LANDSCAPE CHARACTERISTICS INFLUENCE POND OCCUPANCY BY FROGS AFTER ACCOUNTING FOR DETECTABILITY

M. J. Mazerolle,[1,3] A. Desrochers,[1] and L. Rochefort[2]

[1]*Centre de recherche en biologie forestière, Pavillon Abitibi-Price, Faculté de Foresterie et de Géomatique, Université Laval, Québec, Québec, G1K 7P4, Canada*
[2]*Département de phytologie, Pavillon Paul-Comtois, Université Laval, Québec, Québec, G1K 7P4, Canada*

Abstract. Many investigators have hypothesized that landscape attributes such as the amount and proximity of habitat are important for amphibian spatial patterns. This has produced a number of studies focusing on the effects of landscape characteristics on amphibian patterns of occurrence in patches or ponds, most of which conclude that the landscape is important. We identified two concerns associated with these studies: one deals with their applicability to other landscape types, as most have been conducted in agricultural landscapes; the other highlights the need to account for the probability of detection. We tested the hypothesis that landscape characteristics influence spatial patterns of amphibian occurrence at ponds after accounting for the probability of detection in little-studied peatland landscapes undergoing peat mining. We also illustrated the costs of not accounting for the probability of detection by comparing our results to conventional logistic regression analyses. Results indicate that frog occurrence increased with the percent cover of ponds within 100, 250, and 1000 m, as well as the amount of forest cover within 1000 m. However, forest cover at 250 m had a negative influence on frog presence at ponds. Not accounting for the probability of detection resulted in underestimating the influence of most variables on frog occurrence, whereas a few were overestimated. Regardless, we show that conventional logistic regression can lead to different conclusions than analyses accounting for detectability. Our study is consistent with the hypothesis that landscape characteristics are important in determining the spatial patterns of frog occurrence at ponds. We strongly recommend estimating the probability of detection in field surveys, as this will increase the quality and conservation potential of models derived from such data.

Key words: amphibian; detection; field surveys; habitat disturbance; landscape; logistic regression; New Brunswick, Canada; patch; peatland; Rana clamitans; site-occupancy model.

INTRODUCTION

Ecologists have long attempted to explain animal distributions at fine spatial scales through mechanisms such as habitat selection (e.g., Miller 1942, Sexton and Heatwole 1968, Rosenzweig 1973, Anderson and Shugart 1974), competition and predation (reviewed in Connell 1983 and Sih et al. 1985). During the 1980s, however, interest has shifted to patterns at the landscape scale, and much of conservation-oriented research has since focused on predicting the spatial distribution and persistence of organisms through time and disturbances (e.g., Andrén 1994, Fahrig and Merriam 1994, Bender et al. 1998, McGarigal and Cushman 2002). Researchers strived to provide empirical support for various theories on patch dynamics in the landscape (e.g., island biogeography, MacArthur and Wilson 1963; source–sink dynamics, Pulliam 1988; neutral landscape models, With and King 1997). However,

metapopulation theory, where patch recolonization is assumed to depend mainly on the distance between patches (Hanski and Gilpin 1991, 1997), has remained particularly popular among conservation biologists (Hanski and Gilpin 1997, Hastings and Harrison 1994, Marsh and Trenham 2001). Though classical metapopulation theory may hold in some cases (e.g., Harrison and Taylor 1997), these models are likely too simplistic for organisms using resources located in more than a single habitat type (i.e., landscape complementation sensu Dunning et al. 1992), such as pond-breeding amphibians.

Based on the life history of pond-breeding amphibians, we would expect that spatial patterns at ponds depend on both patch (e.g., pond size) and landscape characteristics (e.g., proximity of terrestrial habitat). Indeed, pond-breeding amphibians have complex life cycles, as they use distinct components of the landscape at different developmental stages and periods of the year (Wilbur 1980, Pope et al. 2000, Pilliod et al. 2002). Embryos and larvae are generally confined to ponds and their development is regulated by biotic and abiotic factors such as water chemistry and temperature (e.g., Moore 1939, Gosner and Black 1957, Bridges and Sem-

TABLE 1. Landscape characteristics influence the presence of pond-breeding amphibians at ponds.

Landscape type	Percentage of taxa responding to:			Total no. taxa
	Patch only	Landscape only	Landscape and patch	
Agriculture†	28.2	2.6	56.4	39
Alpine ponds‡	87.5	0	12.5	8
Forest§	16.7	0	83.3	12
Natural desert‖	100	0	0	1
Peatland¶	0	100	0	1

Note: We only considered studies investigating both patch and landscape characteristics on amphibian presence, where the pond was considered as the patch.

