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**MOUVEMENTS ET REPRODUCTION DES
AMPHIBIENS EN TOURBIÈRES PERTURBÉES**

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Résumé court

Les déclin de populations d'amphibiens ont généré de nombreux travaux sur les effets de la perte d'habitats variés, mais peu en milieux naturellement acides. Néanmoins, plusieurs tourbières du sud-est canadien sont perturbées par l'extraction de la tourbe. Dans le premier chapitre, j'ai comparé l'utilisation des milieux tourbeux par les amphibiens à celle des milieux non tourbeux. Dans les quatre chapitres subséquents, j'ai quantifié les effets de l'extraction de la tourbe sur l'utilisation des étangs de tourbières par les amphibiens et mesuré les contraintes liées à leurs déplacements sur des surfaces exploitées. Les résultats indiquent que les amphibiens utilisent les tourbières surtout comme sites d'estivage. De plus, l'intensité de l'exploitation influence la fréquentation des étangs, mais la quantité et la proximité d'habitats complémentaires (i.e., étangs adjacents, forêt) semblent réduire ces effets. Finalement, les surfaces arides associées à certaines activités anthropiques telles que l'exploitation des tourbières ou l'agriculture, entravent les déplacements des grenouilles, bien que ces effets puissent être atténués par la présence de canaux de drainage.

Résumé long

Les déclinés de populations d'amphibiens ont généré de nombreux travaux sur les effets de la perte d'habitats variés, mais peu en milieux naturellement acides. Néanmoins, plusieurs tourbières du sud-est canadien sont perturbées par l'extraction de la tourbe. À travers cinq chapitres, j'ai étudié l'utilisation des milieux tourbeux par les amphibiens, quantifié les effets de l'extraction de la tourbe sur leur utilisation des étangs de tourbières et mesuré les contraintes liées à leurs déplacements sur des surfaces exploitées. Les tourbières se prêtaient moins bien à la reproduction que les milieux moins acides environnants, mais elles étaient toutefois utilisées par les adultes et les juvéniles après la reproduction à l'extérieur des tourbières. Les étangs de tourbières sur les surfaces de tourbe exploitées procuraient un habitat suboptimal pour les grenouilles vertes (*Rana clamitans*). Par contre, les étangs de la zone en préparation à l'exploitation, caractérisée par la présence de canaux de drainage et de végétation, offraient des habitats supplémentaires aux grenouilles. Cet effet positif n'était que temporaire, car ces zones allaient être éventuellement exploitées. Dans une étude effectuée à plus grande échelle et ciblant uniquement les étangs en section naturelle à proximité de la bordure exploitée pour la tourbe, j'ai démontré l'importance de la quantité et de la proximité d'habitats complémentaires (i.e., étangs adjacents, forêt) sur la répartition spatiale des amphibiens aux étangs. Par ailleurs, mes expériences sur les mouvements ont révélé que la probabilité de retour de grenouilles relocalisées sur les surfaces exploitées était inférieure à celle des individus relocalisés sur les surfaces naturelles, et que les risques de déshydratation étaient les plus faibles sur les surfaces naturelles avec couverture végétale. Aucune reproduction des amphibiens ne fut observée dans les canaux de drainage, bien que les taux de survie des grenouilles dans ces structures y étaient élevés. De plus, les canaux de drainage n'entravaient pas les déplacements des individus. Globalement, mes résultats indiquent que les amphibiens utilisent les tourbières surtout comme sites d'estivage. De plus, l'intensité de l'exploitation influence la fréquentation des étangs, mais la quantité et la proximité d'habitats complémentaires pourraient réduire ces effets. Finalement, les surfaces exploitées entravent les déplacements des grenouilles, bien que ces effets puissent être atténués par les canaux de drainage, particulièrement ceux contenant de l'eau en périphérie des tourbières.

Abstract

Global amphibian population declines have generated numerous studies on the effects of habitat loss, but few have been conducted in naturally-acidic environments. Nevertheless, many peatlands are undergoing peat extraction in southeastern Canada. Through five chapters, I have studied the use of bog habitats by amphibians, quantified the effects of peat extraction on amphibian occurrence at bog ponds, and measured the constraints associated with movements over mined surfaces. Bogs were less productive breeding sites than less acidic upland sites, but were used by adults and juveniles following breeding outside bogs. Bog ponds on surfaces actively mined for peat offered suboptimal habitats to green frogs (*Rana clamitans*), whereas bog ponds on surfaces drained for future peat mining, characterized by the presence of drainage ditches and vegetation, provided supplementary frog habitat. However, this positive effect was only temporary, as these surfaces were to be eventually mined. In a study conducted at a larger scale and focusing on bog ponds on unmined surfaces, I showed the importance of the amount and proximity of complementary habitats (i.e., adjacent ponds, forest) on the spatial distribution of amphibian presence at ponds. Moreover, frog movement experiments revealed that frogs translocated on barren peat surfaces had a lower probability of homing successfully than those translocated at a similar distance on an undisturbed surface, and that dehydration risks were the lowest on natural surfaces with vegetation cover. No reproduction occurred in drainage ditches, although frog survival in these structures was high. In addition, ditches did not impede the movements of individuals. Globally, results indicate that amphibians use bogs mostly as summering sites. Furthermore, peat mining intensity influences the occurrence of amphibians at ponds, but the proximity and amount of complementary habitats could mitigate these effects. Finally, barren surfaces associated with certain human disturbances such as peat mining and agriculture impede frog movements, although drainage ditches, particularly those containing water, may facilitate movements across these hostile environments.

Avant-propos

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Introduction générale

La fin de la dernière glaciation (i.e., 10 000 – 12 000 BP) a initié la formation de systèmes accumulateurs de tourbe, les tourbières, qui dominent encore aujourd'hui une partie des continents nord-américain, européen et asiatique (Glaser et Janssens 1986, Gorham 1990, Warner et al. 1991, Vitt 1994, Payette et Rochefort 2001, Payette et Bouchard 2001). Ces milieux humides naturellement acides couvrent environ 4 millions de km² (3-4%) du globe, et la plupart sont répartis dans les régions boréales, principalement au Canada et dans les états de l'ex-Union Soviétique (Maltby et Proctor 1996). On estime que les tourbières constituent 17% de la superficie du territoire canadien (Gorham 1990), alors que les systèmes forestiers en occupent environ 45% (Neave et al. 2002).

De prime abord, les tourbières sont considérées peu accueillantes par bien des gens, en raison des conditions humides qui y prévalent et de l'abondance des insectes piqueurs qu'on y trouve (Larson et House 1990). Néanmoins, elles jouent un rôle important au niveau de plusieurs processus régionaux et globaux. En effet, ces milieux approvisionnent en eau les lacs et les systèmes de rivières et peuvent agir comme tampon contre les sécheresses ou les inondations, tout en réduisant l'érosion (Gorham 1984, Glaser et al. 1997, Price 2001). Les tourbières naturelles sont également des puits de carbone qui influencent considérablement le bilan de carbone à l'échelle du globe (Gorham et al. 1984, Gorham 1991, Moore 2001, Joosten et Clarke 2002). De plus, les tourbières contribuent à la diversité faunique et végétale régionale, plusieurs espèces y étant inféodées ou utilisant ces milieux pendant au moins une partie de leur cycle vital (Rosenberg et Danks 1987, Larson et House 1990, Poulin et al. 1999, Desrochers 2001, Mazerolle et al. 2001, Rochefort 2001). Finalement, les tourbières sont également fréquentées par les gens en quête d'espaces sauvages, pour l'observation de la nature, la chasse, la cueillette de petits fruits ou de plantes médicinales (Rochefort 2001).

On reconnaît deux grands types de tourbières, soient les tourbières minérotrophes et ombrotrophes. Les tourbières minérotrophes, appelées également fens, ont un apport en eau et en minéraux provenant de la nappe phréatique, de l'écoulement de milieux aquatiques adjacents et des précipitations (Vitt 1994, Payette 2001). Elles sont caractérisées par des dépôts de tourbe de moins de 40 cm et d'un pH généralement supérieur à 4,4 (Zoltai 1988).

Dans les tourbières ombrotrophes ou bogs, l'eau et les nutriments proviennent uniquement des précipitations. Les tourbières ombrotrophes, plus pauvres en matières nutritives que les fens et avec un pH oscillant autour de 4,0, se démarquent aussi par la profondeur de leur dépôt de tourbe pouvant atteindre jusqu'à 10 m (Schwintzer 1981, Gorham et al. 1984, Wells et Hirvonen 1988, Vitt 1994, Payette et Rochefort 2001). C'est d'ailleurs la présence de profonds dépôts de tourbe dans les tourbières ombrotrophes qui est en partie responsable du statut précaire de ces tourbières dans certaines régions du globe.

Les tourbières ombrotrophes subissent des pressions croissantes de l'humain. Le drainage pour l'agriculture, l'industrie forestière et l'urbanisation, ou l'inondation pour les développements hydro-électriques, sont responsables de la perte de vastes superficies de tourbières (Prévost et al. 2001, Poulin et Pellerin 2001, Joosten et Clarke 2002). De son côté, l'industrie de l'extraction de la tourbe (i.e., destinée au marché horticole ou utilisée comme combustible) agit sur des superficies généralement plus modestes, mais réduit la végétation de surface à néant. Suite aux pressions industrielles, peu de tourbières sont demeurées intactes en Europe occidentale (Poulin et Pellerin 2001). Bien que moins de 1% des surfaces de tourbières soient exploitées au Canada, l'extraction de la tourbe est concentrée dans le sud-est du pays, la majeure partie de la tourbe extraite étant destinée au marché horticole (Keys 1992, Daigle et al. 2001, Poulin et Pellerin 2001,). Les tourbières des régions du Bas-Saint-Laurent au Québec et de l'Est du Nouveau-Brunswick sont particulièrement touchées par ces perturbations (Keys 1992, Daigle et al. 2001, Pellerin 2003). À l'instar de l'exploitation des forêts progressant de plus en plus vers le nord, l'exploitation des tourbières a débuté dans le sud du pays, en raison de la proximité des milieux urbains (et de main d'œuvre) et d'un réseau de transport bien développé (Payette et Rochefort 2001). Les tourbières méridionales diffèrent en termes de structure et de biodiversité de leurs homologues des régions arctiques et subarctiques qui sont moins accessibles (Zoltai 1988, Payette et Bouchard 2001). Ainsi, l'exploitation systématique des systèmes tourbeux méridionaux a engendré des préoccupations au niveau de la conservation.

Les activités liées à l'extraction de la tourbe modifient radicalement les milieux tourbeux. Lors de la préparation du site, on établit de larges réseaux de canaux de drainage qui perturbent le régime hydrologique et on retire la végétation de surface afin d'accéder à

la tourbe (Wheeler et Shaw 1995, Rochefort 2001). Les surfaces de tourbe sont labourées et la tourbe est ensuite récoltée par couches successives de quelques centimètres à l'aide d'aspirateurs motorisés ou tirés par des tracteurs (Wheeler et Shaw 1995, Rochefort 2001). Dépourvues de couverture végétale, les surfaces de tourbe qui s'assèchent deviennent des milieux potentiellement hostiles pour plusieurs espèces végétales et fauniques (Wheeler et Shaw 1995, Poulin et al. 1999, Delage et al. 2000, Mazerolle 2001, 2003, Campbell et al. 2003).

Tout comme certaines pratiques forestières, l'exploitation des tourbières génère des milieux ouverts de grandes dimensions et peu complexes, dépourvus de couverture végétale et dont l'hydrologie est perturbée, ce qui se traduit, de façon plus immédiate, en une perte d'habitat pour plusieurs espèces floristiques et fauniques (Bury 1983, Chen et al. 1993, deMaynadier et Hunter 1995, Rothwell et al. 1996, Dupuis 1997, Butts et McComb 2000, Price 2001). Les systèmes non tourbeux ont fait l'objet de plusieurs travaux sur la perte d'habitat associée ou non à la fragmentation (p. ex., Andrén 1994, Bender et al. 1998, Mazerolle et Villard 1999, Fahrig 2003). Ces travaux montrent que dans plusieurs cas, la perte d'habitat influence la répartition des organismes dans les milieux adjacents.

