelter in winter. Tumlison et al. (1982) were the first to propose that river otters and beavers were in a commensal relationship, with otters being the beneficiary and beavers not being advantaged or disturbed in any considerable way. Apparently, interactions between the two species are rarely agonistic (Melquist and Hornocker 1983; Reid 1984) and beaver is a very rare component of the river otter's diet (Greer 1955; Reid 1984; Reid et al. 1994*b*).

Reid (1984) observed that some of the beaver sites and ponds in his study area were rarely or never visited by otters. This might be due to ponds being very different from one another, as a consequence of change in their attributes over time. Beavers have diverse diets (Roberts and Arner 1984) but are nonetheless selective foragers in many regards (Gallant et al. 2004). Their preference for particular deciduous species of trees and their tendency to avoid conifers (Donkor and Fryxell 2000; Gallant et al. 2004) make them potential agents of accelerated forest succession along rivers, streams, and lakes by favouring the dominance of conifers (Donkor and Fryxell 1999, 2000; Barnes and Mallik 2001). As an active beaver pond ages, vegetation characteristics at the site change and the pond will get larger because beavers will build up the dam and flood a wider area, gaining better access to other potential food sources as those near the edge of what was the original pond become depleted. Eventually, unless there are aquatic plants that can serve as an additional food source (Svendsen 1980; Fryxell 2001), the pond site will no longer sustain the nutritional needs of beavers because they locally deplete preferred food species such as aspens (genus *Populus* L.) and willows (genus *Salix* L.) (Hall 1960). They will abandon the site (Fryxell 2001) and disperse to colonize other suitable areas (Barnes and Mallik 1997). The unmaintained dam will no longer hold water; the abandoned pond will eventually dry up and the watercourse will resume its original bed (Bradt 1938), resulting in a fertile meadow replacing the pond (Wright et al. 2002). This process of pond creation, development, and eventual abandonment by beavers creates a mosaic of different ponds that will not all offer the same potential benefits to river otters with regard to shelter and prey availability.

Recovering, reintroduced, or endangered river otter populations in North America are under intense scrutiny (e.g., Raesly 2001; Pitt et al. 2003). Therefore, it is important to gain basic knowledge on how the spatiotemporal dynamics of a key species such as the beaver (Fryxell 2001; Wright et al. 2004) may influence the river otter's habitat use in a region. Based on the dynamic nature of beaver pond attributes (Wright et al. 2004), we predicted that river otters would make unequal use of beaver ponds during summer, provided that these ponds differ in characteristics and, consequently, with regard to river otter prey and shelter. The objective of this study was to determine whether there were relations between pond attributes and usage by river otters.

Materials and methods

Study area

The study was conducted in Kouchibouguac National Park of Canada, which is situated on the east coast of New Brunswick (Fig. 1) and covers 238.8 km^2 (Desloges 1980). The territory was representative of the lowlands of the Maritime Plains, with flat topography supporting bogs and swamps (Dubois et al. 1997). The park contained eight major watersheds (from north to south): Portage River, Polly's Brook, Fontaine River, Black River, Rankin Brook, Kouchibouguac River, Major Brook, and Kouchibouguacis River (Desloges 1980). The Kouchibouguac and Kouchibouguacis rivers were tidal (Desloges 1980).