†Sources: Loman (1988), Sjögren-Gulve (1994), Vos and Stumpel (1995), Vos and Chardon (1998), Findlay et al. (2001), Hazell et al. (2001), Joly et al. (2001), Scribner et al. (2001), Hamer et al. (2002), Stevens et al. (2002), Beja and Alcazar (2003), Jansen and Healey (2003).

‡Sources: Houlahan and Findlay (2003).

§Sources: Bosch and Martínez-Solano (2003), Knapp et al. (2003).

‖Source: Bradford et al. (2003).

¶Source: Mazerolle and Cormier (2003).

litsch 2000), hydroperiod (e.g., Rowe and Dunson 1995, Snodgrass et al. 2000, Babbitt et al. 2003), canopy cover (Skelly et al. 2002, Halverson et al. 2003), as well as competitive and predator–prey interactions between conspecifics or heterospecifics (e.g., Wilbur 1972, Morin 1986, Werner and McPeek 1994, Skelly 1995, Mokany and Shine 2003). Following metamorphosis, juveniles disperse across the landscape to later breed at either natal or adjacent ponds (e.g., Gill 1978, Johnson and Semlitsch 2003). Surprisingly, only recently have investigators started to integrate landscape components into models of amphibian occurrence at ponds, generally finding that the hypothesis holds (Table 1).

We identified two potential problems emerging from models based on amphibian occurrence data. First, because most studies on amphibians are nested in agricultural landscapes of temperate regions (Table 1), we could question the predictive value of these models for other landscape types. Our second concern is more serious and relates to the problem of detecting reliably the species of interest in field conditions, an issue rarely addressed by investigators of any animal taxa (e.g., references in Table 1). Given that many amphibians are cryptic and difficult to census, this can have serious implications. Nondetection not only leads to underestimates of species presence, but likely affects inferences and conclusions regarding species' spatial distribution and associations with patch or landscape attributes (Moilanen 2002, Gu and Swihart 2004). Nonetheless, recent developments now allow to incorporate this detection bias into analyses through various approaches (e.g., Boulinier et al. 1998, MacKenzie et al. 2002, 2003, Tyre et al. 2003, Gu and Swihart 2004).

In this paper, we tested the hypothesis that landscape attributes influence amphibian spatial patterns of occurrence after accounting for the probability of detection. Specifically, we illustrate the use of site-occupancy models (MacKenzie et al. 2002, 2003) with data

from a study assessing the effects of patch (i.e., ponds) and landscape characteristics on the occurrence of adult green frogs (*Rana clamitans melanota*) at 70 ponds embedded within peatland-dominated landscapes. We then investigated the costs of not accounting for the probability of detection by comparing our results to more conventional analyses. We chose peatland systems, as they span over a large portion of boreal countries, have received little attention compared to other environments, are increasingly threatened by human disturbances, and are commonly used by amphibians (Maltby and Proctor 1996, Mazerolle 2001, 2003, Chapman et al. 2003).

METHODS

Study area and peat mining development

We conducted this work during 1999 and 2000 in three peatland landscapes undergoing peat mining in eastern New Brunswick, Canada (Fig. 1). Peatlands are acidic wetlands limited to boreal countries, predominantly Canada and Russia, and extend over 4×10^6 km^2 of the Earth's surface (Maltby and Proctor 1996). Through intensive draining for agriculture, forestry, or urbanization, few peatlands remain unaltered in western Europe (reviewed in Poulin and Pellerin 2001). Furthermore, the deep peat deposits associated with certain types of peatlands (i.e., bogs) are facing increasing pressure from the peat mining industry in Europe and North America (Wheeler and Shaw 1995, Chapman et al. 2003). Indeed, this activity supplies the horticultural peat for the global market, and reached over 32×10^6 m^3 of peat in 1997 (Daigle et al. 2001).