Les mouvements des organismes et la perte d'habitat

Les écologistes ont eu recours pendant longtemps à des phénomènes tels que la sélection d'habitat (p. ex., Miller 1942, Sexton et Heatwole 1968, Rosenzweig 1973, Anderson et Shugart 1974) ou la compétition et la prédation (revue dans Connell 1983, Sih et al. 1985) afin d'expliquer la répartition des animaux, et ce, à de fines échelles spatiales. Au cours des années 1980, l'intérêt s'est déplacé progressivement du côté des phénomènes se manifestant à l'échelle du paysage, pour donner naissance à une nouvelle discipline: l'écologie du paysage. Depuis, la majorité des études en conservation vise à prédire la répartition spatiale et la pérennité des organismes dans le temps, ainsi qu'à la suite de perturbations naturelles et anthropiques (p. ex., Andrén 1994, Fahrig et Merriam 1994, Bender et al. 1998, McGarigal et Cushman 2002). Certains ont tenté de démontrer empiriquement différents aspects de la dynamique des parcelles dans le paysage, notamment en utilisant la théorie de la biogéographie insulaire (MacArthur et Wilson

1963), les dynamiques source-gouffre (« *source-sink* », Pulliam 1988, Dias 1996) et les modèles de paysages neutres (« *neutral landscapes* », With et King 1997). Toutefois, la théorie des métapopulations est demeurée la plus populaire auprès des biologistes de la conservation (Hanski et Gilpin 1997, Hastings et Harrison 1994, Marsh et Trenham 2001). Fait remarquable, chacune de ces théories comporte une composante sur les mouvements des organismes.

Pour un animal, la réussite d'un déplacement dans un paysage (p. ex., d'une parcelle d'habitat à une autre) dépend de deux facteurs principaux: sa capacité à détecter la parcelle d'habitat cible et sa capacité à l'atteindre. La détection est un problème de perception (i.e., « *perceptual range* » *sensu* Zollner et Lima 1997) et cette dernière peut varier selon l'espèce, la distance et les conditions météorologiques (Yeomans 1995, Zollner et Lima 1997, 1999, Gillis et Nams 1998). Toutefois, nous ne connaissons pratiquement rien de la variabilité de la capacité de détection des milieux, qu'ils soient perturbés ou non. Une fois la parcelle cible détectée, l'individu doit l'atteindre. L'atteinte d'un milieu dépend de la « résistance » du paysage (*sensu* Ricketts 2001) aux déplacements des organismes. Ici sont impliqués des éléments tels que la nature de la matrice (i.e., le milieu dans lequel sont imbriquées les parcelles), la distance entre les parcelles, la physiologie et le comportement de l'organisme et le risque de prédation (Henein et Merriam 1990, Sjögren-Gulve 1994, Larsen et Boutin 1994, Rosenberg et al. 1998, Bonnet et al. 1999, Rothermel et Semlitsch 2002, Turcotte et Desrochers 2003).

Afin de prédire la variabilité des effectifs de populations suite aux perturbations anthropiques, la plupart des travaux en conservation ont ciblé les patrons d'abondance ou de présence animale dans des parcelles d'habitat (Andrén 1994, Bender et al. 1998, Mazerolle et Villard 1999, Fahrig 2003). Ces patrons ont longtemps servi à inférer les mécanismes (p. ex., les mouvements) de régulation des populations. Néanmoins, l'attention s'est récemment dirigée sur l'évaluation directe des effets de la perte d'habitat et de la fragmentation sur les mouvements de certains organismes, tels que les oiseaux (p. ex., Desrochers et Hannon 1997, Bélisle et al. 2001, Bélisle et Desrochers 2002, Desrochers et al. 2003), les arthropodes (Pither et Taylor 1998, McIntyre et Wiens 1999, Schooley et Wiens 2003) et les mammifères (Diffendorfer et al. 1995, Coffman et al. 2001, Bowman et Fahrig 2002, McDonald et Sinclair 2004). Toutefois, de telles études demeurent encore

rares ou inexistantes pour plusieurs taxons. Ceci est particulièrement vrai pour le groupe des amphibiens (mais voir Vos 1999, Rothermel et Semlitsch 2002, Chan-McLeod 2003) et résulte en partie des contraintes logistiques (p. ex., coût et taille d'émetteurs télémétriques), comportementales et écologiques associées à ce groupe. Étant donné le statut précaire de certaines populations d'amphibiens, il est devenu prioritaire d'étudier ces organismes pour mieux comprendre leurs mouvements et mieux orienter les efforts de conservation.

Les déclinés de populations d'amphibiens

Depuis les deux dernières décennies, on relate des déclinés de populations d'amphibiens à différents points du globe (Barinaga 1990, Vitt et al. 1990, Wyman 1990, Wake 1991, Blaustein et al. 1994*a*, Green 1997, Alford et Richards 1999, Lips 1998, 1999, Houlahan et al. 2000). Les chercheurs ont mis en cause une série d'agents potentiellement responsables de ces baisses d'effectifs. Notamment, on identifie l'augmentation du rayonnement ultraviolet (Blaustein et al. 1994, Starnes et al. 2000, Belden et Blaustein 2002*a, b*), les changements climatiques (Rohr et Madison 2003), les pathogènes et parasites (Laurance et al. 1996, Berger et al. 1998, Johnson et al. 2002), l'introduction d'espèces exotiques (Funk et Dunlap 1999, Adams 2000, Matthews et al. 2001, Doubledee et al. 2003), les pesticides (Davidson et al. 2002) ou une combinaison de plusieurs de ces facteurs (Gendron et al. 2003), comme responsables des déclinés. Toutefois, la perte d'habitat et la fragmentation demeurent les facteurs les plus souvent mentionnés comme causes des déclinés (Alford et Richards 1999, Semlitsch 2000). Plusieurs travaux ont montré que la perte et la fragmentation de l'habitat résultant de la création de routes ou de certaines pratiques forestières et agricoles, réduisent la richesse en espèces et l'abondance des populations d'amphibiens ainsi que leur diversité génétique (Petranka et al. 1993, deMaynadier et Hunter 1995, Dupuis 1997, Findlay et Houlahan 1997, Waldick 1997, Hitchings et Beebe 1998, Vos et Chardon 1998, Koloszyvary et Swihart 1999, Grialou et al. 2000, Joly et al. 2001, Scribner et al. 2001, Davidson et al. 2002). Néanmoins, les mécanismes expliquant ces patrons, tel les mouvements de dispersion, demeurent encore peu étudiés (mais voir Rothermel et Semlitsch 2002, Johnston et Frid 2002), bien qu'ils constituent des éléments essentiels de la dynamique des populations d'amphibiens.

Les déplacements dans le paysage et les risques associés

Les amphibiens qui se reproduisent en étangs utilisent différents éléments aquatiques et terrestres du paysage à différentes périodes de l'année afin de compléter leur cycle vital (Sinsch 1990, Pope et al. 2000; Pilliod et al. 2002). Les amphibiens sont capables de migrations de quelques kilomètres, mais leurs déplacements sont généralement inférieurs à 400 m (Dodd 1996, Semlitsch et Bodie 2003). Ainsi, atteindre les habitats de reproduction, d'estivage ou d'hibernation peut s'avérer risqué pour un individu lorsque ces milieux sont séparés par des environnements hostiles résultant de perturbations anthropiques. Par exemple, la coupe à blanc, l'agriculture et l'exploitation des tourbières, génèrent des milieux ouverts et des conditions sèches (Bury 1983, Chen et al. 1993, Wheeler and Shaw 1995, Dupuis 1997, Price 1997). Ces milieux pourraient entraver les mouvements des individus entre différents habitats. En effet, les déplacements sur ces surfaces comportent des risques: les milieux dépourvus de couvert végétal peuvent augmenter la probabilité de prédation, et plus directement, mener à la déshydratation.

Étant donné la grande perméabilité de leur épiderme, les amphibiens nécessitent des environnements humides, et s'aventurent rarement loin de ces milieux (Sinsch 1990). Ils livrent une bataille perpétuelle contre la déshydratation, et la plupart des espèces ne tolèrent pas des pertes en eau excédant 40% de leur masse corporelle (Thorson et Svihla 1943, Littleford et al. 1947, Ray 1958). En conditions sèches, certaines espèces ont adopté des comportements spécialisés, tels que s'enfouir dans le sol ou se retirer dans des cavités, afin de réduire les pertes en eau (Bentley 1966, Katz 1989, Schwarzkopf et Alford 1996, Prather et Briggler 2001). Le bilan hydrique chez les salamandres et les anoues a fait l'objet de plusieurs recherches (p. ex., Thorson et Svihla 1943, Littleford et al. 1947, Cohen 1952, Ray 1958, Schmid 1965, Claussen 1969, Bentley 1966, Spight 1968, Spotila 1972, Hillman 1980, 1987, Prest et Pough 1989, Jørgensen 1997). Néanmoins, la plupart des expériences sur la déshydratation et la réhydratation ont été effectuées en laboratoire dans des conditions artificielles (mais voir Packer 1963, Dole 1967, Parris 1998, Rothermel et Semlitsch 2002, Seebacher et Alford 2002). À ce jour, peu d'expériences sur le bilan hydrique des amphibiens ont été réalisées afin d'aborder la problématique des perturbations anthropiques, qui génèrent des conditions sèches, et de leurs conséquences sur les populations d'amphibiens (mais voir Rothermel et Semlitsch 2002).

Donc, les déplacements des individus dans les paysages comportent des risques qui peuvent influencer la connectivité fonctionnelle entre les parcelles (*sensu* Taylor et al. 1993), et par le fait même, la pérennité des populations dans le paysage. Afin d'en arriver à des prévisions fiables quant à la viabilité des populations d'amphibiens, il faut tester des hypothèses et effectuer des expériences dans différents types de paysage. En régions tempérées, la plupart des études sur les populations d'amphibiens ont été effectuées en milieux forestiers ou agricoles, alors que très peu l'ont été dans des milieux naturellement acides, qui pourtant occupent une partie importante des régions boréales. Ceci constitue une lacune, car la plupart des travaux du genre se limitent à des milieux soumis à l'acidification anthropique.

Les amphibiens en milieux acides

Pendant les années 1980 et 1990, les préoccupations liées aux effets des précipitations acides ont généré plusieurs travaux sur les amphibiens, particulièrement dans le contexte des déclin de populations d'amphibiens (Pierce 1985, Freda 1986, Wyman 1991, Dunson et al. 1992). La plupart de ces études, effectuées tant en laboratoire qu'en milieu naturel, ont évalué les effets du pH sur les stades embryonnaires et larvaires. Les conditions acides peuvent interférer avec la fertilisation des oeufs (Schlichter 1981), ralentir le développement des embryons et des têtards ainsi que réduire leur survie (p. ex., Gosner et Black 1957, Saber et Dunson 1978, Strijbosch 1979, Dunson et Connell 1982, Clark et Hall 1985, Clark et LaZerte 1985, Gascon et Bider 1985, Pierce 1985, Cummins 1986, Leuven et al. 1986, Pierce et Montgomery 1989, Bradford et al. 1992, Pahkala et al. 2001, Räsänen et al. 2003). Un faible pH entraîne également des pertes de sodium chez les individus, qui dans certains cas, peuvent s'avérer fatales (Haines 1981, Freda et Dunson 1984, McDonald et al. 1984, Moore et Klerks 1998). De plus, les interactions avec d'autres facteurs, tels que la présence de compétiteurs et la concentration de certains métaux influencent également l'effet du pH sur le développement des amphibiens (Sadinski et Dunson 1992, Horne et Dunson 1995; Pehek 1995; Warner et al. 1993, Long et al. 1995, Kiesecker 1996).

Chez les amphibiens, la tolérance à l'acidité varie selon l'espèce (Gosner et Black 1957, Karns 1992), diffère entre et à l'intérieur des populations (Pierce and Wooten 1992, Glos et al. 2003, Räsänen et al. 2003), et augmente au fil du développement (i.e., de l'embryon à l'adulte; Pierce 1985). Néanmoins, les effets du pH sur les individus métamorphosés (i.e., juvéniles et adultes) sont moins bien documentés. Les travaux existants se sont surtout limités à l'observation de la répartition des juvéniles et des adultes de certaines espèces dans des milieux acidifiés par les activités anthropiques (Mushinsky et Brodie 1975, Freda et Dunson 1986, Wyman 1988, Wyman et Hawksley-Lescault 1987, Wyman et Jancola 1992, Sugalski et Claussen 1997, Bunnell et Zampella 1999, Vatnick et al. 1999, Simon et al. 2002).

