



Biogeographic aspects of the distribution of bird species breeding in Québec's peatlands

Sophie Calmé* and André Desrochers *Centre de recherche en biologie forestière, Faculté de Foresterie et de Géomatique, Université Laval, Québec, Canada G1K 7P4*

Abstract

Aim The state of peatlands in eastern Canada is of growing concern. This habitat is in decline due to urban sprawl, agriculture, forestry, and peat mining. Moreover, reduction and fragmentation have led to increasing isolation of remaining peatlands. We determined how bird species distribution in peatlands conforms to expectations drawn from island dynamics. We also determined the factors influencing the occurrence of 10 common peatland bird species, two of which rely mainly on peatlands for nesting in the study region.

Location We sampled sixty-three peatlands in southern Québec, Canada, within a landscape characterized by a mosaic of forest stands and farmland.

Methods We sampled nesting bird populations within peatlands from 4 June to 14 July 1995, using both transect lines and fixed-radius point counts. Each sampled peatland was characterized by area, vegetation structure (microhabitats), and isolation. We used multiple regression to test the relationship between bird species richness, peatland area, heterogeneity, microhabitat richness, and relative isolation, after correction for sampling effort. Relationships between bird species abundances and the variables the environmental variables were investigated with Canonical Correspondence Analyses. We calculated probabilities of occurrence of individual species in peatlands by logistic regression, with the same explanatory variables as mentioned previously.

Results Bird species richness was mainly explained by microhabitat richness, and to a lesser extent, by sampling effort. By contrast, the occurrence of more than half of the species was mainly explained by peatland microhabitat heterogeneity. Palm warbler *Dendroica palmarum* (Gmelin) and upland sandpipers *Bartramia longicauda* (Bechstein) were the only species less frequent in small and isolated peatlands than in other peatlands.

Main conclusions The results for species richness support both the habitat diversity, and passive sampling hypotheses for patchy distribution of birds. By contrast, results from individual species emphasized the difference between factors affecting total species richness and individual species distribution. The distribution of palm warbler, the only species restricted to peatlands regionally, was consistent with expectations from island dynamics.

Keywords

Wetland, peatland, habitat heterogeneity, isolation, passive sampling, biogeography, bird, palm warbler.

INTRODUCTION

Peatlands cover about 170 million hectares in Canada (Gorham, 1990). It is estimated that 20 millions hectares of this ecosystem have disappeared since 1800 in the country,

and that millions of others are degraded (Government of Canada, 1991). While this loss represents a relatively small fraction of all peatlands in Canada, pressure on peatlands is high in inhabited regions, because of drainage for agriculture and forestry, urban sprawl and the harvest of peat moss (Buteau, 2000). In those regions, many peatlands either experienced a reduction of their area or were fragmented or disappeared altogether as a result of human activity, and the process is still ongoing.

*Correspondence: Sophie Calmé, El Colegio de la Frontera Sur, División Conservación de la Biodiversidad, Apartado Postal 424, C.P. 77000, Chetumal, Quintana Roo, Mexico. E-mail: scalme@ecosur-qroo.mx

Will the increasing isolation and reduction of remaining peatlands affect wildlife in the long term? Peatlands are typically distributed as 'islands' in eastern Canadian landscapes. Like real islands, peatlands can be clearly distinguished from the landscape in which they are embedded, and they have been isolated for hundreds of generations of wildlife species. However, unlike oceanic islands, peatlands and other 'island' habitats are not surrounded by a totally inhospitable environment for terrestrial species. Many species may also have important populations in adjacent habitats (Margules *et al.*, 1982). Whether animal populations in eastern Canadian peatlands are truly discrete or act as subdivided populations is not only of ecological, but also of conservation interest, especially for species found primarily in this habitat.

One way to assess the relative importance of 'island' *v.* 'continental' peatland species dynamics is to use island biogeography (MacArthur & Wilson, 1967) and associated hypotheses as a theoretical framework. Even though island dynamics hinge on dispersal ability (Diamond, 1984), which is hard to document, some predictions can be made if organisms use habitat patches like true isolated islands (Gilbert, 1980). The most basic expectation is a positive species-area relationship following the relationship $S = cA^z$, where S rep-

resents species richness, c is a constant, A is the area and z the area effect, respectively. Besides MacArthur & Wilson's (1967) theory however, at least two explanations unrelated to isolation have been proposed to explain the relationship between area and species richness. A first explanation is the habitat diversity hypothesis (Williams, 1964), which states that the number of habitat types increases along with area as a result of spatial changes, e.g. edaphic conditions, and because each habitat supports its own set of species. Another explanation unrelated to isolation is the passive sampling hypothesis (Connor & McCoy, 1979), which states that the chance of encountering a new species increases independently of any ecological process, as sample size increases. Before inferring biogeographical mechanisms, one thus needs to assess Williams's (1964) and Connor & McCoy's (1979) hypotheses.