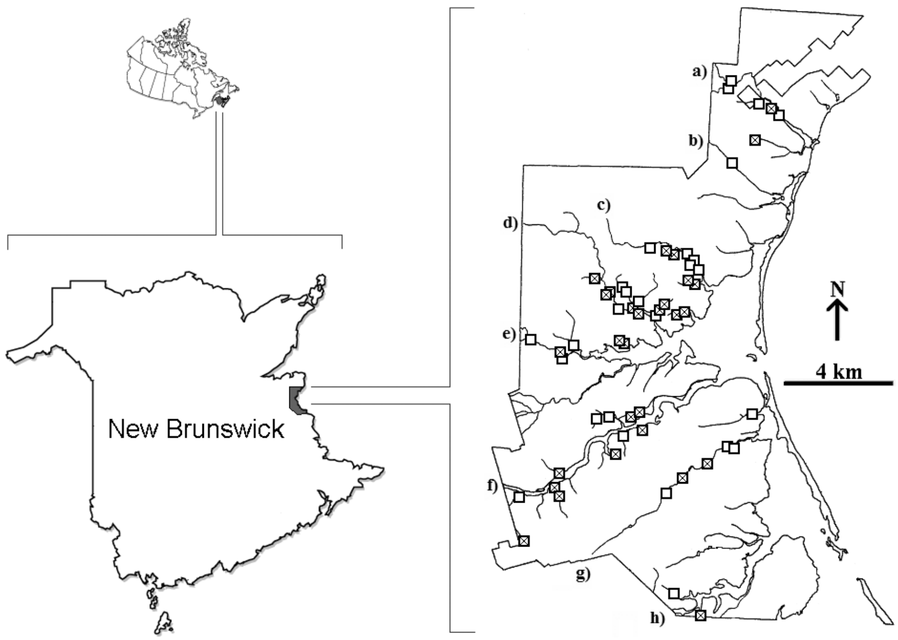
Since the park's creation in 1969, the protected beaver population within its borders increased from 21 active beaver sites in 1971 to 89 active sites in 1993 (Dubois et al. 1997). In 2002, 52 active beaver sites were counted (Léger 2004). Their distribution within the watersheds also varied in time. In 1993, they were located more upstream in the watercourses of the park in comparison with the 1973–1977 period (Dubois et al. 1997; Léger 2004). With as many as 137 inactive beaver sites also counted in 2002 (Léger 2004), the park's territory constituted a mosaic of beaver ponds in various conditions within which we could study what pond characteristics may influence river otter usage. It has also been demonstrated that river otters were present in all watersheds of the park and that beaver ponds were among the most important habitat characteristic they selected in the park (Gallant 2006).

Beaver pond site selection

Beaver ponds used in our study were selected from the 2002 beaver census conducted in the park (Léger 2004). From the 189 colonies in the 2002 database, we preemptively eliminated from the database 67 colony sites that were either too remote or without dams and, hence, without beaver ponds to study. We also did not consider nine colony sites for which the active–inactive status was uncertain. This left 41 active and 81 inactive potential beaver colony sites with ponds to study. We randomly selected 41 inactive sites to study with the 41 active sites to consider an equal number of colonies of both statuses. We randomly selected a particular number of inactive sites per river or tributary so that inactive and active sites were equally represented in a given river. After an initial field visit, we were constrained to eliminate 32 of the 82 sites initially selected because ponds could not be found or did not exist anymore. Some ponds had changed status since 2002. To obtain an equal number of active and inactive sites to the extent possible, we added three known active sites that did not exist in the 2002 database and randomly selected additional inactive sites accordingly. A total of 56 beaver ponds made the final selection (Fig. 1), with 29 of them having active beaver colonies.

Only four ponds changed status during the course of the study (summer 2004). Three active beaver sites were abandoned and one abandoned pond was recolonized by beavers. For these four ponds, the original statuses determined early in the season were not changed for statistical analyses because other than the beavers leaving in the middle of

Fig. 1. Illustration of the watersheds of central and northern regions of Kouchibouguac National Park of Canada with 27 open boxes representing ponds abandoned by beavers (*Castor canadensis*) and 29 marked boxes representing ponds hosting beavers, totalling 56 ponds chosen to search for river otter (*Lontra canadensis*) feces in summer 2004 (map adapted from Dubois et al. 1997). Watercourses with sampled beaver ponds are (*a*) Portage River, (*b*) Ruisseau à Pierrot Brook, (*c*) Carrigan Brook, (*d*) Fontaine River, (*e*) Black River, (*f*) Kouchibouguac River, (*g*) Major Brook, and (*h*) Kouchibouguacis River.



summer, other characteristics of these four ponds would not have changed in the short term.

River otter habitat use

We studied river otter habitat use indirectly by documenting activity signs that they typically leave (i.e., feces deposition) along the banks. River otters concentrate their deposits of urine, feces, and anal secretions at latrine sites. Thus grouped, they constitute conspicuous signs of river otter activity in an area (Mombray et al. 1976). Latrine sites have been defined as a group of two or more feces (Swimley et al. 1998) situated at a metre or more from other feces (Kruuk et al. 1986). According to Bas et al. (1984), the number of feces is a better indicator of otter activity levels than the number of latrine sites.