Bien que certaines espèces d'amphibiens se reproduisent dans les environnements naturellement acides, tels que les tourbières (p. ex., *Rana arvalis*, Andrén et al. 1989; *Hyla andersonii* et *Rana virgatipes*, Freda et Dunson 1986, Pehek 1995, Bunnell et Zampella 1999), les études sur les amphibiens dans de tels milieux sont peu nombreuses (Tableau 1). La diversité en espèces d'amphibiens des milieux naturellement acides est généralement inférieure à celle des milieux environnants, mais on peut y trouver jusqu'à 75% de la richesse régionale de ce taxon (Tableau 1). Ceci est particulièrement vrai pour le Nouveau-Brunswick et la Nouvelle-Écosse, où les milieux naturellement acides, en l'occurrence les tourbières, recouvrent une grande partie du territoire (Tableau 1).

Tableau 1. Composition en espèces d'amphibiens évaluée lors d'études en milieux naturellement acides. Le pourcentage de richesse régionale représente la proportion des espèces d'amphibiens répertoriées dans chacune des régions qui furent également trouvées en milieux naturellement acides.

Référence	Région (nombre de sites)	% de richesse régionale	Composition en espèces d'amphibiens en milieux acides [†]
Marshall et Buell (1955)	Minnesota (1)	33.3	Rapi, Rase, Rasy, Hyve, Pscr, Psni, Buam
Heatwole et Getz (1960)	Michigan (1)	21.7	Racl, Rapi, Rasy, Buam, Amje
Bellis (1965)	Minnesota (1)	28.6	Rana pi, Rasy, Hyve, Pscr, Psni, Buam
Saber et Dunson (1978)	Pennsylvanie (1)	17.6	Racl, Rapa, Rasy, Pscr, Novi, Psru
Dale et al. (1985)	Nouvelle-Écosse (25)	61.5	Raca, Racl, Rapa, Rasy, Pscr, Buam, Amla, Amma
Stockwell et Hunter (1989)	Maine (9)	75.0	Raca, Racl, Rapa, Rapi, Rasy, Pscr, Buam, Novi, Amla, Amma, Defu, Eubi
Karns (1992)	Minnesota (1)	33.3	Rapi, Rasy, Hyve, Pscr, Pstr, Buam, Amla
Bunnell et Zampella 1999	New Jersey (14)	31.2	Racl, Rasp, Rasy, Ravi, Accr, Hyan, Hyve, Pscr, Psfe, Bufo,
Mazerolle 2001	Nouveau-Brunswick (12)	62.5	Racl, Rapi, Rase, Rasy, Pscr, Buam, Novi, Amla, Amma, Plci

[†]Accr: *Acris crepitans*, Amje: *Ambystoma jeffersonianum*, Amla: *Ambystoma laterale*, Amma: *Ambystoma maculatum*, Buam: *Bufo americanus*, Bufo: *Bufo fowleri*, Defu: *Desmognathus fuscus*, Eubi: *Eurycea b. bislineata*, Hyan: *Hyla andersonii*, Hyve: *Hyla versicolor*, Novi: *Notophthalmus v. viridescens*, Plci: *Plethodon cinereus*, Pscr: *Pseudacris crucifer*, Psfe: *Pseudacris feriarum*, Psni: *Pseudacris nigrata*, Psru: *Pseudotriton ruber*, Pstr: *Pseudacris triseriata*, Raca: *Rana catesbeiana*, Racl: *Rana clamitans*, Rapa: *Rana palustris*, Rapi: *Rana pipiens*, Rase: *Rana septentrionalis*, Rasp: *Rana sphenoccephala*, Rasy: *Rana sylvatica*, Ravi: *Rana virgatipes*.

Objectifs et structure de la thèse

Les paysages dominés par les tourbières naturelles et exploitées présentent un intérêt particulier pour les études à grandes échelles, particulièrement dans l'est du continent. En effet, les tourbières de ces régions sont de grandes tailles tandis que les surfaces exploitées sont à la fois démarquées par des bordures bien définies et quadrillées par un réseau de canaux de drainage (Wells et Hirvonen 1988, Wheeler et Shaw 1995, Robert et al. 1999, Payette et Rochefort 2001, Rochefort 2001). De plus, les étangs qui s'y trouvent sont aussi menacés pendant les activités d'exploitation, puisqu'ils sont comblés ou drainés. Le statut précaire des tourbières ombrotrophes du sud-est canadien, le statut précaire des populations d'amphibiens en milieux perturbés, la pénurie de données concernant l'utilisation des milieux naturellement acides par les amphibiens, et l'insuffisance d'information sur les mouvements de ces organismes, particulièrement dans un contexte de perte d'habitat, ont motivé la préparation de cette thèse.

La présente étude est composée de cinq chapitres qui abordent trois objectifs principaux: 1) évaluer l'utilisation par les amphibiens des tourbières et des milieux environnants, 2) mesurer les effets de l'exploitation des tourbières sur la fréquentation par les amphibiens des étangs de tourbières, et 3) quantifier la capacité des amphibiens de se déplacer sur des surfaces naturelles et exploitées de tourbières. Plusieurs des chapitres traitent de la grenouille verte (*Rana clamitans melanota*), une espèce sensible aux perturbations anthropiques et trouvées dans les tourbières (Bonin et al. 1997, Knutson et al. 1999, Koloszvary et Swihart 1999, Mazerolle 2001, 2003, Woodford et Meyer 2003, Renken et al. 2004).

Dans le premier chapitre, je teste l'hypothèse générale que les amphibiens utilisent les milieux tourbeux comme site d'estivage. Pour ce faire, je compare l'utilisation des tourbières et des milieux environnants comme milieux de reproduction de la grenouille verte. Afin d'évaluer si les amphibiens juvéniles et adultes utilisent ou évitent les milieux tourbeux, je quantifie les mouvements des amphibiens entre les tourbières et les milieux forestiers environnants, et je mesure la sélection de différents substrats (i.e., terre, eau, sphaigne).

Dans le cadre du deuxième chapitre, je prédis que la présence des grenouilles aux étangs de tourbières dépend de l'intensité des activités d'extraction de tourbe. Afin de tester cette prédiction, j'étudie la fréquentation et la reproduction des grenouilles vertes dans des étangs de tourbières soumises à différents degrés de perturbation reflétant les différentes étapes de leur exploitation: 1) surface naturelle (i.e., végétation intacte, absence de canaux de drainage), 2) surface exploitée (i.e., absence de végétation, présence de canaux), 3) surface en préparation d'exploitation (i.e., végétation intacte, présence de canaux).

Dans le troisième chapitre, j'avance que les facteurs intrinsèques aux étangs influencent la présence des amphibiens à ces mêmes étangs. En fait, j'évalue l'influence de facteurs intrinsèques aux étangs (p. ex., taille de l'étang, pH) et de facteurs extrinsèques (p. ex., proximité de surface exploitée, quantité de surfaces aquatiques dans un rayon donné) sur la fréquentation des étangs de tourbières par les amphibiens.

Lors du quatrième chapitre, je teste l'hypothèse que les déplacements des amphibiens sur les surfaces de tourbes sont plus difficiles que sur les surfaces naturelles. Ainsi, je quantifie les contraintes aux déplacements de grenouilles vertes (*Rana clamitans melanota*) et de grenouilles léopards (*Rana pipiens*) dans les milieux tourbeux. Pour ce faire, je quantifie la capacité d'orientation et la probabilité de retour d'individus relocalisés sur des surfaces naturelles et perturbés. J'évalue également les taux de déshydratation des grenouilles sur différentes surfaces (i.e., terre, tourbe, sphaigne) afin d'évaluer les contraintes physiologiques imposées par chacune de ces surfaces.

Pour le cinquième chapitre, je teste les hypothèses que les canaux de drainage sont des sites de reproduction d'amphibiens et que ces structures n'influencent ni la survie ni la reproduction des grenouilles. Pour ce faire, j'évalue la reproduction, la survie et les déplacements d'individus marqués dans les canaux de drainage des tourbières exploitées. En utilisant différentes méthodes d'échantillonnage, dont des techniques de marquage-capture-recapture, je détermine l'utilisation de différents types de canaux de drainage par la grenouille verte (*R. c. melanota*).

Plusieurs des résultats des différents chapitres de cette thèse, obtenus à partir des études des patrons et des comportements des amphibiens à différentes échelles spatiales,

sont interprétés et discutés dans une problématique de conservation et de dynamique des populations.

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Chapitre 1

Peatlands and amphibians: a relationship regulated by acidity?

Mazerolle, M. J. En révision. **Peatlands and amphibians: a relationship regulated by acidity?** Écoscience. Centre de recherche en biologie forestière, Pavillon Abitibi-Price, Faculté de Foresterie et de Géomatique, Université Laval, Québec, Québec, Canada G1K 7P4 et Groupe de recherche en écologie des tourbières, Pavillon Paul-Comtois, Université Laval, Québec, Québec, Canada G1K 7P4.

Résumé

Les répercussions des précipitations acides sur les populations d'amphibiens ont été étudiées intensivement pendant les deux dernières décennies. Néanmoins, les amphibiens en milieux naturellement acides, tels que les tourbières menacées par l'industrie de l'extraction de la tourbe, ont reçu très peu d'attention. Lors de deux études sur le terrain et d'une expérience, j'ai évalué l'utilisation de milieux tourbeux par la grenouille verte (*Rana clamitans melanota*), une espèce sensible à l'exploitation forestière et à l'extraction de la tourbe. Premièrement, j'ai comparé la fréquentation et la reproduction des grenouilles en étangs de tourbières à celles des étangs en milieux terrestres. J'ai ensuite caractérisé les mouvements des grenouilles entre les milieux tourbeux et les milieux forestiers adjacents, afin de déterminer s'ils correspondaient à des migrations de reproduction ou de post-reproduction. Finalement, j'ai évalué, par l'entremise d'une expérience de terrain, la valeur des tourbières comme milieux de réhydratation pour les amphibiens, en offrant trois types de médias (i.e., de la mousse de sphaigne, de l'eau, et de la terre saturée en eau) à des grenouilles légèrement déshydratées. La reproduction des grenouilles vertes dans les étangs de tourbières était rare et aucun mouvement net de grenouilles vertes n'a été détecté entre les milieux forestiers et tourbeux. Néanmoins, les grenouilles légèrement déshydratées n'évitaient pas la sphaigne. Malgré la faible probabilité de reproduction des grenouilles vertes en tourbières et l'absence de mouvements *en masse* entre les milieux forestiers et tourbeux, les grenouilles n'évitent pas les substrats tourbeux pour se réhydrater, malgré leur acidité. Ainsi, les tourbières offrent des habitats d'estivage aux amphibiens, ce qui souligne l'importance de ces milieux menacés dans l'écologie terrestre des amphibiens.

Abstract

The effects of site acidification on amphibian populations have been thoroughly addressed in the last decades. However, amphibians in naturally-acidic environments, such as peatlands facing pressure from peat mining industry, have received little attention. Through two field studies and an experiment, I assessed the use of bog habitats by the green frog (*Rana clamitans melanota*), a species sensitive to various forestry and peat mining disturbances. First, I compared the occurrence and breeding patterns of frogs in bog and upland ponds. I then evaluated frog movements between forest and bog habitats to determine whether they corresponded to breeding or postbreeding movements. Finally, I investigated, through a field experiment, the value of bogs as rehydrating areas for amphibians by offering three types of media (i.e., *Sphagnum* moss, water, and water-saturated soil) to acutely-dehydrated frogs. Green frog reproduction at bog ponds was a rare event and no net movements occurred between forest and bog habitats. However, acutely-dehydrated frogs did not avoid *Sphagnum*. Results show that although green frogs rarely breed in bogs and do not move *en masse* between forest and bog habitats, they do not avoid bog substrates for rehydrating, despite their acidity. Thus, bogs offer summering habitat to amphibians, which highlights the value of these threatened environments in terrestrial amphibian ecology.