The patterns observed for whole assemblages, however, might differ from those of individual species, because of interspecific relationships such as competitive exclusion. Thus, it is not trivial to look for factors influencing individual species. It is critical, indeed, to be able to appreciate how conservation measures might influence whole assemblages and species of interest separately, as conservation usually affect two factors here considered, namely size and isolation of peatlands.

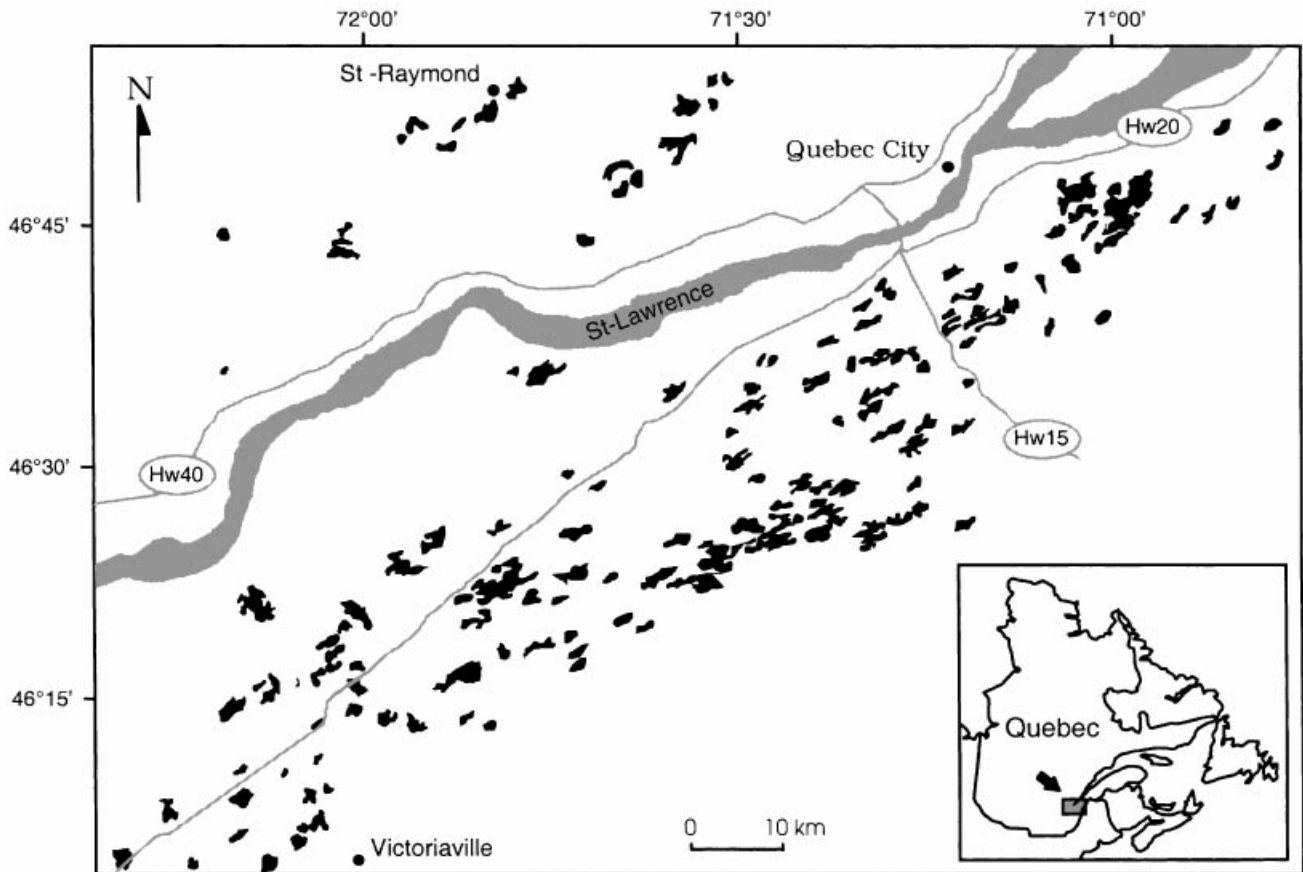


Figure 1 The 'archipelago' of peatlands in the study area, located in southern Québec (see insert). The two most distant peatlands in our sample were separated by approximately 160 km. Only main roads (Highways 15, 20 and 40) were represented for more clarity.