During peat mining, the surface vegetation is removed and large networks of ditches are established to drain the wetland. The peat layers are then sequentially tilled, left to dry, and collected with tractor-pulled vacuums. In addition, ponds occurring in peatlands are drained or filled in before activities begin. Mined peat
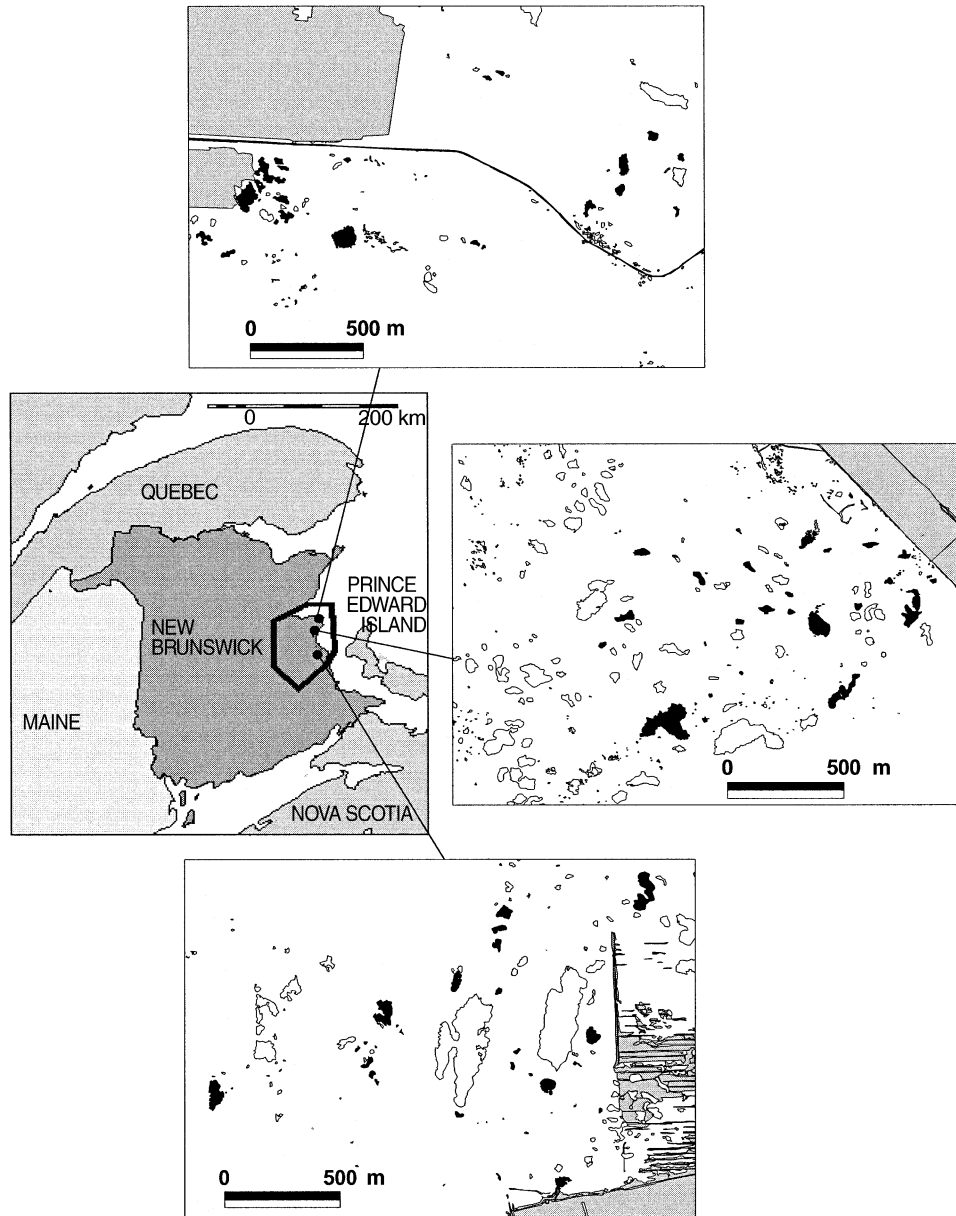
FIG. 1. Location of bog ponds sampled in the three peatland landscapes under study in eastern New Brunswick, Canada, for the study of green frog occurrence. Black polygons correspond to the 70 ponds sampled, empty polygons denote other bog ponds, and shaded areas indicate the surfaces undergoing peat mining.

surfaces are devoid of cover, typically dry, and under regular mechanical disturbance, and therefore strongly contrast with adjacent unmined peatland surfaces.

Each of the three areas under study centered on a peatland covering between 835 and 2315 ha with 6–12% of its surface mined for peat, and extended onto the adjacent areas (Fig. 1). Peatlands were surrounded by mixed forest dominated by black spruce (*Picea mariana*), balsam fir (*Abies balsamea*), birch (*Betula* spp.), and maple (*Acer* spp.). Paved and dirt roads also bordered the peatlands. Mined peat surfaces adjacent to each peatland were undergoing regular mechanical dis-

turbance and had been mined for at least five years. Bog ponds were common in each peatland, but we did not consider ponds on the mined surfaces as they were too scarce. Indeed, ponds are typically drained or filled in when encountered during peat mining. In contrast to upland ponds, bog ponds are typically acidic (i.e., pH = ~4.0) and devoid of fish (Mazerolle 2005). Each study year, we selected a subset of 12 ponds in each peat landscape through randomized stratified sampling across distance of the ponds to the mined edge to ensure that we covered a gradient of distances (Fig. 1). Two of the sampled ponds in one of the landscapes were

later deleted from the data set because both their pH and emergent vegetation cover were considerably greater than is typical for bog ponds (pH > 5.21 vs. ~4.0; emergent cover >43.8% vs. 8.8%). Thus, this paper deals with the 70 remaining bog ponds.