INTRODUCTION

The concern over acidic precipitations, especially in the context of amphibian population declines, has generated an impressive quantity of papers during the late 1980's and early 1990's (e.g., Freda 1986, Wyman 1991, Dunson et al. 1992). Whether in field or laboratory conditions, most investigations on the effects of low pH have focused on the embryonic or larval stages (Gosner and Black 1957, Saber and Dunson 1978), with few studies on juvenile and adult amphibians (but see Wyman 1988, Sugalski and Claussen 1997, Simon et al. 2002). Indeed, several have shown the adverse affects of pH alone or in combination with other variables (e.g., predation or competition, concentrations of certain toxic metals) on amphibian development (Horne and Dunson 1995, Pehek 1995, Pakkala et al. 2001). Although some species successfully breed in naturally-acidic environments (e.g.,

Rana arvalis: Andr n et al. 1989; *Hyla andersonii* and *Rana virgatipes*: Pehek 1995, Bunnell and Zampella 1999), amphibian populations occurring in such habitats have received very little attention. For instance, studies in peatlands (i.e., bogs and fens) remain scarce (e.g., Stockwell and Hunter 1989, Karns 1992a, b).

Peatlands are naturally acidic wetlands covering approximately 4 million km² of the Earth's surface, and occur mostly in boreal countries, mainly Canada and the former states of the Soviet Union (Maltby and Proctor 1996). The deep peat deposits in some types of peatlands, namely bogs, have been facing increasing pressures from the peat mining industry and few have remained unaltered in western Europe (Wheeler and Shaw 1995, Poulin and Pellerin 2001, Joosten and Clarke 2002). This trend is also becoming apparent in bogs of southeastern Canada, where most of the peat mined is intended for horticultural use on the continent or abroad. Although certain amphibian species are known to occur in bogs (Marshall and Buell 1955, Bellis 1965, Stockwell and Hunter 1989, Karns 1992a, b) and are sensitive to peat mining (Mazerolle 2001, 2003a), it remains unclear to what extent they use these habitats (i.e., breeding vs summering) relative to other, less acidic sites.

I evaluated the use of bog habitats (i.e., relative to upland habitats) by the green frog (*Rana clamitans melanota*), a species common in bogs and sensitive to anthropogenic disturbances such as agricultural or urban development (Bonin et al. 1997, Koloszvary and Swihart 1999, Woodford and Meyer 2003) and peat mining (Mazerolle 2001, 2003a). First, I compared green frog breeding and abundance patterns in bog ponds to those in upland ponds. Second, as bogs remain moist throughout summer and could offer valuable amphibian summering habitats during dry periods, I evaluated whether green frogs move *en masse* from forest to bog habitats during their season of activity (i.e., during or after reproduction). Finally, I determined experimentally whether or not acutely-dehydrated frogs select *Sphagnum* as a substrate for rehydration when offered as a choice against water or water-saturated soil.

MATERIALS AND METHODS

Study Area

I conducted this study in eastern New Brunswick, Canada (Fig. 1). The study area

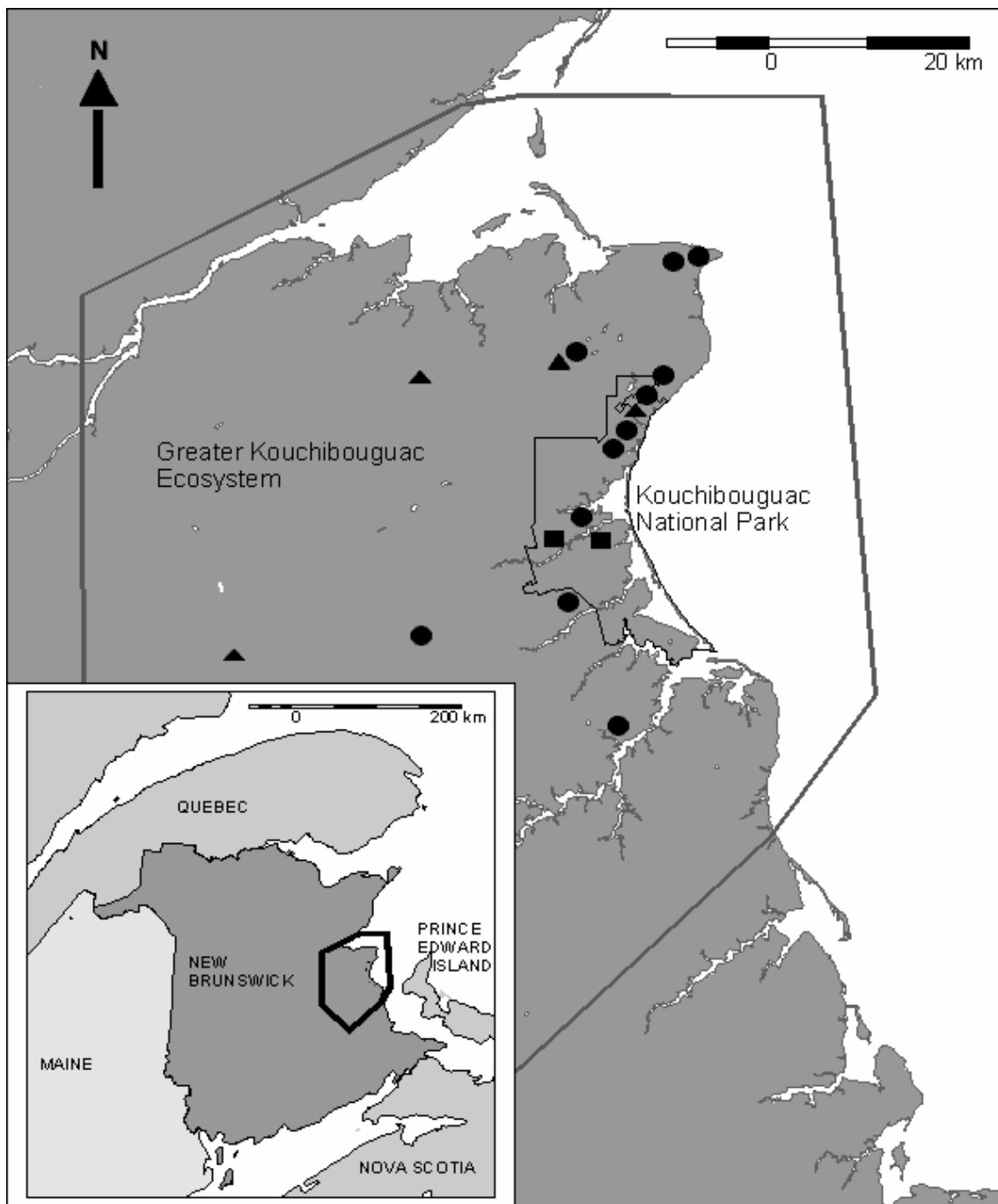


Figure 1. Location of green frog sampling sites in the Greater Kouchibouguac Ecosystem, in eastern New Brunswick, Canada. Circles indicate upland or bog pond sites for the pond use study, triangles indicate drift-fence sites for the study of movements at the bog-forest interface, and squares represent the location of bogs sampled for both studies. Note that a single point can represent several ponds.

includes Kouchibouguac National Park under federal legislation with relatively little disturbance, whereas the surrounding area is subjected to forestry, peat mining activities, and moderate rural development. Peatlands make up 8.6% of the landscape. Most of these consist in ombrotrophic peat bogs, i.e., peatlands with low pH (ca. 4.0) with mineral and water inputs depending chiefly on precipitations (Schwintzer 1981, Gorham et al. 1984, Vitt 1994). Upland habitats mainly consist in mixed forest dominated by black spruce (*Picea mariana*), balsam fir (*Abies balsamea*), white pine (*Pinus strobus*), red pine (*P. resinosa*), maple (*Acer* spp.) and birch (*Betula* spp.), and abandoned fields.

Bog vs Upland Ponds

In order to assess the potential of bogs as breeding habitat for green frogs, I selected 12 bog ponds and 12 upland ponds within the study area (Fig. 1). Bog ponds were chosen to match the size of upland ponds. Upland ponds were located next to roads in the study area in the proximity of mixed forest, whereas bog ponds (i.e., 2 ponds/bog) were all in open bog habitat at least 1 km from peat mining. I recorded the geographic position of each pond in UTM coordinates and accounted for pond location in the analyses (see below).

I characterized each pond according to microhabitat variables. I estimated visually the vegetation cover at each pond: % of pond area with overhanging, floating, and emergent vegetation, as well as the % of pond perimeter with shrub and tree cover. At each pond, I took three water samples within the first 30 cm of the water column to determine pH and conductivity and also measured mean water depth 1 m from the shore. Descriptive statistics for the habitat variables mentioned above are given in Table 1.

Several meters of decomposing peat at the bottom of the bog ponds rendered wading impossible at these sites. Thus, we used anuran calling and trapping surveys to sample amphibians at all ponds. Green frogs were sampled with 15-min call surveys, during which two investigators were placed at opposite ends of the pond. Surveys were conducted after sunset. I used a call index to estimate green frog abundance at ponds: 0 (no frogs calling), 1 (1 individual calling), 2 (> 1 individual calling, and can be counted), 3 (chorus, individuals cannot be distinguished). Each pond was sampled on 2 occasions

during the green frog breeding season, except for 2 upland ponds which dried up. The first sweep was conducted between 5 and 17 July 2002, and the second between 30 July and 4 August 2002. Surveys were conducted under similar weather conditions: mean air temperature (\pm SD) of 19.4 ± 2.6 °C, low wind and no precipitations.

Table 1. Habitat characteristics (mean \pm SD) of bog and upland ponds of eastern New Brunswick, Canada.

Variable	Bog pond (<i>n</i> = 12)	Upland ponds (<i>n</i> = 12)
Perimeter (m)	279.3 \pm 192.2	194.2 \pm 111.6
Depth 1-m from the shore	0.72 \pm 0.23	0.23 \pm 0.12
Water chemistry		
pH	3.67 \pm 0.27	5.54 \pm 0.98
Conductivity (μ S)	55.8 \pm 17.9	271.3 \pm 551.0
Vegetation structure		
Overhanging vegetation (%)	0	0.2 \pm 3.2
Floating vegetation (%)	9.0 \pm 11.9	11.1 \pm 22.5
Emergent vegetation (%)	8.1 \pm 14.3	32.2 \pm 30.5
Trees (> 3 m) on perimeter (%)	0.2 \pm 0.3	60 \pm 27.7
Shrubs (< 3 m) on perimeter (%)	7.7 \pm 9.0	18.4 \pm 21.1

I used minnow traps in each pond to sample tadpoles (see Mazerolle and Cormier 2003 for trap details). The number of traps deployed in each pond was proportional to pond size (i.e., two traps for the first 25 m² and an additional trap each time the area doubled *sensu* Adams et al. 1997). Between 4 and 10 traps were placed in the ponds. These were checked for three consecutive days between 21 and 27 July 2002, for a total trapping effort of 531 trap nights, where one trap night equates to one trap open for one night.

Because two surveys were conducted at each pond, I analysed the call index value across bog and upland ponds using Poisson regression for repeated measures (Diggle et al. 1994, Horton and Lipsitz 1999, Stokes et al. 2000). I included a pond type categorical variable to account for differences between bog and upland pond vegetation and water characteristics. I also included the variables pond perimeter and depth. The x and y UTM coordinates (i.e., divided by 10 000 to obtain smaller values) were used in the models to account for spatial relationships. I considered 13 models based on the above-mentioned variables to explain green frog abundance in the ponds. I ranked the models according to the second-order Akaike Information Criterion (AIC_c). Delta AIC_c values < 2 and high Akaike weights (interpreted as a probability) identified the most likely models given the set of candidate models considered. I then used model-averaging techniques to obtain estimates for each variable and their standard errors and computed 95% confidence intervals to measure the influence of each variable on frog abundance at the ponds (Pan 2001, Burnham and Anderson 2002). Please refer to Appendix 1 for detailed instructions on how to compute and interpret the results of the analysis of ecological data using this approach.

Forest-bog Movements

This component of my study assessed whether mass frog movements occurred between bog and forest habitats, as this would indicate that frogs use bogs either as breeding or summering habitat. I conducted the work in three unmined bogs of Kouchibouguac National Park and three bog remnants adjacent to peat mining operations within the Greater Kouchibouguac Ecosystem (Fig. 1). Bogs of the study area are typically surrounded by black spruce (*Picea mariana*) stands, which can tolerate harsh acidic

conditions. I established two sampling stations within each bog at the interface between the bog and forest habitat. This was the location most likely to intercept frogs moving between the two habitats. For the purpose of the study, I selected only abrupt edges between the bog and forest habitats. I considered the point where trees reached a height > 3 m as the start of forest habitat. Bog habitat, on the other hand, consisted of a continuous cover of *Sphagnum* spp. and shrub layer (10-50 cm) dominated by ericaceous shrubs (*Kalmia angustifolia*, *K. polifolia*, *Chamaedaphne calyculata*, *Rhododendron groenlandicum*, *Andromeda glaucophylla*, *Vaccinium* spp., *Gaylussacia baccata*, and *G. dumosa*). The position of each sampling station was determined randomly across all suitable locations in each bog based on the vegetation structure and composition, the distance to roads (i.e., at least 1 km from road), and the distance to the mined edge for bog remnants (ca. 150 m).