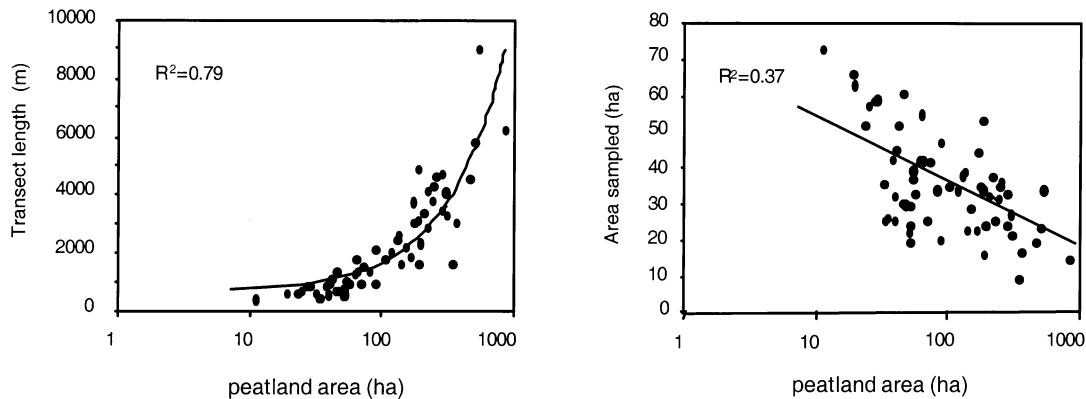


Figure 2 Relationships between, transect length (left), and area sampled (right), and peatland area.

In this paper, we assess how bird species distribution in peatlands conforms to expectations from island dynamics. We quantify the species-area relationship and assess its relationship with habitat size and isolation on species richness, as well as passive sampling, and habitat diversity. Finally, we present the patterns of occurrence and microhabitat preference for nineteen common bird species in peatlands including two peatland specialists, and discuss implications for peatland conservation in eastern Canada.

METHODS

Study area and sites

The study area was located in southern Québec, Canada (Fig. 1), within a landscape characterized by a mosaic of forest stands and farmland. Peatlands in this area range from a few hectares to a thousand hectares. The study area lays within a deciduous forest region characterized by red maple *Acer rubrum* L. stands on sandy substrates (Thibault, 1985), where most peatlands are found. The presence of balsam fir *Abies balsamea* L. (Mill.) is also characteristic, except in the south-east portion of the study area. We sampled sixty-three ombrotrophic peatlands ranging in size from 10.9 to 843 ha. Large peatlands were overrepresented in our sample, as many smaller peatlands were discarded because they were too small to be sampled by transect and/or strongly disturbed by drainage. Most peatlands in the region developed after the icefields of the Wisconsin period melted, around 10,000 years ago, but some expanded between 6000 and 4000 years ago, during a cold and humid climatic event, so larger ombrotrophic peatlands usually also include more recent minerotrophic areas (also called fens).

Bird sampling

We sampled nesting birds populations within peatlands from 4 June to 14 July 1995, using both transect lines and fixed-radius point counts (Ralph *et al.*, 1993). Point counts were conducted using a 100-m-radius and lasted 10 min, during which all birds seen or heard were recorded. Along transect

lines, all birds seen or heard were recorded up to 100 m on either side of the line. The total length of transect lines in each peatland was proportional to peatland area, but sampled ratio was negatively related to area (Fig. 2), so sampling effort was proportionally lower in larger peatlands. Both transect lines and point counts were located at least 150 m from the peatland edge (% trees > 5 m high exceeding 50%), leaving a 50-m wide buffer zone to avoid observation of birds in or near the edge of adjacent habitats.

A total of eighty-one bird species were detected, but only twenty-one species were included in the analyses (Table 1). We retained only (1) species whose breeding is documented in peatlands (Gauthier & Aubry, 1996) (2) species for which the sampling methods were appropriate (3) species breeding during the sampling period, and (4) species whose territories may not encompass the peatland and surrounding habitats. Additional details can be found in Calmé & Desrochers (1999). Two regionally rare species (clay-coloured sparrow *Spizella pallida* Swainson, and field sparrow *Spizella pusilla* Wilson) were included because their presence and territoriality had been confirmed over at least two years at the same site (unpublished data).

Vegetation mapping

We identified ten types of microhabitats found in peatlands in the study area (Calmé & Desrochers, 1999), based mainly on height and density of trees but also on spatial arrangement of trees in the case of clumps of black spruce *Picea mariana* (Mill.) B.S.P. Two microhabitats with fen attributes reflected the presence of open water, and of more diverse vegetation. These two classes are rare in ombrotrophic peatlands, but can be found along edges where decomposition is higher, or in complex peatlands.