Amphibian sampling

We used a combination of visual (Crump and Scott 1994) and call surveys (Scott and Woodward 1994) to detect the presence of adult and juvenile amphibians at the ponds. Because decomposing peat (>1 m deep) on the ponds' bottom rendered wading impossible, we limited our searches to pond perimeters. Sampling effort was standardized across ponds to efficiently search the entire perimeter of each pond. On a given year, each pond was surveyed on five occasions, spread over five sampling periods (mid-May, mid-June, mid-July, late July, and mid-August) during which green frogs (*Rana clamitans*) were active and breeding in the study area (Mazerolle and Cormier 2003). We randomized the sequence of the ponds surveyed within each landscape for each sampling period.

On a given visit, we established a transect (2 m × length of the entire pond perimeter) along the pond perimeter to assess green frog presence. The starting point of the visual survey on the pond perimeter was determined randomly. We then systematically walked along each transect while scanning and listening for amphibians. Call stations were spaced at 20-m intervals on pond perimeters (range: 2–36 stations per pond), and consisted in stopping and listening during 30 s for any green frog calls. Total time spent listening and searching at a pond during a single visit varied between 2 and 98 min. We searched ponds between 16:00 and 24:00 hours, under similar meteorological conditions (i.e., low winds, no precipitation, air temperature >10°C), using a headlamp after dusk.

Pond characteristics

We measured pond perimeter in the field. Water samples were taken within the first 30 cm of the water column at three locations in each pond to determine pH and conductivity. Bog water chemistry typically does not fluctuate greatly across the season (Vitt 1994). Thus, we considered our sampling sufficient to obtain representative values for each pond. We measured water depth within 1 m of the shoreline at the calling stations on pond perimeters (i.e., 20-m intervals). We used the mean values of pH, conductivity, and water depth at each pond in all analyses.

We measured vegetation cover on the shoreline and in the water with 3 × 1-m quadrats centered on each call station (i.e., between 2 and 36 quadrats per pond, proportional to pond size). The center of each quadrat was at the interface of the shore and the water, so that an area of 1.5 × 1 m was sampled on the shoreline and in the water. We categorized vegetation structure on the basis of height and life form: tree layer >3 m; three

shrub layers 0.5–3 m, 30–50 cm, 10–30 cm, and <10 cm; herb layer (herbaceous vegetation); moss layer (*Sphagnum* spp. and lichens); submerged vegetation; emergent vegetation; and floating vegetation. We quantified vegetation cover according to a semi-quantitative scale: <5% but rare, <5% but abundant, 5–25%, 25.1–50%, 50.1–75%, and >75%). See Appendix A for descriptive statistics of microhabitat variables.

Due to the large number of vegetation variables, we used principal components analysis (PCA) to summarize the information with the first four axes explaining a total of 76.6% of the variation (Appendix B). The first axis (VEG1) was strongly correlated with the cover of tall shrubs and emergent vegetation, and the second (VEG2) was an index of low shrubs and moss cover. Herbs and floating vegetation were summarized by the third axis (VEG3), whereas the fourth axis (VEG4) represented submerged and floating vegetation. The principal component scores for ponds on the PCA axes were used in subsequent analyses.

Landscape characteristics

We used georeferenced digital 1:10 000 orthophotomaps based on 1996 aerial photographs and obtained from the New Brunswick provincial government (Service New Brunswick 2001) to build a geographic information system in ArcView 3.1 (ESRI 1996) for each of our three peat landscapes. After classifying each habitat type, we created buffer areas (i.e., concentric measures sensu Vos and Stumpel 1995) of 100, 250, 500, and 1000 m around each of the ponds we sampled. We limited our analyses to 1000 m because most pond-breeding amphibians move <1 km within the landscape to reach breeding, summering, and hibernation habitats (Dodd 1996, Semlitsch and Bodie 2003). We then calculated the area of forest habitat, pond habitat, and surfaces mined for peat in the buffer areas surrounding each of the ponds we sampled. Correlations of cover among scales varied between $r = -0.07$ (pond cover at 100 and 1000 m, $n = 70$) and $r = 0.93$ (mined surface cover at 250 and 500 m, $n = 70$). However, spatial overlap between scales was not considered an issue here, as our analyses did not assume independence of the regressors. We also measured the distance of each pond to the nearest adjacent pond, forest patch, mined surface, and road. Appendix C summarizes the descriptive statistics for each landscape-scale variable.

Statistical analyses

Because each pond was surveyed on five occasions, we used site-occupancy models (MacKenzie et al. 2002) to assess green frog occurrence at ponds across microhabitat and landscape variables. This type of model, analogous to capture–recapture models, allows to distinguish between the probability of occurrence (ψ) and the probability of detection (p) (MacKenzie et al. 2002). These models enable the inclusion of site variables (e.g., patch size, habitat type) as well as time-

TABLE 2. Set of candidate models considered to explain green frog occurrence at 70 bog ponds sampled either in 1999 or 2000 in mined peat landscapes.