A straight-line aluminum drift fence (10 m x 60 cm in height, 20 cm of which was below ground) was erected parallel to the forest and bog edge at each sampling station in 2001 (Fig. 2). Each fence was associated with 6 pitfall traps: 3 on each side of the fence at 5 m intervals. I added 55-cm wide side-flaps (aluminum flashing) at the end of each fence to avoid capturing the amphibians that moved along the forest-bog edge. Pitfall traps consisted of 11.4-L plastic buckets with rims as described in Mazerolle (2003b). Traps were visited every 4 days. Each captured frog was measured to snout-vent length (SVL), marked with a toe-clip, before being released 5 m on the other side of the fence. Trapping was conducted in 2001 from 18 May to 1 September, and in 2002, from 30 June to 2 September, for a total capture effort of 11 880 trap nights. Traps were closed with tight-fitting lids when not in use.

Each year was divided in two trapping periods (i.e., before/during breeding vs following breeding), based on the dates at which green frogs are known to breed in the study area (Oseen and Wassersug 2002, Mazerolle unpubl. data). At each site and for each trapping period, I summed the captures from the bog side of the two fences (i.e., excluding recaptures), then did the same for captures on the forest side. This yielded the number of individuals moving from the bog to the forest (and vice versa) at each site during and following breeding. I then assigned a value of 1 to sites where more individuals came from the bog than the forest, and 0 otherwise. This value can also be considered as the probability that frogs moved from the bog to the forest (i.e., analogous to presence/absence

data). It was used as the response variable in logistic regressions for repeated measures (Diggle et al. 1994, Horton and Lipsitz 1999, Stokes et al. 2000), because each site had a datum for each trapping period (i.e., repeated measures).

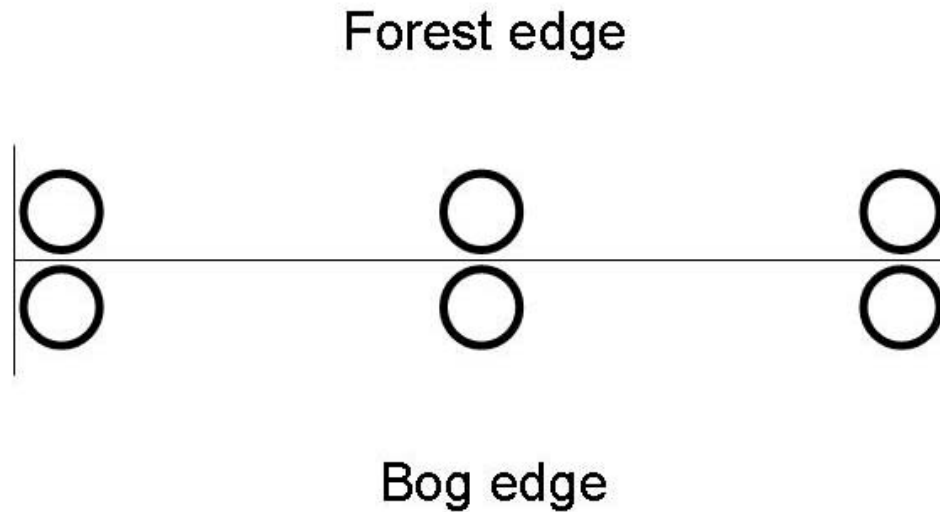


Figure 2. Design of 5-m drift-fence with side flaps and pitfall traps with rims used to detect green frog movements between bog and forest habitats. Lines represent aluminum flashing fence, circles denote pitfall traps.

I analyzed the two years of data separately. For each, I considered a set of 3 plausible models explaining the patterns of green frog captures based on mining disturbance (undisturbed vs adjacent peat mining) and period (breeding vs post-breeding). One model contained the intercept only, whereas the second and third consisted of the intercept with either the period or disturbance variable. Conclusions were based on the AIC_c and related measures (Appendix 1).

Selection of Rehydration Substrate

Bogs, unlike upland habitats, generally remain humid during dry periods and could offer rehydration habitat for amphibians in the summer. However, *Sphagnum* moss releases hydrogen ions (Clymo 1963, 1964, Andrus 1986) which generates acidic conditions that could deter juvenile and adult amphibians from using bogs. To test this hypothesis, I evaluated experimentally whether acutely-dehydrated green frogs actively avoid bog substrates (i.e., living *Sphagnum* moss). Frogs were captured between 29 July and 8 August 2001 at a large flooded quarry in the study area. The individuals were temporarily housed in plastic containers with water for no more than 24 h before starting the experiments.

To simulate dehydrating conditions during dry periods, frogs (weighed to the nearest 0.1 g) were placed singly in containers (54.5 x 39 x 22 cm in depth) covered with window screening. These containers lay in the shade under an opaque tarpaulin in an open mowed field devoid of any vegetative cover > 1 cm. Individuals were allowed to dehydrate for 2 h before their mass lost in water was assessed. Preliminary trials revealed that this procedure prevented green frogs from dehydrating beyond the vital limits recorded for the species by Thorson (1955) and Schmid (1965). Thus, I refer to frogs submitted to the 2-h desiccation period as acutely-dehydrated frogs. Once dehydrated, individuals were immediately transferred to the substrate selection experiment.

The selection experiment was conducted in a plastic container (54.5 x 39 x 14 cm depth) divided into three compartments of equal dimensions with wooden lathes and silicone. One compartment contained soil, another *Sphagnum* moss, and a third held well water. All substrates were saturated with well water prior to trials, but in all cases, the water level remained below the substrate surface to provide a clear choice between water and the substrates. The height of the dividers matched the depth of the substrate (i.e. ca. 5 cm), allowing the frog to move freely across the three media. The container was covered with window screening and placed in the shade under an opaque tarpaulin during trials.

At the start of a substrate selection trial, a frog was introduced in a container on one of the three rehydration media (determined randomly). I subsequently recorded the position of the frog (i.e., the medium selected) at 15-min. intervals during 3 h for a total of 12 observations for each individual. Twenty-one frogs (mean SVL \pm SD: 5.39 \pm 1.55 cm) were

submitted to the substrate selection experiment. Each was used only once and released at its point of capture at the end of the trial. All trials were conducted between 29 July and 8 August 2001 between 1200 and 1800.

I tabulated the frequencies of occurrence on each substrate to determine which was most often selected by each individual. I then used logistic regressions (McCullagh and Nelder 1989) to evaluate whether substrate selection (i.e., *Sphagnum* vs other media) in acutely-dehydrated frogs depended on initial frog mass, the type of medium on which the frog was placed at the start of the trial, or the state of dehydration (i.e., mass lost by frog during acute dehydration).

RESULTS

Bog vs Upland Ponds

I detected calling male green frogs in 33% of the bog ponds, whereas males were heard calling in 75% of the upland ponds. Male abundance was greater in upland ponds than in bog ponds (Figure 3, Table 2). Large ponds also had a greater number of calling males, regardless of the pond type (Table 2). In contrast, neither pond depth nor geographic position influenced the abundance of calling frogs. No tadpoles were caught with minnow traps in bog ponds, but 58% of upland ponds had at least one captured green frog tadpole. Although leopard frogs (*Rana pipiens*) also occurred at some bog ponds, spring peepers (*Pseudacris crucifer*), mink frogs (*Rana septentrionalis*), wood frogs (*Rana sylvatica*), red-spotted newts (*Notophthalmus viridescens*), spotted salamanders (*Ambystoma maculatum*) and blue-spotted salamanders (*Ambystoma laterale*) heard or detected during trapping surveys were limited to upland ponds. Large invertebrate predators (*Belostoma* sp., *Dytiscus* sp., Nepidae, and Odonata) occurred in all ponds.

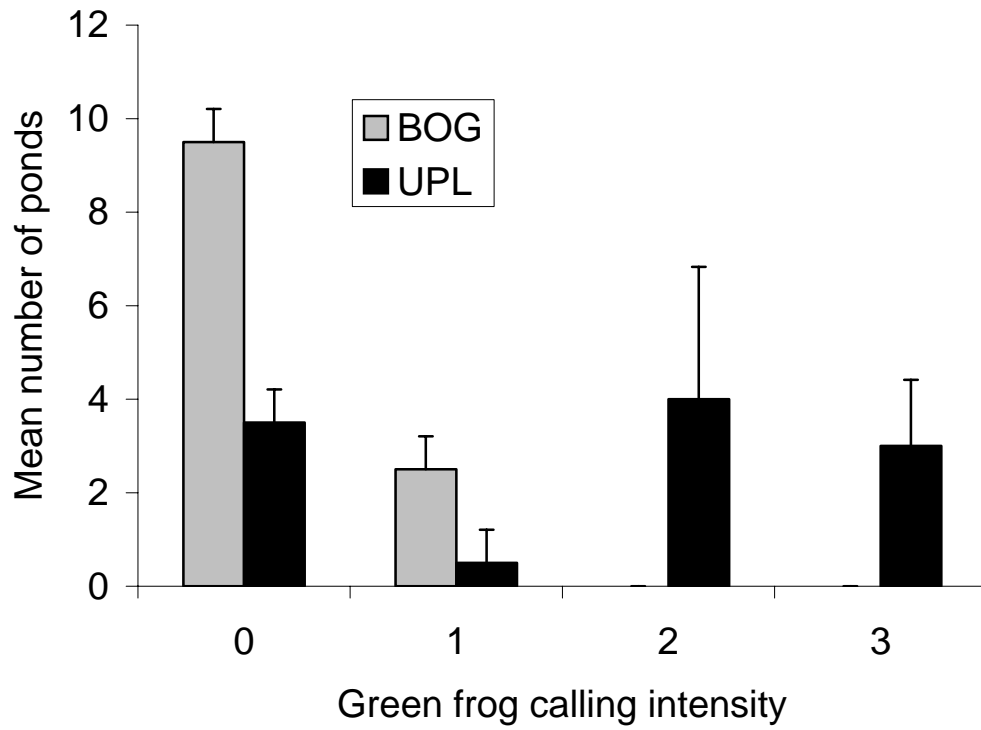


Figure 3. Green frog calling rate at bog (BOG) and upland (UPL) ponds sampled in 2002. Mean number of ponds \pm SD are shown for each calling class.

Table 2. Ranking of Poisson regression models for repeated measures (based on AIC_c) assessing green frog abundance at bog and upland ponds. Model-averaged estimates in bold indicate that 0 is excluded from the 95% confidence interval and that the variable influences pond use. X and Y denote the UTM coordinates of each pond; logperimeter: natural log of pond perimeter.

Model	Number of parameters	Delta AIC _c	Akaike weight
Pondtype logperimeter	3	0	0.59
Pondtype x y logperimeter	5	1.76	0.25
Pondtype x y	4	4.58	0.06
Pondtype x y depth	5	5.92	0.03
Pondtype	2	6.17	0.03
Logperimeter depth	3	7.30	0.02
Pondtype depth	3	7.32	0.02
Logperimeter x y depth	5	7.65	0.01
Depth x y	4	18.76	0.00
Depth	2	19.63	0.00
X y logperimeter	4	24.05	0.00
X y	3	26.90	0.00
Logperimeter	2	31.53	0.00

Estimates (\pm unconditional SE) obtained from model averaging

Pond type (bog vs upland)	Log perimeter	of Depth	X	Y
-2.3043	0.8588	-0.0033	-0.4772	-2.3868
(0.5247)	(0.2597)	(0.0282)	(2.3887)	(1.6400)

Forest-bog Movements

A total of 159 green frogs were captured across all sites and years, with trap rates (mean \pm SD) of 0.021 ± 0.041 and 0.014 ± 0.020 green frogs per trapnight for 2001 and 2002, respectively (Fig. 4). The other amphibians and reptiles captured consisted of leopard frogs (*Rana pipiens*), wood frogs (*Rana sylvatica*), American toads (*Bufo americanus*), spring peepers (*Pseudacris crucifer*), blue-spotted salamanders (*Ambystoma laterale*), spotted salamanders (*Ambystoma maculatum*), red-spotted newts (*Notophthalmus v. viridescens*), red-backed salamanders (*Plethodon cinereus*), smooth green snakes (*Opheodrys vernalis*), northern red-bellied snakes (*Storeria o. occipitomaculata*), and Maritime garter snakes (*Thamnophis sirtalis pallidulus*), but were too infrequent to consider in the analyses. Neither the trapping period (i.e., breeding vs postbreeding) nor the presence of adjacent mining influenced the amphibian movement patterns from the bog to the forest (i.e., 95% confidence interval included 0 for the estimate of the variables for both years, Table 3). The intercept-only models were the most parsimonious, between 2.1 and 4.5 times more likely to explain frog movements than models including either period or mining disturbance (i.e., based on the ratio of Akaike weights). There was no indication that individuals predominantly moved from the forest into bog habitats during the summer (i.e., 95% confidence interval for the intercept included 0 for both years, indicating an overall proportion not different from 0.5).