We mapped microhabitat types with recent 1 : 15,000 aerial photographs. Photointerpretation was validated in the field for all peatlands by verifying whether both classification and limits between microhabitats were accurate. Finally, the maps were digitized in a geographical information system. We considered that optical distortion on aerial photographs was negligible since we mostly used the orthogonal

Order	Species name	Species codes	Species occurrence
Falconiformes	Northern harrier <i>Circus cyaneus</i> (L.)	noha	23
Charadriiformes	Upland sandpiper <i>Bartramia longicauda</i> (Bechstein)	upsa	4
	Common snipe <i>Gallinago gallinago</i> (L.)	cosn	4
Passeriformes	Alder flycatcher <i>Empidonax alnorum</i> (Brewster)	alfl	27
	Eastern kingbird <i>Tyrannus tyrannus</i> (L.)	eaki	19
	Tree swallow <i>Tachycineta bicolor</i> (Vieillot)	trsw	15
	Hermit thrush <i>Catharus guttatus</i> (Pallas)	heth	45
	American robin <i>Turdus migratorius</i> (L.)	amro	24
	Nashville warbler <i>Vermivora ruficapilla</i> (Wilson)	nawa	57
	Magnolia warbler <i>Dendroica magnolia</i> (Wilson)	mawa	14
	Yellow-rumped warbler <i>Dendroica coronata</i> (L.)	yrwa	13
	Palm warbler <i>Dendroica palmarum</i> (Gmelin)	pawa	56
	Common yellowthroat <i>Geothlypis trichas</i> (L.)	coye	63
	Clay-coloured sparrow <i>Spizella pallida</i> (Swainson)	ccsp	1
	Field sparrow <i>Spizella pusilla</i> (Wilson)	fisp	1
	Savannah sparrow <i>Passerculus sandwichensis</i> (Gmelin)	sasp	45
	Song sparrow <i>Melospiza melodia</i> (Wilson)	sosp	27
	Lincoln's sparrow <i>Melospiza lincolnii</i> (Audubon)	lisp	61
	Swamp sparrow <i>Melospiza georgiana</i> (Latham)	swsp	11
	White-throated sparrow <i>Zonotrichia albicollis</i> (Gmelin)	wtsp	59
	Red-winged blackbird <i>Agelaius phoeniceus</i> (L.)	rwbl	12

Table 1 List of the twenty-one bird species considered for analyses and their frequency of occurrence in the sixty-three peatlands studied.

parts of photo-graphs, and because the peatlands had little or no relief.

Measuring peatland relative isolation

Relative isolation of peatlands was measured as the total area of peatlands present in a 10-km radius around the approximate centroid of each peatland, excluding the area of sample peatland (< 0.03% of sampled region). This measure provides an estimate of the availability of the habitat regionally, and we assume that it better reflects isolation of the habitat in the landscape than does the distance to the next patch (Vos & Stumpel, 1995), as the regional amount of habitat is thought to influence the rate of dispersal (Askins *et al.*, 1987).

Measurements were made with an electronic planimeter and recent aerial photographs. To allow direct interpretation of the variable, i.e. the greater the value, the more isolated the peatland, we assigned a minus to all calculated values in all analysis.

Assessing the relationship between peatland metrics and species use

We used multiple regression to test the relationship between bird species richness, peatland area, number of microhabitats (microhabitat richness), and relative isolation, after correction for sampling effort. The contribution of each variable to the model after the effects of all other variables have been factored out was assessed using type III sums of squares

(Littell *et al.*, 1991). To normalize variables and stabilize the variance, peatland area, sampling effort and relative isolation were log-transformed, while species and microhabitat richness were transformed by square root.

Relationships between bird species abundances and variables that may influence their distribution (referred to as environmental variables) were investigated with Canonical Correspondence Analyses (CCA; Ter Braak, 1988). Environmental variables were peatland area, microhabitat richness, and relative isolation. The significance of the first canonical axis was tested by way of a Monte Carlo test with ninety-nine permutations.

Because individual bird species have different requirements, we calculated their individual probabilities of occurrence in peatlands by logistic regression, with the same explanatory variables as mentioned previously. Stepwise logistic regressions were performed on eighteen species, after excluding ubiquitous (common yellowthroat *Geothlypis trichas* L.) and rare species (clay-coloured sparrow, field sparrow). We selected explanatory variables by setting the level of significance at $\alpha = 0.10$. The goodness of fit of the relation was assessed using a coefficient of determination modified for discrete models (Nagelkerke, 1991), and the Hosmer-Lemeshow statistic (Hosmer & Lemeshow, 1989). All models presented were well adjusted to the data, based on the residual deviance/degrees of freedom ratio, $P > 0.1$.

RESULTS AND DISCUSSION

Role of peatland metrics on species richness

Area, microhabitat richness, isolation, and sampling effort jointly accounted for 54.8% of the variation in bird species richness (adjusted R^2). Peatland area and microhabitat richness were strongly intercorrelated ($r > 0.70$; Fig. 3), but peatland isolation, the last key variable, was poorly correlated with other variables ($r < 0.20$).

