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Building for the future: Abandoned beaver ponds promote bird diversity[1]

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Abstract: We examined beaver (*Castor canadensis*) pond dynamics and associated riparian bird communities, based on call-response surveys. Following water disappearance, abandoned beaver ponds were invaded by grassy areas and alder shrubs and supported higher bird species numbers than nearby riparian areas. We detected a total of 49 species. At abandoned beaver ponds, the mean number of species was 6.4, whereas it ranged between 2.4 and 3.1 species for active beaver ponds, rivers, and lakes. Density of deciduous shrubs and graminoid cover, higher in abandoned beaver ponds, was positively associated to the number of species of birds. However, riparian avian diversity was lower near clearcuts and large water areas. Beaver population control or geographic confinement may suppress both spatial and temporal dynamics of beaver pond creation and abandonment, and could impact riparian vegetation and birds.
Keywords: beaver pond dynamics, *Castor canadensis*, forestry, logging, Québec, species richness, songbirds.

Résumé : Nous avons examiné la dynamique d'étangs de castors (*Castor canadensis*) et les communautés d'oiseaux riverains à partir de relevés de type appel-réponse. Après la disparition de l'eau, les étangs de castors abandonnés ont été envahis par des herbes et des arbustes d'aulne et supportaient un plus grand nombre d'espèces d'oiseaux que les aires riveraines des alentours. Nous avons détecté 49 espèces au total. Dans les étangs de castors abandonnés, le nombre moyen d'espèces était 6.4 et ce nombre variait de 2.4 à 3.1 pour les étangs de castors actifs, les rivières et les lacs. La densité d'arbustes feuillus et la couverture de graminées étaient plus élevées dans les étangs de castors abandonnés, elles étaient aussi associées positivement au nombre d'espèces d'oiseaux. Cependant, la diversité aviaire riveraine était inférieure près de coupes totales et de grandes étendues d'eau. Le contrôle des populations de castors ou leur restriction géographique pourraient faire disparaître la dynamique spatiale et temporelle associée à la création et à l'abandon d'étangs de castors et ainsi avoir un impact sur la végétation riveraine et les oiseaux.
Mots-clés : *Castor canadensis*, coupe forestière, dynamique d'étangs de castor, foresterie, oiseaux chanteurs, Québec, richesse en espèces.

Nomenclature: Gauthier & Aubry, 1996.

Introduction

Disturbance plays a central role in determining the spatial and temporal dynamics of plant and animal communities (Sousa, 1984; Pickett & White, 1985). The interfaces between terrestrial and aquatic ecosystems, the riparian areas, are subject to disturbances that produce irregular patches of vegetation and control plant species composition and biodiversity (Naiman, Decamps & Pollock, 1993; Miller *et al.*, 1995; Scott, Auble & Friedman, 1997). Periodic fluvial disturbances by flooding and migration of the channel and meanders of the river (Gregory *et al.*, 1991) help sustain ecosystem integrity of flowing water systems (Karr, 1991; Poff *et al.*, 1997; Shafroth, Stromberg & Patten, 2002). Riparian areas are also modified by non-fluvial disturbances such as resource exploitation by humans, fire, wind, insect outbreaks, and herbivory by large mammals (Peinetti, Kalkhan & Coughenour, 2002).

In northeastern America, beavers induce major disturbances to the hydrology and vegetation patterns in 20–40% of the total length of second- to fifth-order streams (Ford & Naiman, 1988). Heavy trapping pressure in the past led to extirpation of beaver populations, but in recent decades, beavers have increased in northeastern America (Ingle-Sidorowicz, 1982; Naiman, Johnston & Kelley, 1988; Rosell *et al.*, 2005). Selective foraging by beaver themselves decreases habitat suitability and in turn induces site abandonment (Fryxell, 2001). In boreal forests, dynamics of beaver populations result in a diversity of successional pathways, leading to the formation of emergent marshes, bogs, and forested wetlands, depending on existing vegetation, hydrology, topography, fire, disease, and herbivory (Naiman, Johnston & Kelley, 1988).