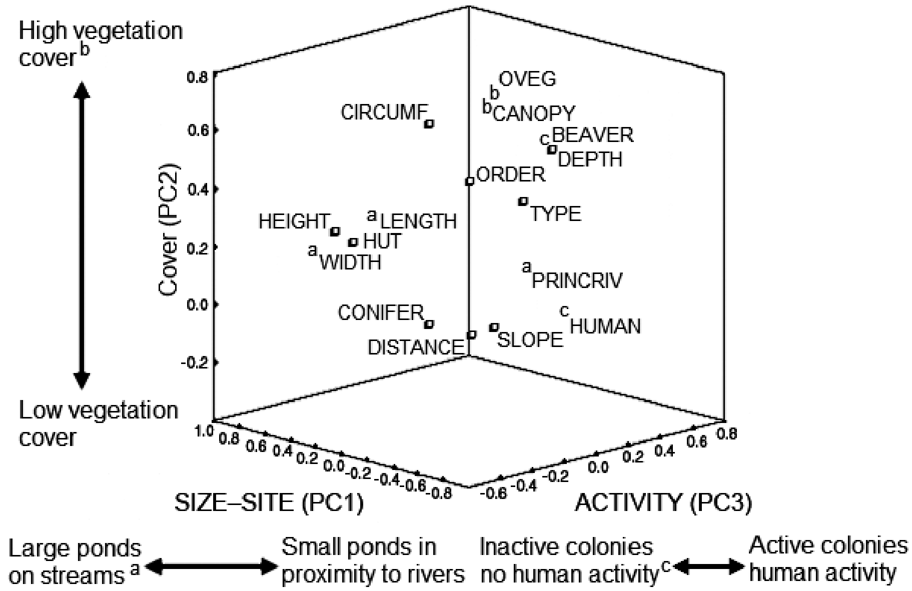
We used the abundance of feces found around beaver ponds as an index of the degree of utilization of particular ponds by river otters. In June, July, and August 2004, we conducted three systematic surveys of the 56 selected beaver ponds and counted all feces detected. Around each pond, we scrutinized within a 4 m band from the pond's edge. This was judged sufficient to document most feces because they were mostly found within a few metres of the water (Swimley et al. 1998). After each search, all feces found were crushed where they were located to avoid recounting the same feces during subsequent searches (Newman and Griffin 1994). We considered that river otters were absent or did not use a pond when no feces were detected around it during the three searches (Lodé 1993). This method of documenting activity levels permitted the maximization of the number of ponds that we could visit. Abundant feces at a pond could be produced by many otters (e.g., large family group) having used the pond site for a short time, or a small number of otters having continuously used the pond for an extended period of time. Therefore, we interpreted fecal counts as an index of habitat use, not as an abundance index.

Habitat characterization

The status of each pond was revised by characterizing them as having or lacking resident beavers (factor: BEAVER). We determined this by searching each pond for signs of beaver activity, such as high water levels, well-maintained lodges and dams, recently cut woody stems, and fresh territorial mounds, as well as beaver sightings. This inspection was done each time we visited a pond. We recorded the location of each beaver pond with a portable geographical positioning system (GPS Garmin 12-XL), and noted for each pond the watershed to which it belonged and whether it was situated upstream in a tributary or in proximity to principal rivers of the study area (factor: PRINCRIV). We also noted the presence–absence of beaver lodges at each pond (factor: LODGE). We measured the distance (in metres) separating each pond from respective rivers where the concerned tributary empties (factor: DISTANCE). We used the type and size categories of watercourses associated to each pond (factors: TYPE and ORDER, respectively) from Léger (2004) and Desloges (1980).

We measured the circumference (in metres) of each pond with a hip chain (factor: CIRCUMF). Data on length, width, and height of beaver dams (in metres) were taken from Léger (2004) (factors: LENGTH, WIDTH, and HEIGHT, respectively). We measured these variables ourselves with a measuring tape as in Léger (2004) for ponds not present in the 2002 census. We also measured water depth (in metres) at four locations in each pond with a wooden metre stick

Fig. 2. Distribution of loadings for 16 factors representing habitat characteristics at 56 beaver ponds in Kouchibouguac National Park of Canada relative to three principal components (PCs) obtained from the principal component analysis (PCA). Superscript letters indicate which factors constitute a specific PC.