Bird species richness was significantly related to microhabitat richness and sampling effort, which explained 7.6% ($F_{1,58} = 4.77$, $P < 0.05$) and 6.3% ($F_{1,58} = 3.88$, $P < 0.10$) of the total variation, respectively, all other effects being factored out. Our result thus supports both the habitat diversity (Williams, 1964), and the passive sampling hypotheses (Connor & McCoy, 1979). In comparison, other factors such as peatland area and isolation were relatively unimportant (both $F_{1,58} < 1.94$, $P > 0.10$). It is likely that the species-area relationship within peatlands was due to high correlations between peatland area and the two significant variables explaining species richness: microhabitat richness (Fig. 3) and sampling effort (Fig. 2). Stockwell (1994) also found vegetation

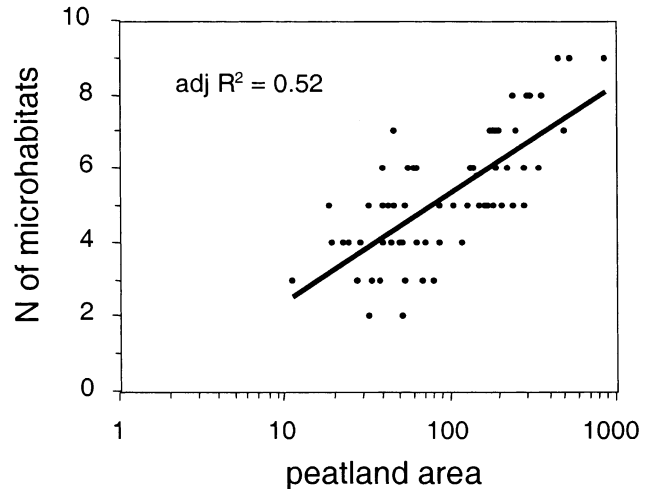


Figure 3 Relationships between peatland area and microhabitat richness ($n = 63$). R^2 values was adjusted for the number of variables entered in the model.

diversity to be more important than area as an explanation of peatland bird species richness and abundance in eight peatlands in Maine, USA. We therefore support the view of Simberloff & Levin (1985) that if habitat diversity explains species richness, area *per se* is probably a secondary factor.

Distribution of individual bird species

Both the CCA on bird species abundances and logistic regression on individual bird species occurrences generally tallied, and therefore will be discussed jointly. Peatland area was strongly and positively correlated with the first environmental axis in the CCA, whereas isolation was correlated with the second axis, and microhabitat richness to the third axis (Table 2). The first three environmental axes explained, respectively, 67.5%, 26.6% and 5.9% of the variance of the species-environment relationship. The first canonical axis was significant according to the Monte Carlo test ($P = 0.01$). All environmental variables accounted for 12.2% of the variance in the model ($P < 0.01$).

Higher abundances of forest bird species appeared to be related to smaller peatland area, as all these species were on the left of Axis 2 (Fig. 4). By contrast, species associated with wet or open habitats in the literature (reviewed by Gauthier & Aubry, 1996) were on the right hand portion of the graph, indicating a positive relationship with peatland area, and microhabitat richness. Large peatlands, which are also characterized by more diverse microhabitats, tended

Table 2 Correlation matrix (Kendall's Tau) of the environmental variables with the first three environment axes in the Canonical Correspondence Analysis.

	Peatland area	Microhabitat richness	Peatland isolation
Axis 1	0.89	0.57	-0.60
Axis 2	0.42	0.22	0.75
Axis 3	0.16	0.79	0.28

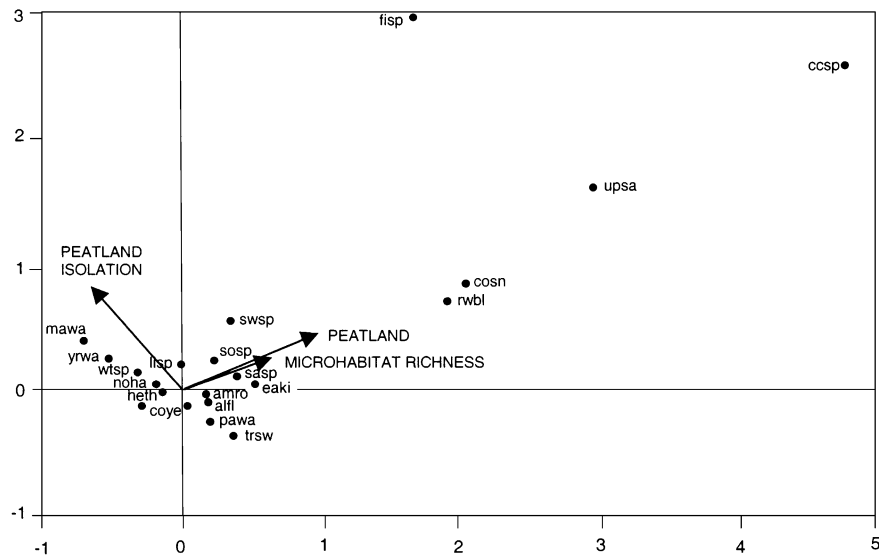


Figure 4 CCA biplot showing the distribution of bird species in the multivariate environmental space. Species codes are as in Table 1.