Selection of Rehydration Substrate

Acutely-dehydrated frogs did not discriminate between *Sphagnum* and the other rehydration media (Table 4). Indeed, substrate choice was independent of frog mass before rehydration, mass lost during dehydration, and the nature of the substrate on which the frog was introduced at the start of a trial.

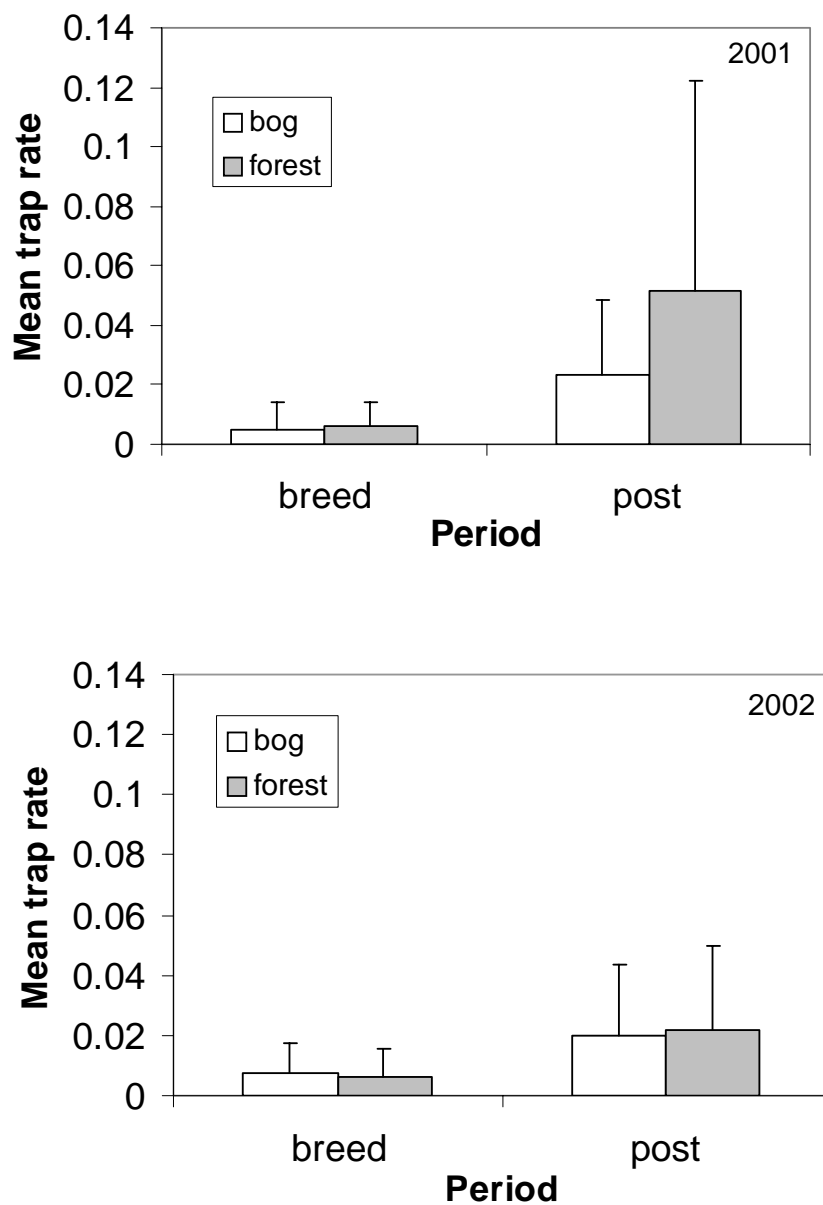


Figure 4. Mean green frog trap rates (number of frogs per trap night) of individuals moving out of the bog (bog) and out of the forest (forest) during 2001 and 2002. Total trapping effort is of 11 880 trap nights. The bars represent 1 SD around each mean ($n = 6$ for each group).

Table 3. Ranking of logistic regression models for repeated measures (based on AIC_c) explaining the probability of frogs moving from the forest to bog habitats across the season (breeding vs postbreeding period) and disturbance (presence vs absence of adjacent peat mining). Akaike weights, also interpretable as probabilities, indicate that intercept-only models are better than models with either period or disturbance variables at explaining frog movements.

Year	Model	Number of parameters	Delta AIC_c	Akaike weight
2001	Intercept only	1	0	0.63
	Period	2	2.48	0.18
	Disturbance	2	2.48	0.18
2002	Intercept only	1	0	0.58
	Period	2	1.38	0.29
	Disturbance	2	2.93	0.13

Table 4. Ranking of logistic regression models (based on AIC_c) and model-averaged estimates explaining the probability of green frogs of choosing *Sphagnum* moss more often than other substrates for rehydration ($N = 21$). Massloss: mass lost during dehydration; mass: body mass before rehydration; firstsubstrate: substrate on which frog was placed at start of rehydration experiment. Frogs selected *Sphagnum* as often as the other media, regardless of covariables.

Model	Number of parameters	of Delta AIC_c	Akaike weight
Mass	2	0	0.46
Mass massloss	3	0.84	0.30
Massloss	2	3.07	0.10
Mass firstsubstrate	4	3.52	0.08
Firstsubstrate	3	5.93	0.02
Mass massloss firstsubstrate	5	6.43	0.02
Massloss firstsubstrate	4	6.93	0.01

Estimates (\pm unconditional SE) obtained from model averaging

Intercept	Mass	Massloss	First substrate	
			<i>Sphagnum</i> moss	Soil
0.5532	-0.3624	2.6585	1.8572	1.1905
(1.8636)	(0.4049)	(3.6624)	(1.4342)	(1.7847)

DISCUSSION

Bogs as Breeding Sites

Green frogs rarely bred in bog ponds relative to upland sites, as indicated by calling and minnow trapping surveys. This is consistent with other studies conducted in bogs of the same region. Indeed, Mazerolle and Cormier (2003) and Mazerolle (unpubl. data) reported captures of green frog tadpoles at 19.0% of the 21 ponds, and 12.9% of the 70 ponds sampled, respectively. Although green frog tadpoles have a high tolerance to low pH (50%

mortality at pH 3.36: Freda and Taylor 1992; see also Dale et al. 1985), the average bog pond pH of 3.67 presumably reduced the successful development of embryos and larvae. Similarly, Saber and Dunson (1978), Dale et al. (1985), and Karns (1992a) observed few successful breeding attempts of wide-ranging species of amphibians in peatlands.

Although some species predominantly use naturally acidic systems (Bunnell and Zampella 1999), no such species occurred in the study area. Indeed, the *Sphagnum*-associated four-toed salamander (*Hemidactylium scutatum*) occurs 100 km from the sites (Woodley and Rosen 1988). Thus, results of my study, along with those of previous investigations in eastern and central North America, indicate that peat bogs (with pH ca. 4.0) are not productive breeding sites for most amphibians.

Bogs as summering sites

I did not detect any net frog movements into bogs from adjacent forest habitats neither during, nor following the breeding period. This was unexpected, as upland habitats in both summers (i.e., mid June – September) were particularly dry with less than 217 mm of total rainfall, whereas bogs remained humid throughout the season. Bellis (1962), Schroeder (1976), and Karns (1992b) also suggested that amphibians summer in bogs after leaving upland ponds. Nonetheless, I found as many individuals moving into bogs than out of bogs and few individuals were recaptured (ca. 14%). Thus, it seems that some individuals moved into bogs from upland sites during the summer. Furthermore, during the substrate-selection experiment, frogs did not discriminate against *Sphagnum* to rehydrate, which suggests that bogs provide adequate substrates for rehydration. Previous observations of increased amphibian captures in bogs following the breeding period further support this hypothesis (Karns 1992b, Mazerolle 2001).

Most investigations conducted on adult amphibians and their response to pH suggest that individuals of certain species avoid acidic conditions (Vatnick et al. 1999, Karns 1992b), and that low pH can disrupt sodium balance (e.g., Wyman and Hawksley-Lescault 1987, Frisbie and Wyman 1992) and result in lower abundances (Wyman 1988). This seemingly contradicts the notion of amphibians using bogs. Nonetheless, amphibian pH tolerance increases with the developmental stage (Pierce 1985), and also varies among as

well as within populations (Pierce 1985, Glos et al. 2003, Räsänen et al. 2003). Furthermore, differences between populations may evolve after exposure to acidic conditions for several generations (Andrén et al. 1989, Pierce and Wooten 1992). I assume such a process has operated on amphibian populations in my study area, as acidic conditions have been prevalent since the formation of peatlands over 8 000 yr ago (Glaser and Janssens 1986, Warner et al. 1991). Yet, such a hypothesis needs to be tested formally with populations from regions with and without naturally-acidic environments.

Although bogs of eastern New Brunswick are not productive amphibian breeding sites, at least 10 species frequent these habitats during summer (Mazerolle 2003a). Similarly, other investigators have reported between 5 and 12 amphibian species in naturally acidic habitats of central and eastern North America (Marshall and Buell 1955, Heatwole and Getz 1960, Bellis 1965, Saber and Dunson 1978, Dale et al. 1985, Stockwell and Hunter 1989, Karns 1992a, Bunnell and Zampella 1999, Zampella and Bunnell, 2000). Mazerolle (1999) and Karns (1992b) reported that amphibian abundance in peatlands was generally lower than that reported in upland habitats. Nonetheless, data indicate that juvenile and adult amphibians exploit acidic environments close to their physiological limits, particularly in summer. Furthermore, despite their acidity, bogs harbor an abundance of arthropods (Danks and Rosenberg 1987, Larson and House 1990) and moist refugia potentially useful for amphibians. Karns (1992b) also suggested bogs provide valuable hibernation sites, but this requires further investigations.

Peat Mining and Amphibians

Frog movements between forest and bog habitats did not differ between bog remnants and undisturbed bogs. In contrast, Mazerolle (2001, 2003a) showed that adjacent peat mining negatively influences green frog abundance and movement patterns, but these effects seem to lessen after 100 m. Drift fences in the present study were generally further from mined edges and closer to forest habitat than in earlier investigations (i.e, Mazerolle 2001, 2003a). These conditions could have mitigated the effects of proximate peat mining on green frog movement patterns in this study and would be consistent with the existing evidence. In a concurrent study, Mazerolle et al. (Chapter 3) observed that the occurrence

of amphibians at bog ponds increased with the proximity and amount of adjacent ponds, but was independent of the proximity of mined edges.

During their season of activity, pond-breeding amphibians move between hibernation, breeding, and summering sites, which are generally spatially-distinct elements of the landscape (e.g., Pope et al. 2000, Pilliod et al. 2002). Each is critical in the amphibian life cycle and must be considered in amphibian management (e.g., Semlitsch 1998, Gibbons 2003, Semlitsch and Bodie 2003). Thus, the loss of one of these habitats, or the presence of human-related disturbances such as agriculture or forestry practices between habitats could disrupt amphibian movements and put populations at risk. To this effect, Mazerolle and Desrochers (this thesis, Chapter 4) have reported that surfaces mined for peat are efficient barriers to amphibian movements.