Model name	Model structure†		No. parameters†
	ψ	p	
Pond-scale models			
Pond size	year perim depth	effort airtemp	7
Pond vegetation structure group 1	year VEG1 VEG2	effort airtemp	7
Pond vegetation structure group 2	year VEG3 VEG4	effort airtemp	7
Pond water	year pH cond	effort airtemp	7
Landscape-scale models			
Distance to adjacent habitat	distforest distpond	effort airtemp	7
Distance to disturbance	distroad distmined	effort airtemp	7
Percent cover of adjacent habitat‡	forestcov watercov	effort airtemp	7
Percent cover of adjacent disturbance‡	minedcov	effort airtemp	6
Hybrid models§			
Pond scale + distance to habitat		see models above	9
Pond scale + cover of habitat		see models above	9
Pond scale + distance to disturbance		see models above	9
Pond scale + cover of disturbance		see models above	8

Note: Terms in the columns for ψ, the probability of occurrence, and p, the probability of detection given the presence of the species, are the variables included for each.

† Intercept parameters for ψ and p were included in all models. Fifty-four models were run for three scenarios of p (i.e., effort and airtemp, effort only, and p constant).

‡ This model was run for each of the four landscape scales (i.e., 100, 250, 500, and 1000 m).

§ These consisted of every combination of a pond-scale model (e.g., vegetation, pond size, water chemistry) with a landscape-scale model (e.g., habitat cover, proximity of disturbance).

varying covariates (e.g., air temperature at a site on a given visit) and show great promise for use in field studies (see Mackenzie et al. 2002 for a thorough discussion of these models).

Initially, we considered a set of 54 site-occupancy models consisting of microhabitat and landscape variables, either alone or combined, to determine to what extent landscape variables influence species occurrence (Table 2). These included four microhabitat models likely to explain frog presence at the ponds: pond size, pond water chemistry, cover of shrubs and moss (VEG1 and VEG2), and cover of herbs and aquatic vegetation (VEG3 and VEG4). Two landscape models consisted of the distance to either the nearest potential habitat or disturbance. The other landscape models included the cover of either habitat or mined surfaces within 100, 250, 500, and 1000 m of each sampled pond (Table 2). More complex models were then built by combining microhabitat and landscape-scale variables. All models included the intercept on both ψ and p. Because the probability of detecting green frogs could be influenced by the sampling effort (i.e., observer hours) and air temperature at each pond, models were run once with effort and air temperature on p, then with effort only, and finally, with p constant (i.e., intercept only). Thus, our total set of models consisted of 162 candidate models. Mantel tests (Manly 1997, Bonnet and van de Peer 2002) of the geographic distance between sampled ponds and the frog presence suggested a very low spatial autocorrelation ($r = -0.0039$, $P = 0.4009$, 100 000 permutations). Based on this evidence, we did not include any covariate to account for spatial dependence

among ponds. We systematically added a categorical year variable (i.e., 1999 vs. 2000) as a covariate in all models.

Site-occupancy analyses were run with program PRESENCE (Mackenzie et al. 2003) which is specifically designed for site-occupancy data. All continuous variables were standardized (i.e., the mean was subtracted from each value and then divided by the SD) before being entered in analyses. Collinearity diagnostics did not reveal any confounding effects between independent variables. The estimated c-hat value for site-occupancy models was close to 1 and did not suggest overdispersion or lack of fit (Burnham and Anderson 2002). We ranked each site-occupancy model based on the second-order Akaike Information Criterion (AIC_c) and we computed delta AIC_c and Akaike weights to determine the strength of evidence for each model (Burnham and Anderson 2002). We then performed model averaging to obtain estimates and associated standard errors for each parameter of interest (Burnham and Anderson 2002).

We compared the results of site-occupancy models (i.e., accounting for the probability of detection) to those obtained using conventional logistic regression (McCullagh and Nelder 1989). For the logistic regression analyses, we designated a site as occupied when green frogs were detected on a least one of the five visits. We used the same model-building approach as described above for the site-occupancy models (Table 2). Here, however, each regression model had 1–3 parameters fewer than its site-occupancy counterpart, because logistic regressions did not account for the prob-

TABLE 3.   Highest-ranked occupancy models of green frogs at ponds in peat landscapes undergoing peat mining.