(factor: DEPTH). The locations were at each extremity of the dam and at each side of the tributary on the side of the pond opposing the dam. We calculated a mean from the four measurements for each beaver pond.

We used estimations of percent conifer around beaver ponds (factor: CONIFER) from Léger (2004), who recorded respective percentages of observed woody species for a radius of approximately 50 m, with beaver dams as the reference point. We measured the percentage of canopy closure using a model-A densiometer (R.E. Lemmon, Forest Densiometers©, Bartlesville, Oklahoma) at the same four points where we measured water depth and calculated a mean for each pond (factor: CANOPY). We also noted the relative abundance of overhanging vegetation at each pond (absent, a few trees, or abundant) (factor: OVEG). The mean slope of the banks at each pond was obtained from Léger (2004), who visually categorized it as being weak, moderate, or steep (factor: SLOPE). We noted the presence of all human disturbances encountered within 50 m of ponds (factor: HUMAN). These disturbances in the park are roads, cycling trails, and hiking trails.

Statistical analyses

To determine whether temporal variations in the number of feces deposited by river otters at each pond existed, Friedman's test was performed to compare data from the three rounds of visits made at each pond. We used a Mann–Whitney test to compare river otter usage (i.e., fecal counts) in active versus inactive beaver ponds. To determine how other pond attributes and habitat characteristics around them influence river otter usage, we first used principal component analysis (PCA) to obtain components. Such factorial groups of variables represented the principal tendencies in our data, which implicated intercorrelated variables. We then used the scores of these principal components as explanatory variables and tested their potential correlation with river otter usage of beaver ponds. We applied forward stepwise multiple regressions with total fecal counts at each beaver pond as the response variable. We also used the presence–absence of feces as a response variable in logistic regressions. Analyses were done using SPSS® for Windows version 11.5 (SPSS Inc. 2002) and α = 0.05 as the significance level chosen to consider effects as being statistically significant.

Results

During the course of the summer, a total of 1186 feces were found around visited beaver ponds. A total of 384 feces were found during the first round of visits conducted in June, while 442 and 360 feces were found during subsequent rounds of visits in July and August, respectively. Friedman's test revealed that there was no statistically significant difference in the number of feces found during the three rounds of visits for each individual pond ($\chi^2_{[2]}$ = 4.705, p = 0.095, n = 56). Subsequent analyses were thus conducted with data from all three visits summed together to represent otter usage of beaver ponds over the course of the entire summer.

The abundance of river otter feces was significantly higher at active beaver ponds (92.16% of feces) than at inactive ones (7.84% of feces; U = 231.500, p = 0.006, n = 29 active ponds + 27 inactive ponds). Six principal components were obtained through PCA to identify principal tendencies in our data, of which three were important and had highly correlated variables (Fig. 2). The first principal component (SIZE–SITE, 18.16% of total variance) represented three significantly intercorrelated variables. Location of ponds (in tributary streams or in proximity to rivers) was negatively correlated to both the length and width of the dams (Table 1, Fig. 2). Beaver ponds vary in size and shape; they can range from shallow and spread over a large area to deep and narrow. The three-dimensional aspects of pond sizes are a combined effect of the size of dams and the topography of concerned watersheds. Our pond circumference

Table 1. Loadings of 16 factors describing beaver (*Castor canadensis*) pond characteristics and their surroundings in Kouchibouguac National Park of Canada relative to three PCs obtained by applying PCA.