Table 3 Relationships between peatland area, isolation and microhabitat richness and species occurrence in sixty-three peatlands, as calculated by stepwise logistic regression. Linear parameter estimates are shown with their standard errors in parentheses. Significant parameters are in bold typeface. Species are ranked from the most to the least associated to large peatlands. Microhabitat codes are defined in footnote. Microhabitat–species associations were all positive unless indicated otherwise (–).

Species	Area	Relative isolation ($\times 1000$)	Microhabitat richness	Associated microhabitats†
Upland sandpiper	0.077 (0.004)	-2.77 (0.49)	0.58 (0.29)	
Palm warbler	0.057 (0.022)	-2.65 (0.77)	0.17 (0.35)	6
Savannah sparrow	0.026 (0.008)	0.80 (0.59)	-1.65 (0.54)	1, 5, 8
Common snipe	0.011 (0.004)	-0.43 (0.60)	-0.21 (0.37)	
Swamp sparrow	0.010 (0.004)	0.88 (0.61)	-0.24 (0.34)	9
Alder flycatcher	0.010 (0.004)	-0.25 (0.54)	-0.43 (0.35)	1, 8(–)
American robin	0.008 (0.004)	0.60 (0.55)	-0.17 (0.33)	6
Red-winged blackbird	0.007 (0.004)	-0.49 (0.57)	-0.08 (0.31)	9
Northern harrier	0.007 (0.004)	0.73 (0.58)	0.10 (0.32)	7(–)
Nashville warbler	0.004 (0.006)	-1.00 (0.64)	0.22 (0.36)	
Eastern kingbird	0.004 (0.004)	0.65 (0.59)	0.67 (0.33)	10(–)
Tree swallow	0.003 (0.003)	-0.39 (0.55)	0.03 (0.30)	
Song sparrow	0.001 (0.003)	0.20 (0.57)	0.35 (0.35)	5, 10(–)
Magnolia warbler	0.001 (0.003)	0.94 (0.58)	-0.30 (0.37)	3, 6
White-throated sparrow	0.000 (0.004)	-0.15 (0.62)	0.88 (0.45)	8(–)
Hermit thrush	-0.004 (0.004)	0.55 (0.59)	0.51 (0.35)	3, 6
Lincoln's sparrow	-0.006 (0.006)	-0.15 (0.65)	1.19 (0.47)	
Yellow-rumped warbler	-0.011 (0.004)	-0.05 (0.51)	1.64 (0.50)	2(–), 4(–)

†Microhabitat codes: 1, tree cover < 5%; 2, tree cover < 20% and height < 5 m; 3, tree cover < 15% and height > 5 m; 4, tree cover < 50% and height < 5 m; 5, tree cover < 40% and height > 5 m; 6, tree cover variable and clumped distribution of layers of black spruce; 7, tree cover > 60% and height > 2 m; 8, fen-lag; 9, fen; 10, forest soil.

to have relatively less habitat available for forest species, because they supported a smaller proportion of peripheral forested habitat. Thus, abundances of forest species tended to decrease with peatland area. The converse was also true for abundances of species of open/wet habitats.

Of the eighteen species for which probabilities of occurrence were calculated, sixteen were significantly associated with independent variables (Table 3). All single-species model

R-squares were > 0.08. Individual microhabitat association was the factor most frequently related to species occurrence (thirteen times), while peatland area, microhabitat richness, and relative isolation explained, respectively, the occurrence of nine, six, and two species. Thus, factors related to the occurrence of individual species contrasted from those related to total species richness. More specifically, area and isolation were significant predictors of individual species distributions,

whereas it was not significant for predicting total species richness. However, microhabitat richness was a critical factor for both species richness and various individual species distributions.

The occurrence of upland sandpiper, eastern kingbird, white-throated sparrow, Lincoln's sparrow, and yellow-rumped warbler was positively related to microhabitat richness, while the occurrence of savannah sparrow was negatively related to this variable. Some of these species, like upland sandpiper and Lincoln sparrow, were not microhabitat specific so that their increased presence in rich microhabitat peatlands can be interpreted as a lack of specificity towards the microhabitat categories we defined. Eastern kingbird, white-throated sparrow and yellow-rumped warbler were not specific to microhabitats, but were rather avoiding some of them. Eastern kingbirds were also more abundant in microhabitat-rich peatlands.