Model structure		No. parameters	ΔAIC_c	Akaike weight
ψ	p			
year VEG3 VEG4 forestcov1000 watercov1000	effort	8	0	0.52
year VEG3 VEG4 forestcov1000 watercov1000	effort airtemp	9	1.61	0.23
year VEG3 VEG4 forestcov500 watercov500	effort	8	3.63	0.09
year VEG3 VEG4 forestcov250 watercov250	effort	8	4.67	0.05
year forestcov100 watercov100	effort	6	4.71	0.05

Notes: Notation follows Table 2; AIC_c of the highest-ranking model = 288.08. Models with Akaike weights <0.05 are not shown for clarity.

ability of detection (i.e., no parameter for either the intercept, effort, or air temperature). We ran a first series of 54 models with the log of the total time spent searching and listening at each pond as an offset variable to account for the sampling effort, whereas a second series of 54 models did not account for effort. As in the analyses above, we computed the AIC_c and associated measures of strength of evidence for each logistic regression model before computing model-averaged estimates and standard errors. Based on the Hosmer and Lemeshow statistic (Hosmer and Lemeshow 1989), logistic regression models did not significantly lack fit.

RESULTS

We detected green frogs at 51.4% of the ponds during the surveys. Site-occupancy models, which accounted for the probability of detection, suggested that 77.0 ± 5.8% (model-averaged estimate ± 1 unconditional SE) were occupied by green frogs, with a detection rate of 21.4 ± 12.9%. Models including pond vegetation structure (herbaceous and submerged vegetation) and the amount of potential neighboring habitat ranked high in explaining green frog occurrence at ponds (Tables 3 and 4). The ''best'' model given our set of candidate models consisted of pond vegetation structure and the percent cover of forest and ponds within 1000 m, with effort on p. This model was followed relatively closely (Akaike weight = 0.23) by the one consisting of the same variables for the probability of occurrence, but with effort and air temperature on the probability of detection.

Ranking of the variables based on their relative importance, denoted as the sum of Akaike weights (w_+) of the models that include the variable of interest, revealed that herb cover and the cover of floating and submerged vegetation were the most important (w_+ = 0.93) in explaining the probability of frog occurrence at the ponds. They were followed by the amount of adjacent pond and forest cover within 1000 m (w_+ = 0.76). There was little evidence of an effect of the other microhabitat and landscape variables we considered in our study, as these variables had a low relative importance (i.e., w_+ < 0.09). Sampling effort was the most important variable explaining the probability of detection (w_+ = 1), whereas air temperature was far less important (w_+ = 0.27).

Based on model averaging, the probability of green frog occurrence increased strongly with the pond cover within 100, 250, and 1000 m (Tables 3 and 4). Frogs were likely to occur at ponds that had high forest cover within 1000 m of their perimeter. At a finer scale however, forest cover within 250 m decreased the occurrence of frogs. To a lesser degree, the proximity of adjacent mining decreased pond occupancy (model-averaged estimate ± 1 unconditional SE, −1.202 ± 0.797). Similarly, the cover of floating and submerged vegetation (VEG4) tended to affect frog occurrence at the ponds (model-averaged estimate ± 1 unconditional SE, −6.506 ± 4.282). Sampling effort strongly influenced the probability of detecting green frogs at the ponds during surveys, whereas air temperature did not have such an effect.

Site-occupancy vs. logistic regression

The logistic regression analyses, which did not account for the probability of detection, revealed patterns different from the ones observed in site-occupancy models. Though two of the highest-ranked logistic regression models (i.e., Akaike weights = 0.06–0.28)

TABLE 4.   Model-averaged beta estimates for parameters of the site-occupancy models of green frogs at ponds in peat landscapes undergoing peat mining.

Parameters on ψ					Parameter on p
Pond cover (%)			Forest cover (%)		
100 m	250 m	1000 m	250 m	1000 m	Effort
38.550 (14.618)	11.203 (5.996)	7.291 (3.313)	−5.112 (2.573)	4.218 (2.286)	0.782 (0.163)

Notes: Values in parentheses are unconditional standard errors. Parameters for which 0 is excluded from the 90% confidence interval are shown.

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TABLE 5. Highest-ranked logistic regression models of green frogs at ponds in peat landscapes undergoing peat mining.

Model name	Inclusion of effort as offset	Number of parameters	ΔAIC_c	Akaike weight
Year VEG3 VEG4 minedcov100	yes	7	0	0.28
Year minedcov100	yes	5	1.41	0.14
Year perim watdepth minedcov100	no	7	1.62	0.12
Year perim watdepth minedcov100	yes	7	2.29	0.09
Year VEG3 VEG4	yes	6	3.14	0.06
Year pH cond minedcov100	yes	7	3.63	0.05

Notes: The intercept was included in all models, and notation follows Table 2; AIC_c of highest-ranking model = 84.07. Models with Akaike weights <0.05 are not shown for clarity.

included pond vegetation structure, they suggested that the amount of mined surfaces within 100 m of the pond influenced frog presence (Tables 5 and 6). Indeed, the amount of mined surfaces within 100 m had a greater relative importance than the vegetation structure (i.e., 0.69 vs. 0.49). These variables were followed by pond perimeter and pond depth, which both had a relative importance of 0.27. Model averaging revealed that out of the original variables considered, only two pond variables (VEG3 and VEG4) had a strong effect on green frog occurrence, as their 90% confidence intervals excluded 0. Based on the analyses, frog occurrence was influenced to a lesser degree by pond perimeter (model-averaged estimate ± 1 unconditional SE, 0.893 ± 0.568), distance to mined edge (−0.624 ± 0.382), pond cover within 100 m (0.568 ± 0.364) and cover of mined surfaces within 100 m (1.390 ± 0.893) and 250 m (0.591 ± 0.380). Few of these variables were deemed important based on the site-occupancy analyses.