Factor	SIZE–SITE (PC1)	COVER (PC2)	ACTIVITY (PC3)
DISTANCE	0.479	–0.214	0.406
PRINCRIV[a]	–0.730	0.251	–0.218
BEAVER[c]	0.234	0.442	0.668
ORDER	–0.333	0.500	–0.254
TYPE	–0.501	0.425	–0.061
LODGE	0.512	0.204	–0.314
HEIGHT	0.323	0.301	–0.584
LENGTH[a]	0.753	0.218	–0.012
WIDTH[a]	0.523	0.212	–0.573
CIRCUMF	0.423	0.567	0.091
OVEG[b]	0.085	0.705	0.235
DEPTH	–0.364	0.547	0.233
CANOPY[b]	0.044	0.669	0.163
SLOPE	–0.182	–0.058	0.018
CONIFER	0.406	–0.124	0.077
HUMAN[c]	0.040	–0.127	0.631

Note: See text for factor definitions.

[a]Factors that constitute the SIZE–SITE (PC1) component.

[b]Factors that constitute the COVER (PC2) component.

[c]Factors that constitute the ACTIVITY (PC3) component.

Table 2. Results of forward stepwise multiple regressions testing selectivity of river otters (*Lontra canadensis*) towards 56 beaver ponds in Kouchibouguac National Park of Canada according to factorial groups of variables obtained with PCA.

Factor	b^a	SE	p
Constant	21.145	6.825	0.003
SIZE–SITE	19.009	6.687	0.008

Note: $F_{[54,54]} = 7.617$, $p = 0.008$; $R^2 = 0.126$.

[a]The dependent variable tested was the number of feces at respective beaver ponds.

Table 3. Results of a logistic regression testing selectivity of river otters towards 56 beaver ponds in Kouchibouguac National Park of Canada according to factorial groups of variables obtained with PCA.

Factor[a]	b^b	SE	Wald's statistic	p
Constant	0.330	0.362	0.833	0.361
SIZE–SITE	1.347	0.462	8.497	0.004
COVER	1.137	0.453	6.287	0.012

Note: $\chi^2_{[1]} = 16.274$, $p = 0.012$; $R^2 = 0.342$.

[a]Factors were entered in a single step.

[b]The dependent variable tested was the presence–absence of feces at respective beaver ponds.

measurements were correlated to the width and length of dams but to a smaller degree (SIZE–SITE component, Table 1), indicating an influence of topography. Therefore, the aspect of pond size that the SIZE–SITE component represents is mainly the size of the impoundment, as linked to dam dimensions, and less so with regard to the surface area of ponds. The second principal component (COVER, 16.00% of total variance) represented two strongly positively correlated variables, overhanging vegetation and canopy cover (Table 1, Fig. 2). The third principal component (ACTIVITY, 12.78% of total variance) represented two correlated types of activity at the pond sites, the presence of beavers (active ponds) and anthropogenic disturbances such as roads, cycling trails, and hiking trails (Table 1, Fig. 2).

When considering total fecal counts at respective beaver ponds as an index of use by river otters, multiple regressions indicated that the first component (size and location of beaver ponds) had a statistically significant influence on the degree of use by river otters (Table 2). More feces were found at large ponds located farther inland on streams, as opposed to smaller ponds in proximity to major rivers. When considering presence–absence of feces as an indication of usage or avoidance of particular ponds by river otters, logistic regressions indicated that not only size and location of ponds but also vegetation cover around them had a statistically significant influence on whether or not a given pond will be frequented by river otters (Table 3). River otters more readily frequented ponds that had more vegetation cover around them.

Discussion

Our finding of greater river otter activity in ponds hosting resident beavers is consistent with previous work by Dubuc et al. (1992), who found that river otters used watersheds that had active beaver ponds and avoided those that did not. However, our findings show that river otters will not necessarily avoid inactive beaver ponds. Reid (1984), in the boreal ecoregion of Alberta, found that in winter river otters mainly used inactive beaver lodges and burrows. This contrasts with our summer results that link river otter activity with active beaver ponds mostly. It is possible that river otters spend more time in inactive ponds in winter to take advantage of vacant lodges and burrows for shelter from the elements (Reid 1984), while our summer study may have principally documented otter activity related to prey acquisition in active, well-maintained beaver ponds.