Along riparian corridors, vegetation is typically denser, has a more complex structure, and supports a greater number of plant and animal species than in the neighbouring upland forest (Gregory *et al.*, 1991; Naiman, Decamps & Pollock, 1993). Beavers act as a keystone species or "habitat engineers" by increasing the area and modifying the structure of riparian habitat (Remillard, Gruendling & Bogucki, 1987; Naiman, Johnston & Kelley, 1988). Beaver ponds affect communities of aquatic plants (Hill, 1982; Ray, Rebertus & Ray, 2001), invertebrates (McDowell &

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Naiman, 1986), fish (Snodgrass & Meffe, 1998; Schlosser & Kallemeyn, 2000; Collen & Gibson, 2001), amphibians (Skelly & Freidenburg, 2000; Metts, Lanham & Russell, 2001), and mammals (Hill, 1982; Peinetti, Kalkhan & Coughenour, 2002). Several authors have reported that open water areas provide habitats for waterfowl (Nummi, 1992) and densities can be up to 5 times higher in beaver-dominated areas (McKinstry, Caffrey & Anderson, 2001). Grover and Baldassare (1995) and Medin and Clary (1990) reported increased diversity of nesting birds near active beaver ponds relative to riparian areas unused by beaver or abandoned ponds. These 2 studies thus suggest that benefits of beaver ponds to birds are of short duration, despite lasting changes in riparian vegetation associated to beaver ponds.

The effect of beaver ponds on associated wildlife may change in the presence of clearcutting and associated buffer strips. The latter, often found alongside beaver ponds, are thought to limit adverse effects of harvesting practices on water quality, aquatic habitat, and wildlife (Whitaker, Carroll & Montevecchi, 2000). But buffer strips sometimes provide inadequate habitat for riparian wildlife (Vander Heagen & DeGraaf, 1996; Whitaker & Montevecchi, 1999; Lambert & Hannon, 2000; Darveau *et al.*, 1995).

We hypothesized that breeding birds are indirectly affected by beaver pond dynamics through changes in vegetation composition (*e.g.*, graminoids, ericaceous and alder shrubs). We examined breeding songbird species occurrence and species richness along riparian habitats associated to vegetation dynamics and beaver activity (potential, current, former), and the presence of logging near the riparian zone.

Methods

Study area

The study area (50 × 50 km) was located within a forested landscape 200 km north of Montréal (45° 31' N, 73° 39' W), Québec, Canada (Figure 1). The bedrock consists of metamorphic rocks of Archean age, with a mix of sandstones and limestone deposit, covered by sandy loam soils. Mean annual precipitation is 1016 mm. Most of the precipitation falls from April through July. The mean temperatures of July and January are 14.8 °C and –14.6 °C, respectively (Environment Canada). Our study area was entirely within the balsam fir-white birch bioclimatic domain. Dominant tree species include black spruce (*Picea mariana*), balsam fir (*Abies balsamea*), and white birch (*Betula papyrifera*). Occasional species include white pine (*Pinus strobus*) and yellow birch (*B. alleghaniensis*). Logging clearcuts were located 50 km to the north prior to the 1980s but are now found throughout the study area.

Sampling design

In the study area, we identified 39 adjacent 2-km transects (elevation range: 450–550 m) that were potentially accessible and located on first- and second-order streams. We randomly selected 26 transects for bird and vegetation sampling. We placed sampling stations regularly along transects (100 m apart), in the forest edge alongside bodies of water including rivers, streams (0.5–5 m width), beaver ponds, and lakes. Each transect was sampled once.

Bird counts

Between 4 June and 3 July 2001, we surveyed 19 transects (318 point count stations), one per day, on days without rain or strong winds from sunrise to 1100 EST. Between 1 and 7 June 2003, we sampled 7 other transects (130 stations). The point count number was 15–21 per transect, depending on access by foot. We used a variant of call-response surveys (Gibbs & Melvin, 1993; Turcotte & Desrochers, 2002) by simulating a mobbing event with a recording of mobbing chickadees (*Poecile atricapillus*) and nuthatches (*Sitta canadensis*) to attract non-singing birds to each point count station. Playbacks were broadcast at full volume from a 5-W amplifier. The amplifier was oriented skyward, 1.5 m high. The recording was inaudible to humans 30 m from the point count station. Playbacks lasted 5 min and began 1 min after the arrival of the observer, who remained stationed > 5 m from the amplifier. All birds seen or heard during the 1-min precalling period and the 5-min call interval within 15 m of the amplifier were recorded. We made specific searches for secretive birds in low and dense vegetation. We assume that species detectability was constant across habitats. We cannot infer that undetected species were absent from sites sampled; thus, our data provide information on avian activity at the point count stations rather than true species occupancy. Because of the short duration and range of the recording, we assumed it only drew birds present in the immediate vicinity (< 30 m) of each point count.