In conclusion, most amphibians of eastern Canada rarely breed in bogs, but use these habitats during the summer. As the movement study and substrate choice indicate, frogs neither prefer nor avoid bogs over upland habitats. Several aspects of amphibian ecology in naturally-acidic environments need further investigation, such as between-population variation in acid tolerance, especially in the context of increasing pressures on peatlands of southeastern North America from the peat mining industry.

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Chapitre 2

Effects of peat mining intensity on green frog (*Rana clamitans*) occurrence in bog ponds

MAZEROLLE¹, M. J., Cormier², M. 2003. **Effects of peat mining intensity on green frog (*Rana clamitans*) occurrence in bog ponds.** *Wetlands* 23:709-716. ¹Centre de recherche en biologie forestière, Pavillon Abitibi-Price, Faculté de Foresterie et de Géomatique, Université Laval, Québec, Québec, Canada G1K 7P4 et Groupe de recherche en écologie des tourbières, Pavillon Paul-Comtois, Université Laval, Québec, Québec, Canada G1K 7P4. ²Département de biologie, Pavillon Vachon, Université Laval, Québec, Québec, Canada G1K 7P4. *Ce chapitre est le fruit du travail du candidat. Mario Cormier a effectué en partie le travail de terrain du projet et à aussi collaboré à la rédaction de ce chapitre.*

Résumé

Nous avons évalué les effets de l'intensité de l'extraction de la tourbe sur l'utilisation des étangs de tourbières par les grenouilles vertes (*Rana clamitans*). Pour ce faire, nous avons sélectionné 21 étangs dans trois zones soumises à différentes intensités d'exploitation: 1) zone exploitée (végétation absente avec surface de tourbe à nue, présence de canaux de drainage avec peu ou pas d'eau), 2) zone en préparation à l'exploitation (végétation intacte mais présence de canaux de drainage remplis d'eau), et 3) zone naturelle (végétation intacte, absence de canaux de drainage). Nous avons évalué l'abondance ainsi que la reproduction de grenouilles vertes à l'aide d'une combinaison de techniques d'échantillonnage. Les grenouilles vertes ont été détectées plus souvent dans les étangs de la zone en préparation à l'exploitation que dans les étangs des zones exploitées ou naturelles. De plus, aucun chant de grenouille n'a été entendu dans les étangs de la zone exploitée, contrairement aux étangs des zones naturelles ou en préparation à l'exploitation. Des têtards ont été détectés uniquement dans la zone en préparation à l'exploitation. Ceci suggère que les étangs sur la zone exploitée procurent un habitat suboptimal pour les grenouilles vertes. Dans la zone en préparation à l'exploitation, les canaux de drainage offrent possiblement un habitat de reproduction supplémentaire et pourraient faciliter les déplacements entre les étangs. Néanmoins, si cet effet positif est réel, il n'est que temporaire car les zones en préparation à l'exploitation sont inévitablement exploitées. Bien que le maintien des corridors de végétation autour des étangs de la zone exploitée n'augmentera pas nécessairement à court terme l'utilisation des étangs par les amphibiens,

il pourrait faciliter la phase de restauration en procurant une source d'individus d'espèces végétales et fauniques, incluant les amphibiens.

Abstract

We assessed whether peat mining intensity influences the use of bog ponds by green frogs (*Rana clamitans*). We selected 21 ponds in three areas undergoing different levels of peat mining: 1) mined (vegetation completely removed exposing bare peat, presence of drainage ditches with little or no water), 2) in preparation to be mined (vegetation intact but presence of drainage ditches filled with water), and 3) natural (vegetation intact, absence of drainage ditches). We estimated green frog abundance and reproduction using a combination of sampling techniques. Green frogs were detected more often at ponds in the moderately disturbed section than at ponds in either the mined bog or natural sections. Furthermore, no green frogs called at ponds on mined surfaces, as opposed to ponds on either natural or moderately disturbed surfaces. Tadpoles occurred only in the moderately disturbed section. This suggests that ponds on mined surfaces provide suboptimal habitat for green frogs. Within the moderately disturbed section, drainage ditches may provide additional breeding habitat and facilitate movements between ponds. However, if this positive effect occurs, it is only temporary because moderately disturbed sections are inevitably mined. Although preserving vegetated corridors or buffer zones around bog ponds within mined surfaces may not necessarily increase pond use by amphibians in the short term, it will facilitate the restoration phase of mined sites by providing a source of dispersers of bog plants and wildlife, including amphibians.

INTRODUCTION

Widespread amphibian declines have been reported during the last 30 years (Barinaga 1990, Vitt et al. 1990, Wyman 1990, Wake 1991). Habitat loss and fragmentation are the most frequently mentioned agents believed responsible for these declines. Wetlands provide a diversity of habitats for amphibians to complete their life cycle, and habitat degradation has serious repercussions on the persistence of amphibian

populations (Gibbs 1993). Physiological constraints (water balance and thermoregulation), combined with short dispersal distances and a high fidelity towards breeding sites, make amphibians vulnerable to local extinction in recently drained wetlands (Sinsch 1990, Blaustein et al. 1994). The degradation of habitats adjacent to breeding sites is also problematic, as amphibian movements in disturbed and dry environments are more strongly correlated with climatic variables than in less disturbed habitats (Martof 1953a, Bellis 1962, Sinsch 1988, Mazerolle 2001). Thus, amphibian movements over hostile habitat are limited to optimal weather conditions.

Peat mining radically modifies the structure of bogs by introducing networks of drainage trenches and removing the living vegetation layer. This generates dry conditions over the peatlands to facilitate the extraction of the peat (mostly used in horticulture or as fuel) with tractor-pulled vacuums (Wheeler and Shaw 1995). This type of habitat loss is most extensive in boreal countries with deep peat deposits, mainly Russia, Finland, Germany, Canada, and Ireland (Lawton 1996, Rubec 1996, Poulin and Pellerin 2001). In certain European countries, such as the Netherlands, Denmark, Poland, and Germany, less than 15% of the original surface of peatlands remain undisturbed, whereas ca. 90% of Canadian peatlands are still intact, mostly in the northern part of the country (Poulin and Pellerin 2001). The peatlands of southeastern Canada, especially those of Quebec and New Brunswick, face the greatest pressures from peat mining because infrastructures are already in place (i.e., roads, rails, ports) that facilitate access to sites. Certain amphibian species occurring in bogs of eastern Canada are negatively influenced by peat mining, with more individuals found in natural bogs as opposed to the periphery of bog remnants (Mazerolle 2003).

Ponds are characteristic of large coastal bogs of eastern Canada (Wells and Hirvonen 1988). Certain amphibian species occur in these ponds, although the degree of use for breeding or summering remains unknown (Mazerolle 1999). During peat mining, ponds are usually drained or filled in. We hypothesized that the degree of peat mining decreases amphibian abundance patterns at bog ponds. Using call surveys, visual encounter surveys, and funnel traps in ponds within a disturbed bog, we determined whether the intensity of peat mining influences the abundance, probability of calling, and reproduction of green frogs (*Rana clamitans melanota* Rafinesque), a species of amphibian typically

found in bogs and sensitive to peat mining (Mazerolle 2001, Mazerolle 2003). We also studied the effectiveness of ponds remaining within mined bogs (i.e., completely surrounded by peat fields) as refugia for green frogs.

METHODS

Study Site

The study was conducted in Saint-Charles Bog (46°39'N, 64°55'W), an ombrotrophic bog (i.e., water and nutrients are solely derived from precipitation) in eastern New Brunswick, Canada. Originally 2315 ha, 138.9 ha (6%) of the bog are now actively mined for peat. Over 170 bog ponds occur at the site (i.e., most are located in the natural section of the bog, see below), with perimeters ranging from a few meters to over 1 km. Mixed forest, dominated by black spruce (*Picea mariana* (Mill.) B. S. P.), balsam fir (*Abies balsamea* (L.) Mill.), and birch (*Betula* spp.), occurs at the bog periphery.

Selection of Bog Ponds

Ponds were selected throughout the bog, in sections differing in mining intensity (Fig. 1). We used the degree and type of disturbance to describe the intensity of mining, as either mined, moderately disturbed, or natural. Mined peat fields are devoid of any vegetation cover, subject to regular disturbance by heavy machinery, and separated by trenches containing little or no water, (hereafter, mined section). The moderately disturbed section consists of areas to be mined in a few years that are still covered with living vegetation, but a network of trenches filled with water drain the area. The natural section consists of the natural bog surface, characterized by intact vegetation and the absence of drainage trenches (most ponds occurred in this section). These study sections reflect the typical steps involved in peat mining across eastern Canada.

Two ponds overlapped the mined sections and moderately disturbed sections. We classified these ponds according to the proportion of the pond perimeter adjacent to the mined surface. A pond with more than 50% of its perimeter adjacent to the mined surface was considered as being in the mined section; otherwise, the pond was classified in the moderately disturbed section.



Figure 1. Example of bog ponds sampled in three sections of bogs differing in mining intensity. From top to bottom: pond on natural section, pond on moderately-disturbed section, and pond within peat surface.

We selected the only six ponds (perimeter ranging between 119 and 342 m) remaining in the mined section. These were located on peat fields over which mining had begun 2-3 years before and was still continuing. The ponds in the other two sections were selected randomly, with the only restriction that ponds had to be similar in size to those on the mined surface. We chose seven ponds in the moderately disturbed section and eight ponds in the natural section, for a total of 21 ponds. Two upland breeding sites occurred around the bog: a ditch leading to a large pond on the east side and a small brook north of the site. The minimum distance between ponds selected and an upland breeding site was 2.3 ± 0.6 km (mean \pm SD). The minimum distance separating the ponds selected was 190.8 ± 129.1 m (range = 35-508 m). Green frogs have a mean home range of 60 m^2 (range = 20-200 m^2) and return to the same breeding, summering, and hibernation sites across years (Martof 1953a). In addition, as all ponds were surveyed on each survey night, we assumed that the detection of the same individual at different ponds was unlikely as individuals would have stayed in close proximity to the ponds. Therefore, we considered ponds independent from one another.

Pond Characteristics

Vegetation cover was determined in 1.0- x 1.5-m quadrats spaced at 20-m intervals along the pond perimeter (i.e., side of the quadrats against the water's edge). Similarly, we measured vegetation cover 15 m from the pond edge in quadrats of identical dimension (i.e., spaced at 20-m intervals) to characterize the vegetation in the vicinity of the pond. The number of quadrats on the pond perimeter ranged between 3 and 20 quadrats, whereas 6 to 40 quadrats were established 15 m from the pond edge. We estimated the percent ground cover of vascular plants (all species combined) in two height categories (3-30 cm and > 30 cm), as well as the percent cover of *Sphagnum* spp. using the following scale: < 5% with few individuals (i.e., individuals are rare), < 5% with many individuals (several individuals but less than 5% cover), 5-25%, 25.1-50%, 50.1-75%, and > 75%. At each pond, the mean percent cover for each strata was used in subsequent analyses.

We measured the pH of pond water (within first 30 cm of water column) at three locations in each pond with a HI 9024 pH meter fitted with a temperature probe (Hanna Instruments Inc., Rhode Island, USA). The pH of bogs typically does not vary greatly

across the season (Vitt 1994, Vitt et al. 1995, but see Tahvanainen and Tuomaala 2003) and we considered our sampling sufficient to obtain representative values for each pond. We also took water-depth measurements within 1 m of the shoreline at 20-m intervals on pond perimeters. The mean values for pH and water depth at each pond were used in further analyses.

Green Frog Detection

Visual and Call Surveys.—We censused ponds between mid-June and mid-August 2000 using a combination of visual encounter and call surveys (adapted from Crump and Scott 1994, Scott and Woodward 1994, and Zimmerman 1994). Four surveys were conducted at each pond during the breeding season (2 and 14 July 2000, 1 and 18 August 2000). We surveyed all ponds in early to late evening (between 1530 and 2400) under similar meteorological conditions (i.e., low winds, no precipitation, air temperature > 10°C). A headlamp was used after dusk. Green frogs call more intensely during the evening and night (Oseen and Wassersug 2002), but several investigators have observed green frogs calling during the day (Wright and Wright 1949, Martof 1953*b*). We did not detect any relationship between time of day and probability of calling at bog ponds of our study site. The sampling effort (i.e., number of investigators x time to conduct survey) at each pond was recorded and accounted for in the analyses (see Statistical Analyses).