Peatland area was positively related to the occurrence of upland sandpiper, palm warbler, savannah sparrow, common snipe, swamp sparrow *M. georgiana* Latham, alder flycatcher *Empidonax alnorum* Brewster, American robin *Turdus migratorius* L., and red-winged blackbird *Agelaius phoeniceus* L. It is noteworthy that red-winged blackbirds and swamp sparrows depended on the presence of fen areas in peatlands (Stockwell, 1994; Calmé & Desrochers, 1999; this study). Though we did not find a significant effect of individual microhabitat for upland sandpiper and common snipe, these species are also preferentially found in large peatlands that contain poor fen habitat (Calmé & Haddad, 1996, personal observation). Calmé & Desrochers (1999) demonstrated that microhabitats were distributed in a nested pattern among peatlands, and that fen areas occurred more frequently in large peatlands than in small ones. We hypothesize that the importance of peatland area for red-winged blackbirds, swamp sparrows, and possibly upland sandpipers and common snipes resides in the presence of their preferred microhabitats in larger peatlands. Similarly, savannah sparrows were found in large open or semiopen habitat patches within peatlands, which are more likely to be found in large peatlands (Calmé & Desrochers, 1999).

Palm warbler and upland sandpiper's occurrences were negatively correlated to peatland isolation, and positively to peatland area. As palm warblers are strongly and almost exclusively associated with peatlands (Wilson, 1996; Calmé & Desrochers, 1999), this result is fully consistent with MacArthur & Wilson's (1967) prediction that immigration rates should drop with increasing isolation in insular systems, while extinction should increase with decreasing island area, thus leading to depauperate populations in small, isolated islands. According to Calmé & Haddad (1996), upland sandpiper's populations in this region are also mostly found in peatlands, although they likely use surrounding habitats. However, the absence of upland sandpipers in small peatlands or isolated peatlands can be explained by its semicolonial behaviour rather than by increased extinction or decreased immigration.

It is striking that palm warbler, the species most strongly associated with peatlands (Calmé & Desrochers, 1999 and

references therein), should also be one of the two that show both isolation and area trends consistent with MacArthur & Wilson's (1967) theory. Area and isolation-sensitivity by palm warbler may stem from their occurrence in very small numbers (< ten pairs) in peatlands (personal observation), which contrasts with all other songbirds frequently found in peatlands. However, behavioural work will be required to assess whether it is too costly for dispersing palm warblers to reach isolated, small peatlands or whether they simply avoid these habitats.

Conservation implications

Peatlands bird assemblages were richest in peatlands presenting the greatest diversity of habitat types (Stockwell, 1994; Calmé & Desrochers, 1999; this study), and habitat-rich peatlands tended to be large. This double correlation makes area a good predictor of species richness, though the causality was only partially direct (Calmé & Desrochers, 1999).

Even though the distribution of peatland birds was consistent with that expected from a set of islands, our results do not support the use of the equilibrium theory of island biogeography as a tool for conservation of all peatland bird species. As in Margules *et al.* (1982), many of the species found in habitat islands such as peatlands have substantial populations in surrounding habitats. As a matter of fact, among all the bird species we studied only palm warblers and possibly Lincoln's sparrows only occurred in peatlands regionally (Calmé & Desrochers, 1999). The distribution of palm warblers depended both on peatland area and the amount of peatland habitat available in a 10-km-radius around a peatland it was found in. We argue that the trend might be under-evaluated due to the time lag in species adaptation occurring during habitat relaxation (Opdam, 1991) resulting from recent losses and drainage of peatlands, which exceed 50,000 ha in our study area and its vicinity (Buteau 2000). For other species whose occurrence was related to peatland area, the presence of habitat features specific to large peatlands explained most area-occurrence relationships. Besides, we showed elsewhere that species- and habitat-rich peatlands supported species and habitats not found in poorer ones, but the hypothesis that nestedness was caused by extinction was not supported (Calmé & Desrochers, 1999). As suggested by Stockwell (1994), microhabitat richness within peatlands might thus be used as a simple indicator of peatland biological diversity, as it should reflect diversity both in plants and animals communities.

ACKNOWLEDGMENTS

We thank Marc-André Villard, Bruno Drolet, Marcel Darveau and Jean-Pierre Savard, and one anonymous reviewer for their comments on earlier versions of this manuscript. We are indebted to David Avellaneda and Bruno Drolet for their contribution to the computerization and analysis of spatial data. Stephanie Haddad, Jean-François Rousseau and Nicolas Wampach helped with the fieldwork. We greatly appreciated

their dedication. Financial support was provided by the Canadian Wildlife Service, Wildlife Habitat Canada, the Province of Quebec Society for the Protection of Birds, and the Natural Science and Engineering Research Council of Canada through a fellowship to S. Calmé.