Beaver ponds and vegetation

Each station was categorized as (1) river and stream, (2) lake and natural pond, (3) active beaver pond, or (4) abandoned beaver pond. The number of stations in each category was 180, 68, 50, and 150, respectively. Stations were classified as river when the width of open water was < 5 m with no evidence of beaver activity (past or present). The main characteristic of lakes and occupied beaver ponds was the presence of large (> 5 m wide) areas of water. Rivers, lakes and active beaver ponds were characterized by the absence of a transitional zone between water and riparian forest. Ponds abandoned by beavers rapidly lose water, leaving easily recognizable mudflats progressively invaded by specific emergent transitional vegetation located between the water's edge and riparian forest: (1) graminoid, (2) ericaceous plants (a group of low shrubs), and

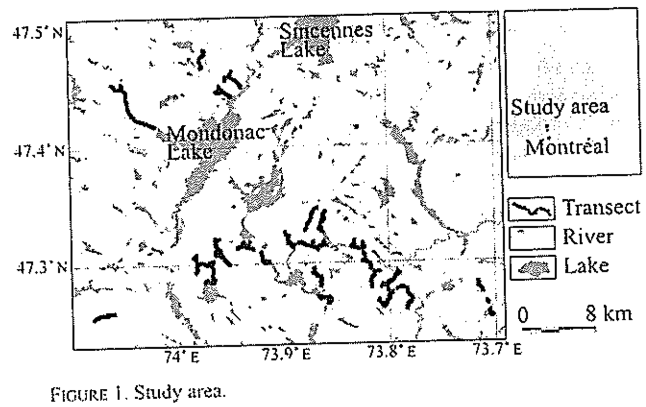

FIGURE 1. Study area.

We select models using Akaike's Information Criterion (AIC) and Akaike weights (w_i) following Burnham and Anderson (2002). The final, most parsimonious models were selected at each level using w_i, which reflects the likelihood that a particular model was best among those considered. Given the large sample size and the lack of overdispersion in the data, there was no need to use adjusted AIC values. We used model-averaged coefficients and their unconditional standard errors, which account for uncertainty in model selection. There was no evidence of multicollinearity ($r < 0.6$ in all pairwise comparisons among regressors).

Results

Beaver pond dynamics

In the study area, 45% of the sampled stations were influenced by beaver. Abandoned beaver ponds with a residual water surface represented 75% of these. Beaver ponds occurred with a frequency of 4.5 ponds·km^{-1} on transects. Three characteristic transitional vegetation assemblages were observed: (1) dense alder shrubs; (2) graminoid cover; and (3) low shrub ericaceous cover. Alder and graminoid covers were strongly associated to abandoned beaver ponds (Figure 2). These vegetation types were observed 72 and 97% of the time, respectively, on mudflats created by the disappearance of water. Low ericaceous shrubs occurred in abandoned beaver ponds and near lakes (49% and 51%, respectively). The number of presences of many species was higher at abandoned beaver ponds than at other habitat types (Appendix I), suggesting that birds colonized preferentially this habitat type. Bird species richness was also higher at abandoned beaver ponds (Figure 2), with a mean of 6.4 species, compared to ranges of 2.4–3.1 for active beaver ponds, rivers, and lakes (pairwise comparisons between abandoned beaver ponds and other habitats: Mann–Whitney U-test, $P < 0.0001$).

Species richness and species composition

Species richness was associated to both coarse- and fine-scale variables. At the coarse scale (Table II), species richness was negatively associated to the area of water (within 80 m). At a finer scale (Table III), arbustive (alder shrubs) and low transitional vegetation assemblages (graminoid cover) were associated to high species richness. The hierarchical model retained (Table IV) comprised a combination of the same variables: gap and transitional vegetation. In this model, the area of clearcut decreased significantly the number of species. Species richness was consistently higher at stations without large areas of open water and undisturbed by logging than at stations where only a 30-m width corridor of riparian vegetation remained. By contrast, the number of species increased significantly with the width of 2 transitional vegetation types: alder and graminoids.