Well-maintained dams will impound the flow of water and create stable water reservoirs (Alexander 1998), which is a key environmental attribute for semi-aquatic animals such as otters (Dubuc et al. 1990; Barbosa et al. 2001; Prenda et al. 2001). Upon hearing water flowing through the dam, beavers will instinctively seek to clog holes and repair dams (Reid 1984) that would otherwise gradually deteriorate. Tumlison et al. (1982) argued that beaver ponds having higher water levels (i.e., active ponds) facilitate hunting for river otters. The hunting behaviour of otters involves diving in pursuit of prey (Beckel 1990; Ben-David et al. 2000; D. Gallant, personal observation) and sufficiently deep water is necessary for this behaviour (Tumlison et al. 1982). Active ponds with maintained dams offer deeper water levels than neighbouring non-impounded stream sections. Water current in beaver ponds is weaker because of the dam and this permits sedimentation (Gard 1961; Allred 1980). The lentic environment created by beavers (i.e., ponds) constitutes a good habitat for slow-swimming fish species that will be potentially easier to catch for river otters (Melquist and Hornocker 1983).

Prey availability is among the most important factors that define habitat use by river otters (Melquist and Hornocker 1983). Ponds with dams maintained by beavers constitute habitats that can be beneficial to organisms preyed upon by river otters. The biomass of benthic organisms in active beaver ponds can be very high compared with non-pond habitats (Gard 1961; McDowell and Naiman 1986). Aquatic insects lay eggs in beaver ponds, which will have plenty of food for emerging larvae (Alexander 1998). These insects may be eaten by otters (Greer 1955) or by species that fall prey to otters, such as brook trout (*Salvelinus fontinalis* (Mitchill, 1814)), which can be found in beaver ponds (Alexander 1998). This abundance of biomass in small organisms, coupled with higher and more stable water temperatures (Gard 1961; Alexander 1998), might explain why fish growth (Alexander 1998) and total biomass of fish (Gard 1961) in active beaver ponds can be higher than in adjacent habitats. There can also be concentrations of fish at the bottom of active beaver ponds during periods of low water levels in rivers (Swimley et al. 1998). This fish abundance appears to be linked to ponds having beavers that keep dams functional. For example, Gard (1961) documented large declines of species such as brown trout (*Salmo trutta* L., 1758) and brook trout following removal of beaver dams by a flood. However, there can be adverse effects of beaver ponds on some fish species (reviewed in Collen and Gibson 2001). For example, dams hinder movements of migratory fish and water temperature in ponds can become too high for cold-water fish species.

Other than activity status of beaver ponds, our results revealed that otters frequented larger ponds more than smaller ponds. As beaver ponds age, they will get progressively larger because beavers will build up and extend the dam, which increases water impoundment. Larger, older beaver sites could have more lodges and underwater burrows built, which otters can use. An example of this in our study area was an old, well-established active beaver site that had three lodges built in the same pond. The other potential benefit of larger, older ponds is in the availability of prey. Schlosser and Kallemeyn (2000) found that ponds with a large, deep body of water had the largest abundance of fish. Snodgrass and Meffe (1998) were able to document a shift from lotic to lentic species of fish in older beaver ponds, as well as a shift towards larger predatory fish in larger ponds. Both slow swimmers and larger fish are potentially easier to capture for river otters. As beaver ponds age and get larger, they potentially become sources of abundant or easy prey.

Large ponds in our study were not located in the same type of environment as small ponds, as was shown by the SIZE–SITE principal component obtained through PCA. Of the 56 ponds that we studied, the largest ones tended to be in tributary streams and the smallest ones were situated adjacent to major rivers of the park. The portions of rivers within the borders of Kouchibouguac National Park of Canada (Fig. 1) constitute estuarine habitats (Desloges 1980). River otters will frequently use these productive regions (Gallant 2006). Ponds situated in proximity to these habitats were less used by river otters compared with those located away from major rivers. River otters are very mobile, with seasonal home ranges ranging from several tens of square kilometres (Melquist and Hornocker 1983; Bowyer et al. 1995) to over one or two hundred square kilometres (Reid et al. 1994*a*). The location of ponds in our study area of limited geographical scale is not a factor that would have limited their accessibility. Consequently, it is likely that the size of beaver ponds was the element in the SIZE–SITE principal component responsible for the statistically significant correlation that we observed.