REFERENCES

- Askins, R. A., Philbrick, M. J. & Sugeno, D. S. (1987) Relationship between the regional abundance of forest and the composition of forest bird communities. *Biological Conservation*, **39**, 129–152.
- Bureau, P. (2000) Les tourbières du Québec: nature et répartition. *Écologie des tourbières. Du Québec-Labrador* (ed. by S. Payette). Presses de l'Université Laval, Sainte-Foy, Québec.
- Calmé, S. & Desrochers, A. (1999) Nested bird and micro-habitat assemblages in a peatland archipelago. *Oecologia*, **118**, 361–370.
- Calmé, S. & Haddad, S. (1996) Peatlands: a new habitat for the Upland Sandpiper, *Bartramia longicauda*, in eastern Canada. *Canadian Field-Naturalist*, **110**, 326–330.
- Connor, E. F. & McCoy, E. D. (1979) The statistics and biology of the species-area relationship. *American Naturalist*, **113**, 791–833.
- Diamond, J. M. (1984) Distributions of New Zealand birds on real and virtual islands. *New Zealand Journal of Ecology*, **7**, 37–55.
- Gauthier, J. & Aubry, Y. (eds) (1996) *The breeding birds of Québec: atlas of the breeding birds of Southern Québec*. Association Québécoise des Groupes d'Ornithologues, The Province of Québec Society for the Protection of Birds, and Canadian Wildlife Service, Environment Canada (Québec region), Montréal.
- Gilbert, F. S. (1980) The equilibrium theory of island biogeography: fact or fiction? *Journal of Biogeography*, **7**, 209–235.
- Gorham, E. (1990) Biotic impoverishment in northern peatlands. *The Earth in transition: patterns and processes of biotic impoverishment* (ed. by G. M. Woodwell), pp. 65–98. Cambridge University Press, Cambridge.
- Government of Canada (1991) *The federal policy on wetland conservation*, 4 pp. Environment Canada, Ottawa.
- Hosmer, D. W. & Lemeshow, S. (1989) *Applied logistic regression*. Wiley, New York.
- Littell, R. C., Freund, R. J. & Spector, P. C. (1991) *SAS® system for linear models*, 3th edn. SAS Institute Inc., Cary.
- MacArthur, R. & Wilson, E. O. (1967) *The theory of island biogeography*. Princeton University Press, Princeton.
- Margules, C., Higgs, A. J. & Rafe, R. W. (1982) Modern biogeographic theory: are there any lessons for nature reserve design? *Biological Conservation*, **24**, 115–128.
- Nagelkerke, N. J. D. (1991) A note on general definition of the coefficient of determination. *Biometrika*, **78**, 691–692.
- Opdam, P. (1991) Metapopulation theory and habitat fragmentation: a review of holarctic breeding bird studies. *Landscape Ecology*, **5**, 93–106.
- Ralph, C. J., Geupel, G. R., Pyle, P., Martin, T. E. & DeSante, D. F. (1993) *Handbook of field methods for monitoring landbirds*. USDA Forest Service, Albany. Pacific Southwest Research Station General Technical Report PSW-GTR-144.
- Simberloff, D. & Levin, B. (1985) Predictable sequences of species loss with decreasing island area—Land birds in two archipelagoes. *New Zealand Journal of Ecology*, **8**, 11–20.
- Stockwell, S. S. (1994) *Habitat selection and community organization of birds in eight peatlands of Maine*. PhD Thesis, University of Maine, Orono.
- Ter Braak, C. J. F. (1988) CANOCO—A FORTRAN program for canonical community ordination by [partial] [detrended] [canonical] correspondence analysis, principal components analysis and redundancy analysis, Version 2.1. Agricultural Mathematics Group, Wageningen. Technical report LWA-88-02.
- Thibault, M. (1985) *Les régions écologiques du Québec méridional*, 2nd approximation. Ministère Des Ressources Naturelles, Direction de la Recherche, Québec, carte (1/1, 250,000).
- Vos, C. C. & Stumpel, A. H. P. (1995) Comparison of habitat-isolation parameters in relation to fragmented distribution patterns in the tree frog (*Hyla arborea*). *Landscape Ecology*, **11**, 203–214.
- Williams, C. B. (1964) *Patterns in the balance of nature*. Academic Press, New York.
- Wilson, W. H. Jr (1996) Palm Warbler (*Dendroica palmarum*). *The birds of North America*, No 238 (ed. by A. Poole and F. Gill). The Academy of Natural Sciences, Philadelphia, PA, and The American Ornithologists' Union, Washington.

BIOSKETCHES

Sophie Calmé is Associate Professor at El Colegio de la Frontera Sur, in Southern Mexico. She is interested in the effects of land use change on wildlife ecology, at the community, population and individual levels. Her current work includes the effect of tropical forest fragmentation on dispersal of an endemic bird, and wildlife conservation in rural communities.

André Desrochers is Associate Professor at the Faculty of Forestry and Geomatics, Université Laval, Québec. His main research area is the ecology of bird behaviour and distribution patterns in relation to landscape structure and fragmentation. Dr Desrochers also conducts research on peatland wildlife conservation in Eastern Canada.