We detected a total of 49 species, none of which were strictly associated to one specific habitat type. Presences of 80% of the species encountered were modelled but only

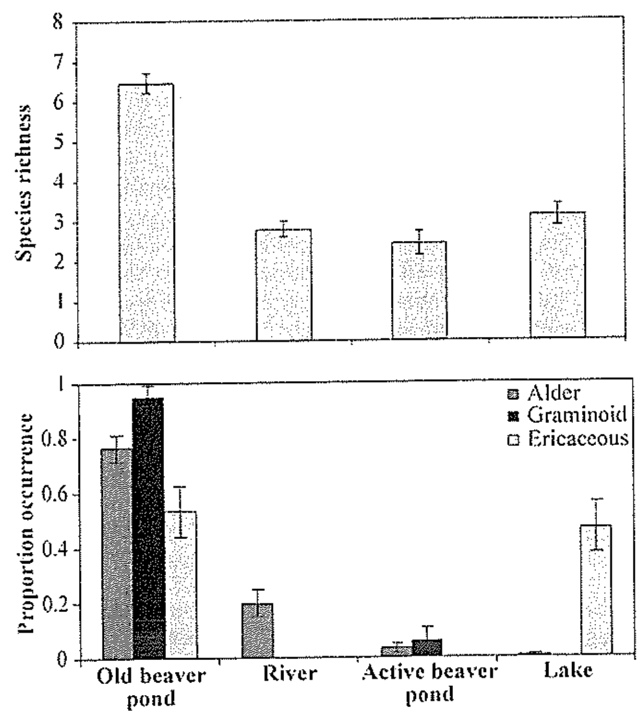

FIGURE 2. Riparian vegetation and species richness related to the shoreline typology. Standard errors were calculated on the set of 26 transects.

TABLE II. Model-averaged parameter estimates for the relation between birds and coarse-scale models. All models shown performed better than null models (ΔAIC > 4) and had Akaike weights > 0.8. Parameter estimates whose confidence intervals (in parenthesis) exclude zero are shown in bold type. Competing models are listed and defined in Table I. Species codes are defined in Appendix I.

Best model	Clr	Wtr	Mix	Reg	Dec
For					
LISP			-0.22 (0.81)	-1.23 (1.29)	-0.061 (0.25)
BLJA			-0.94 (0.94)	-0.77 (0.60)	-0.54 (0.43)
Gap					
COWA	0.07 (0.55)	0.51 (0.48)			
BTGW	**1.66 (0.43)**	-1.55 (1.60)			
PHVI	0.38 (0.47)	-1.36 (1.27)			
Species richness	-0.24 (0.13)	**-0.61 (0.14)**			
Rip					
CHSP	-0.54 (0.31)	**0.48 (0.22)**	0.35 (0.22)	**-1.04 (0.33)**	0.06 (0.10)
LEFL	-0.66 (1.06)	**1.54 (0.70)**	0.32 (0.84)	0.55 (0.74)	0.10 (0.47)
NOPA	-1.44 (1.00)	**-1.81 (0.86)**	**1.71 (0.24)**	-0.42 (0.66)	-0.27 (0.24)
NOWA	-2.54 (1.57)	-1.07 (0.86)	**1.11 (0.46)**	-0.19 (0.51)	0.28 (0.36)

creates a variety of habitats, favourable to some species and unfavourable to others (Neff, 1957; Snodgrass & Meffe, 1998; Maisonneuve & Rioux, 2001; Ray, Rebertus & Ray, 2001). Our original contribution here is that beaver ponds have effects on bird communities lasting longer than the actual occupancy by beavers. However, the relation between beavers and birds was studied indirectly via the density of transitional vegetation. To better document this relation, a more complete understanding of beaver pond vegetation dynamics is needed.

Contrary to what has been suggested in previous papers, beaver ponds in this study did provide lasting benefits to riparian bird communities, through slowly shifting patterns of vegetation, especially alder, following exposure of previously flooded areas. Thus, to conserve overall forest integrity at the landscape scale, it would be useful to preserve the small-scale natural dynamics of beaver ponds.

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APPENDIX I. Number of presences recorded for each species from 448 riparian point counts adjacent to riparian habitats north of Montéal, Canada.