DISCUSSION

Pond characteristics

Few pond microhabitat variables influenced the occurrence of green frogs at ponds. Indeed, only the cover of floating and submerged vegetation tended to affect frog occurrence. Although the importance of pond size on frog presence has been well documented for amphibians in other systems (e.g., Dickman 1987, Laan and Verboom 1990, Bradford et al. 2003), we did not detect such a relationship in peatland systems. This suggests that frogs frequent both small and large bog ponds. Other patch quality characteristics often explain

TABLE 6. Model-averaged beta estimates for parameters of the logistic regression models of green frogs at ponds in peat landscapes undergoing peat mining.

VEG3	VEG4
0.624 (0.350)	−0.708 (0.369)

Notes: Values in parentheses are unconditional standard errors. Parameters for which 0 is excluded from the 90% confidence interval are shown. VEG3, cover of herbs and floating vegetation; VEG4, cover of floating and submerged vegetation.

occurrence patterns of amphibians at ponds (e.g., Hecnar 1997, Hecnar and M'Closkey 1998, Pope et al. 2000), but not in our study. For instance, water chemistry (pH and conductivity), a well known determinant of amphibian distribution (e.g., Gosner and Black 1957, Freda 1986), did not influence pond occupancy. This probably results from the low variability of pond-scale characteristics among ponds.

Landscape characteristics

Landscape-level variables substantially explained pond occupancy. Two types of measures of pond isolation influenced frog occurrence: adjacent pond cover and forest cover. Pond occupancy increased with the percent cover of ponds within a radius of 100, 250, and 1000 m. Although pond cover was weakly correlated across these scales ($-0.07 < r < 0.48$; $n = 70$), frogs responded consistently at the scales we investigated. This agrees with amphibian spatial patterns observed in other systems (e.g., Marsh et al. 1999, Joly et al. 2001, Johnson and Semlitsch 2003) and could result from a metapopulation structure of green frogs. However, pond occupancy should be investigated on a longer time scale to support this hypothesis.

The effect of forest cover is more difficult to interpret, however. At 250 m, high forest cover decreased frog occurrence at ponds, whereas it increased frog occurrence at 1000 m. Skelly et al. (2002) and Werner and Glennemeier (1999) observed that high canopy cover at ponds can reduce the development of certain amphibian species, but it is unclear how far this effect extends from the pond. Alternately, the importance of forest cover at 1000 m may result from the confounding effects of high forest cover at the periphery of peatlands associated with low cover of disturbed surfaces (e.g., roads, mined surface, residential areas). Regardless, experiments are required to further investigate this phenomenon. Based on their recent review, Marsh and Trenham (2001) suggested that isolation from terrestrial habitat (e.g., proximity of terrestrial habitat) could be even more important than isolation from other ponds. In our study however, the effect of forest cover within different radii of the pond was weaker than pond cover and differed across scales.

Dry environments can impede the movements of amphibians, given their physiology (Rothermel and Semlitsch 2002; M. J. Mazerolle and A. Desrochers, *unpublished manuscript*). However, the amount and proximity of peat mining did not greatly influence pond occupancy by green frogs, which was unexpected. Though the relationship was not as strong as the ones relating pond occupancy and the amount of adjacent habitat at a given radius, frogs tended to occur most often at ponds near mined edges. Thus, the presence of peat mining seems to favor the use of ponds near edges and suggests mined surfaces are a barrier to amphibian movement. In support of this hypothesis, Mazerolle and Desrochers observed that green frogs released on mined surfaces were less likely to home successfully than those released on natural bog areas, and that when given a choice, most individuals avoided peat surfaces (M. J. Mazerolle and A. Desrochers, *unpublished manuscript*). Similar movement patterns have also been observed in amphibians in logged forests and old fields (Johnston and Frid 2002, Rothermel and Semlitsch 2002, Chan-McLeod 2003).

Management implications

Our model predicts that pond occupancy by green frogs in peatland systems depends on pond cover within 100, 250, and 1000 m (i.e., pond isolation) as well as the amount of forest cover within radii of 250 and 1000 m. Results not only highlight the importance of the amount and proximity of adjacent ponds, but also of forest cover, though the latter relationship seems to vary greatly across scales. In addition, frogs did not avoid ponds near mined edges, which suggests they are valuable conservation areas in peatlands undergoing disturbance.