Vegetation cover (overhanging vegetation and canopy closure) was a factor influencing whether otters frequented a given pond or not. Otter selection of sites with vegetation cover along shorelines has also been reported in other studies (Bowyer et al. 1995; Madsen and Prang 2001). According to Jenkins and Burrows (1980), vegetation cover along riverbanks is among the most important factors influencing otter occurrence. River otters are top-level predators in aquatic systems, but as specially adapted semi-aquatic mammals, they are less agile on land and may fall prey to various terrestrial predators such as bobcats (*Lynx rufus* (Schreber, 1777)), eastern cougars (*Puma concolor couguar* (Kerr, 1792)), coyotes (*Canis latrans* Say, 1823), dogs (*Canis familiaris* L., 1758), and wolves (*Canis lupus* L., 1758) (reviewed in Larivière and Walton 1998). Vegetation can provide cover for otters when they have to access terrestrial burrows (Melquist and Hornocker 1983; Reid et al. 1994*a*) or travel from one tributary to another. Patches of dense vegetation can also be used as shelter from the elements (Jenkins and Burrows 1980; Bowyer et al. 1995) and otters can even use such patches as natural den sites under which to rest, even in winter (D. Gallant, personal observation). Also, having overhanging vegetation around beaver ponds will reduce water temperature fluctuations, especially during warmer months. Cover can thus be beneficial to fish that constitute potential prey for otters (Kozel and Hubert 1989; Durbin 1998).

Our variable of percent conifers around beaver ponds did not explain important differences in our study. Others reported that conifers provide cover used by otters (Newman and Griffin 1994; Bowyer et al. 1995; Swimley et al. 1998). Their importance may be diminished when beaver ponds are considered rather than riparian habitats in general. Beaver burrows and lodges already provide excellent shelter opportunities and beavers tend to be associated to deciduous species (Fryxell 2001). However, conifers in our study are also represented in variables such as overhanging vegetation and direct measurements of canopy closure (second principal component), which better documented vegetation cover at the aquatic–terrestrial interface.

It appears controversial that river otter activity is associated with vegetation cover around ponds while beavers cut down trees around them. Beavers do not necessarily create barren lands. They are selective generalists that use few trees of species less palatable to them such as conifers (Donkor and Fryxell 2000; Gallant et al. 2004) and deplete preferred species such as quaking aspen (*Populus tremuloides* Michx.) (Hall 1960; Barnes and Mallik 2001). They also cut less-palatable deciduous species such as red maple (*Acer rubrum* L.) (Doucet and Fryxell 1993; Gallant et al. 2004), possibly in reaction to depletion of preferred woody species (Fryxell and Doucet 1993). Least cut and avoided species have an advantage in terms of persistence and regeneration, potentially leading to their dominance (Donkor and Fryxell 1999, 2000; Barnes and Mallik 2001). Sometimes, preferred species persist and community structure does not totally convert to nonpreferred species. McGinley and Whitham (1985) documented this for cottonwood (*Populus fremontii* S. Wats.), where browsing by beavers caused them to regenerate into a bushier structure.

This study contributes information on a possible commensal relationship between two vertebrates. Commensal relationships are rarely reported or studied outside of marine environments (e.g., Caley et al. 2001; Edgurton et al. 2002; Browne and Kingsford 2005) and microbial flora of digestive tracts (e.g., Hentschel et al. 2003; DeFrancesco et al. 2004), where it is more common. Our results have possible implications for understanding river otter population and distribution dynamics in beaver-dominated aquatic systems. Because beaver pond attributes influence river otter habitat use, this suggests that the source–sink dynamics of beavers (Wright et al. 2004) may influence the river otter's own pattern of habitat use and distribution. Our summer results, coupled with the winter findings of Reid (1984), expose the possibility that there also may be a seasonal dynamic in the way river otters use beaver ponds, and support Reid's (1984) conclusion that river otters benefit from regions that have a history of beaver occupations, with both active and inactive beaver sites. To contribute further knowledge about the relationship between these two species, future studies should have a long-term scope and aim to directly document the dynamics of beavers and the ponds that they create, as well as how this influences the actual dynamics of river otters in terms of population fluctuations and patterns of habitat use. Such studies will have to take advantage of available long-term survey data on both species for a given area where they occur sympatrically.

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