Common name	Species name	AOU	Abandoned beaver pond	Active beaver pond	Lake	River	Overall
Black capped chickadee	*Poecile atricapillus*	BCCH	92	27	31	93	243
Yellow rumped warbler	*Dendroica coronata*	YRWA	79	15	20	28	142
Ruby crowned kinglet	*Regulus calendula*	RCKI	47	21	11	54	133
Magnolia warbler	*Dendroica magnolia*	MAWA	55	7	15	51	128
Red Breasted nuthatch	*Sitta canadensis*	RBNU	53	3	15	35	106
White throated sparrow	*Zonotrichia albicollis*	WTSP	59	9	33	-	101
Boreal chickadee	*Poecile hudsonica*	BOCH	40	9	10	41	100
Golden crowned kinglet	*Regulus satrapa*	GCKI	34	9	10	44	97
Nashville warbler	*Vermivora ruficapilla*	NAWA	45	-	-	21	66
Swainson's thrush	*Catharus ustulatus*	SWTH	33	2	-	21	56
Connecticut warbler	*Oporornis agilis*	COWA	38	-	13	-	51
Bay breasted warbler	*Dendroica castanea*	BBWA	36	4	4	4	48
Red eyed vireo	*Vireo olivaceus*	REVI	23	2	-	16	41
Common yellowthroat	*Geothlypis trichas*	COYE	37	-	2	-	39
Swamp sparrow	*Melospiza georgiana*	SWSP	17	1	15	-	33
Blue headed vireo	*Vireo solitarius*	BHVI	16	2	-	12	30
Palm warbler	*Dendroica palmarum*	PAWA	25	-	2	-	27
Blue jay	*Cyanocitta cristata*	BLJA	20	-	-	4	24
Black throated blue warbler	*Dendroica caerulescens*	BTBW	23	-	-	-	23
Wilson's warbler	*Wilsonia pusilla*	WIWA	16	-	-	5	21
Gray jay	*Perisoreus canadensis*	GRJA	13	-	1	6	20
Ovenbird	*Seiurus aurocapilla*	OVEN	8	-	-	9	17
Blackburnian warbler	*Dendroica fusca*	BLWA	16	1	-	-	17
Least flycatcher	*Empidonax minimus*	LEFL	12	-	-	4	16
Northern parula	*Parula americana*	NOPA	4	-	-	12	16
Canada warbler	*Wilsonia canadensis*	CAWA	9	2	1	3	15
Chestnut sided warbler	*Dendroica pensylvanica*	CSWA	13	-	1	1	15
Black and white warbler	*Mniotilta varia*	BWWA	14	-	-	1	15
Philadelphia vireo	*Vireo philadelphicus*	PHVI	8	-	-	7	15
American redstart	*Setophaga ruticilla*	AMRE	12	-	-	2	14
Downy woodpecker	*Picoides pubescens*	DOWO	5	-	-	-	5
Dark eyed junco	*Junco hyemalis*	DEJU	7	2	2	2	13
Lincoln's sparrow	*Melospiza lincolnii*	LISP	8	3	1	-	12
Black throated green warbler	*Dendroica virens*	BTGW	4	-	1	6	11
Chipping sparrow	*Spizella passerina*	CHSP	6	-	4	-	10
Northern waterthrush	*Seiurus noveboracensis*	NOWA	2	-	-	8	10
Veery	*Catharus fuscescens*	VEER	3	-	-	5	8
Hairy woodpecker	*Picoides villosus*	HAWO	4	1	2	1	8
Northern flicker	*Colaptes auratus*	NOFL	5	2	-	-	7
Winter wren	*Troglodytes troglodytes*	WIWR	-	-	-	7	7
Cedar waxwing	*Bombycilla cedrorum*	CEWA	6	-	-	-	6
Belted kingfisher	*Megaceryle alcyon*	BEKI	4	-	-	2	6
Yellow bellied sapsucker	*Sphyrapicus varius*	YBSA	11	-	-	3	14
Ruby throated hummingbird	*Archilochus colubris*	RTHU	3	-	-	1	4
Pine siskin	*Carduelis pinus*	PISI	2	2	-	-	4
Common grackle	*Quiscalus quiscula*	COGR	-	3	-	-	3
Northern harrier	*Circus cyaneus*	NOHA	-	-	2	-	2
Ruffed grouse	*Bonasa umbellus*	RUGR	1	-	1	-	2
Red breasted merganser	*Mergus serrator*	RBME	2	-	-	-	2