The loss of wetlands, accompanying increasing land use, remains a serious concern in a variety of landscapes and many investigators have raised the need to preserve both large and small isolated wetlands (e.g., Semlitsch and Bodie 1998, Gibbs 2000, Snodgrass et al. 2000). However, the sole protection of ponds is insufficient for amphibian conservation and additional landscape components such as terrestrial habitat must be included (e.g., Pope et al. 2000, Guerry and Hunter 2002, Gibbons 2003, Houlahan and Findlay 2003, Johnson and Semlitsch 2003). Based on our data and the evidence from a number of amphibian studies (e.g., Vos and Stumpel 1995, Vos and Chardon 1998, Pope et al. 2000), including such parameters in models of amphibian distribution in the landscape will improve their efficiency. Our study reinforces that maintaining a complex of ponds as well as adjacent terrestrial habitat should enhance amphibian movements between ponds and their persistence in the landscape.

The value of bog ponds near mined edges in conservation remains problematic. Indeed, it is possible that ponds near mined edges have higher rates of extinction and colonization than other ponds far from such a disturbance. Unfortunately, we could not measure such population parameters because each pond was sampled for only one season. Long-term investigations with multiple visits each year are required to assess whether ponds near mined edges function as sinks sensu Pulliam (1988) or are truly valuable assets for conservation in peatlands.

Site-occupancy models vs. logistic regressions

Many differences arose between the two modelling approaches. For instance, few of the variables identified by logistic regressions as efficient predictors of frog presence at ponds were important based on site-occupancy analyses. Furthermore, ignoring the detectability of green frogs either overestimated or underestimated the influence of certain variables on frog occurrence at the ponds in our study system. Gu and Swihart (2004) also reported that nondetection produces biased logistic regression parameter estimates. For data with randomly distributed nondetections, they found that a negative habitat coefficient can lead to overestimation, whereas a positive coefficient can lead to underestimation. Similarly, in our data, where detectability depended strongly on sampling effort, the logistic regressions underestimated the effect of most variables for which the site-occupancy analyses yielded a positive coefficient. However, VEG3, as well as the cover of mined surfaces within 100 and 250 m were overestimated, despite having a positive coefficient. In addition, logistic regressions overestimated the effect of VEG4, for which site-occupancy analyses had yielded a negative sign. These results indicate that the behavior of estimates in analyses omitting detectability require further study.

We strongly recommend using site-occupancy models, or at least formally addressing the issue of detectability in future studies, as a number of methods to do so have been developed (e.g., Boulinier et al. 1998, Kéry 2002, MacKenzie et al. 2002, 2003, Tyre et al. 2003, Gu and Swihart 2004). The alternative is risking the introduction of errors in spatial models derived from the data. For instance, Moilanen (2002) reported that using empirical data without properly accounting for detectability can greatly overestimate all metapopulation model components, which can have serious implications in conservation. The degree of overestimation will likely depend on the detectability of the species investigated, but requires further investigation. We do not question the validity or the need for studies in landscape ecology based on field surveys, if anything, we encourage more studies of the sort, but emphasize that care should be taken when analyzing and interpreting data without accounting for the probability of detection, or at least provide evidence addressing the issue.

Conclusion

In conclusion, our study conducted in peatland landscapes undergoing peat mining revealed that the oc-

currence of frogs at ponds increases with pond cover within 100, 250, and 1000 m (i.e., pond isolation), as well as with forest cover within 1000 m. At 250 m, however, forest cover decreases frog occurrence. Frogs were slightly more likely to occupy ponds near mined edges, which may indicate their value in conservation. However, we did not detect any effect of the amount of mined surfaces on frog occurrence at any given scale. Based on our results, preserving a complex of bog ponds and adjacent habitat may mitigate the effect of peat mining on amphibian populations in peatlands. In addition, we showed that failing to account for probability of detection in field studies can overestimate the effects of certain variables, and has serious implications on the value of models derived from them.

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APPENDIX A

A table showing descriptive statistics of microhabitat variables at bog ponds ($N = 70$ ponds) sampled within mined peatlands in eastern New Brunswick, Canada, is available in ESA's Electronic Data Archive: *Ecological Archives* A015-021-A1.

APPENDIX B

A table showing factor loadings of principal components analysis (PCA) used to summarize vegetation structure data at bog ponds of eastern New Brunswick, Canada, is available in ESA's Electronic Data Archive: *Ecological Archives* A015-021-A2.

APPENDIX C

A table showing descriptive statistics of landscape-scale variables around bog ponds ($N = 70$ ponds) sampled within mined peatlands in eastern New Brunswick, Canada, is available in ESA's Electronic Data Archive: *Ecological Archives* A015-021-A3.