During each survey, the investigator moved discretely toward the water's edge and walked along the perimeter while scanning a 2 m-wide transect and recording every individual seen. As in other studies using similar sampling techniques (Heyer et al. 1994), we assumed that the number of green frog detections was an appropriate surrogate measure of true frog abundance at ponds. During visual surveys, we also stopped at 20-m intervals to listen for calling males for 30 s. All ponds were surveyed on the same night to avoid differences in meteorological conditions. During each survey, the 21 ponds were grouped in clusters of 2-4 ponds (ponds within ca. 500 m of each other), and each cluster was sampled in a random sequence.

Funnel Traps.—To determine if reproduction was occurring in ponds, we conducted two

trapping sessions to detect the presence of tadpoles: the first session between 18 June and 1 July 2000, the second between 19 July and 25 July 2000. We used funnel-shaped plastic minnow traps (43 cm x 23 cm width at largest diameter) with an opening of 2.2 cm diameter and a mesh size of 4.8 mm². Because green frog tadpoles typically overwinter in ponds, our sampling strategy targeted individuals having spent one year in the pond. Traps were placed at pond edges (i.e., near water's edge) and partially submerged to avoid the drowning of metamorphosed individuals. The number of traps deployed in each pond was determined by its surface area (i.e., two traps for the first 25 m² and an additional trap each time the area doubled *sensu* Adams et al. 1997). Traps were set for three consecutive days and checked daily.

STATISTICAL ANALYSES

Pond Characteristics

We first used one-way ANOVA on each of the explanatory variables to detect variations in microhabitat characteristics among the ponds located in the different parts of the bog (i.e., mined, moderately disturbed, or natural surface). The log transformation was applied where warranted to homogenize variances. Where significant differences were detected ($\alpha = 0.10$ to reduce the probability of committing a type-II error), we performed Tukey *a posteriori* multiple comparisons for unequal sample sizes to find where differences occurred among pond categories (Zar 1984, Day and Quinn 1989). We removed variables related to pond location from subsequent analyses to avoid problems of multicollinearity (see below).

Pond Use

We used generalized estimating equations (Diggle et al. 1994, Stokes et al. 2001) to analyze green frog abundance and the occurrence of calling across ponds within sections differing in mining intensity, as each pond was sampled on four occasions. Generalized estimating equations are an extension of generalized linear models and are especially designed for longitudinal data (i.e., repeated measures), yielding robust estimates of parameters and their standard errors. Generalized estimating equations also enable the model to incorporate the error distribution (normal, gamma, binomial, or Poisson) most

adequate to the data. For the frog detection data, the Poisson distribution was selected given the many zeros in the data set (i.e., Poisson regression for repeated measures), whereas the occurrence of green frogs calling at ponds was modeled with the binomial distribution (i.e., logistic regression for repeated measures). We accounted for differences in the sampling effort (time to conduct survey at pond x number of investigators) by including it (after log transformation) as an offset variable in the models. Furthermore, we only included pond characteristic variables that were unrelated to pond location (based on univariate ANOVA). The regression models obtained from generalized estimating equations were computed with the Genmod procedure in SAS 8.01.

Using the information-theoretic approach detailed in Burnham and Anderson (1998), we considered a set of candidate models for the abundance and calling data (i.e., from the set of variables unconfounded with pond location). This framework is based on parsimony, a trade-off between model fit and the number of parameters in the model that favors the least number of parameters required to adequately describe the data. The strength of evidence of each model was assessed with measures derived from the second-order Akaike Information Criterion (AIC_c) and Akaike weights (Burnham and Anderson 1998, Pan 2001). Akaike weights are a relative measure of model uncertainty (i.e., the probability that a given model is the “best” among the models considered and given the data at hand). Akaike weights can also be used to assess the strength of evidence for a variable by summing the weights across all models that include the variable. Please refer to Appendix 1 for detailed instructions on how to compute and interpret the results of the analysis of ecological data using this approach.

We then calculated model-averaged parameters and unconditional standard errors for each variable of interest (Burnham and Anderson 1998). Model-averaging consists of calculating a weighted estimate for a given variable across all models in which it appears. Estimates obtained in this fashion typically have better precision and less bias than when based on a single model (Anderson et al. 2000). Model fit was assessed with the most complex model for each amphibian response variable.

RESULTS

Pond Characteristics

Ponds in each section differed in water depth, *Sphagnum* cover, and cover of vascular plants 3-30 cm in height (Table 1). Ponds in the natural section had a greater percent cover of *Sphagnum* both along the perimeter and 15 m from the edge. Cover of vascular plants (mostly ericaceous shrubs) on pond perimeters was generally lower at ponds in the natural section than on the other sections. Vegetation cover 3-30 cm high 15 m from ponds on the mined surface was lower than in the less disturbed sections. Ponds in the natural section were considerably deeper than in the other sections, and ponds in the moderately disturbed section were deeper than those in the mined section. These differences are directly linked to changes associated with the presence of trenches and mining activity. The mean pond water pH was also slightly higher in ponds of the natural section. Thus, the pond location variable (i.e., mined, moderately disturbed, and natural sections) also included the effect of several pond characteristics.

Pond Use

During the four visual surveys, we recorded a total of 84 green frog observations. The mean detection rate (number of individuals observed/person-hours \pm 1 SD) for the mined section was 0.011 ± 0.017 , whereas the moderately disturbed section and the natural section had a mean detection rate of 0.152 ± 0.124 and 0.047 ± 0.059 , respectively. There was evidence for an overall effect of pond location (mined, moderately disturbed, and natural sections) on green frog abundance based on the sum of Akaike weights. Indeed, the models including pond location had a considerably higher sum of weights (0.81 vs 0.19) than the models without this variable. Ponds on the moderately disturbed surface yielded more individuals than the ponds located on the natural surface (Table 2). However, there was no difference in frog abundance between mined and natural sections. Larger ponds did not yield more frogs than smaller ones. The number of frogs observed did not vary with the percent cover of vegetation 3–30 cm high 15 m from the pond, the only vegetation variable retained in the analysis.

Table 1. Descriptive statistics of pond microhabitat variables (mean \pm SD) within the three sections of a bog undergoing peat mining. Letters in parentheses denote significant differences between the means of the different sections (Tukey multiple comparisons, $\alpha = 0.10$).

Microhabitat	Section			<i>F</i>
	Mined (n = 6)	Moderately Disturbed (n = 7)	Natural (n = 8)	
pH	3.95 \pm 0.09 (a)	3.95 \pm 0.05 (a)	4.05 \pm 0.06 (b)	5.51*
Depth (cm) [¶]	4.6 \pm 2.5 (a)	15.4 \pm 8.2 (b)	41.8 \pm 19.1 (c)	26.28***
Perimeter (m) [¶]	239.4 \pm 86.2	181.5 \pm 100.1	196.7 \pm 116.9	0.70
Vegetation cover on pond perimeter (%)				
<i>Sphagnum</i>	27.7 \pm 13.3 (a)	39.3 \pm 25.8 (a)	83.2 \pm 4.4 (b)	22.30***
Vegetation 3-30 cm [¶]	22.7 \pm 10.5 (a)	21.9 \pm 5.4 (a)	10.3 \pm 4.4 (b)	9.66***
Vegetation > 30 cm [¶]	2.5 \pm 4.8 (ab)	4.1 \pm 4.4 (a)	0.1 \pm 0.2 (b)	3.68*
Vegetation cover 15 m from pond edge (%)				
<i>Sphagnum</i>	0 \pm 0 (a)	10.4 \pm 7.9 (a)	63.5 \pm 19.3 (b)	44.62***
Vegetation 3-30 cm [¶]	14.2 \pm 21.2 (a)	43.7 \pm 7.5 (b)	41.1 \pm 15.7 (b)	10.11***
Vegetation > 30 cm [¶]	4.1 \pm 6.6	12.7 \pm 14.2	9.5 \pm 11.1	1.48

[¶] Data log-transformed before analysis.

* $P < 0.05$, *** $P < 0.001$.

Table 2. Ranking of Poisson regression models for repeated measures (generalized estimating equations) considered for green frog abundance in ponds submitted to different disturbance levels from peat mining in eastern New Brunswick. A total of 21 ponds were sampled on 4 occasions[†].

Model	K	Delta AIC _c ¹	Akaike weight
Section	3	0	0.271
Section logperim	4	0.05	0.264
Section logcov30	4	1.23	0.146
Section logperim logcov30	5	1.49	0.128
Logperim	2	2.29	0.086
logperim logcov30	3	3.17	0.056
Logcov30	2	3.42	0.049
Model-averaged parameters (\pm unconditional standard error) ²			
Pond location ³		Natural log of	Natural log of
Mined area	Moderately disturbed area	Pond perimeter	vegetation cover 15 m from pond (3 – 30 cm)
-0.4721	1.9589	-0.8538	0.1903
(0.6075)	(0.5718)	(0.4415)	(0.3070)

[†] AIC_c calculated as in Pan (2001).

¹ AIC_c of highest-ranked model = 67.365.

² Typescript in bold indicates 0 is excluded from 95% confidence interval.

³ Natural area used as reference level.

Given the set of models considered, there was strong evidence for an overall effect of pond location on the probability of green frogs calling at a pond (sum of Akaike weights of 0.90 for models with pond location vs 0.10 for models without the variable). However, model-averaging estimates and confidence intervals could not provide additional

information on the source of the difference (Table 3). Green frog calls were heard at four of seven (57%) ponds on the moderately disturbed section, and at four of eight (50%) ponds on the natural portion of the bog. However, no calls were heard at ponds within the mined area. Neither pond size (perimeter) nor vegetation cover (3–30 cm high 15 m from pond) influenced the probability of green frogs calling (Table 3).

Table 3. Ranking of logistic regression models for repeated measures (generalized estimating equations) considered for green frog calling in ponds submitted to different disturbance levels from peat mining in eastern New Brunswick. A total of 21 ponds were sampled on 4 occasions[¶].

Model	K	Delta AIC _c ¹	Akaike weight
Section logcov30	4	0	0.562
Section logperim logcov30	5	1.79	0.230
Section	3	4.48	0.060
Section logperim	4	4.97	0.047
Logperim	2	5.31	0.039
logperim logcov30	3	5.57	0.035
Logcov30	2	6.08	0.027
Model-averaged parameters (\pm unconditional standard error) ²			
Pond location ³		Natural log of	Natural log of
Mined area	Moderately disturbed area	Pond perimeter	vegetation cover 15 m from pond (3 – 30 cm)
-2.7144	-0.1434	-0.5617	-0.6363
(1.4341)	0.7602	(0.5744)	(0.3265)

[¶] AIC_c calculated as in Pan (2001).

¹ AIC_c of highest-ranked model = 81.800.

² Typescript in bold indicates 0 is excluded from 95% confidence interval.

³ Natural area used as reference level.

Funnel trapping yielded too few tadpoles for adequate analysis. Tadpoles were only captured at four ponds, all within the moderately disturbed section.

DISCUSSION

Pond Use

Green Frog Abundance.—Although green frogs were more numerous in ponds within the moderately disturbed section, there were no differences in abundance between the ponds of the mined and the natural sections. This suggests that ponds within the mined section can provide refugia for green frogs, but do not necessarily result in positive population growth rates. Furthermore, the greater abundance of frogs in ponds of the moderately disturbed section probably stems from the additional aquatic habitat offered by the drainage ditches spaced at 30-m intervals, all containing water. Alternatively, results could also be explained by the presence of a crowding effect similar to the one observed in forest birds shortly after habitat loss (Hagan et al. 1996, Schmiegelow et al. 1997). Following the beginning of peat mining 2-3 years before the study, frogs using ponds in the mined section may have moved into the moderately disturbed section (adjacent to it), thereby increasing the densities in ponds located in the latter section. This would require further investigation.

Green Frog Calling.—Pond location (i.e., mined, moderately disturbed, and natural sections) did not strongly influence the probability of green frogs calling. However, the absence of calling males in the mined section, as well as the regression estimate \pm SE associated with the mined section variable (i.e., -2.7 ± 1.4), suggests that frogs were more likely to call in ponds within the natural section than the mined section. Thus, ponds within mined areas may be considered unsuitable breeding habitat by male green frogs, or alternately, males may call less often in ponds of the mined section.

Green Frog Development.—A recent study of ponds on bog remnants adjacent to mined surfaces in the same region revealed the presence of tadpoles in 12 (17%) of these bog ponds (M. J. Mazerolle unpublished data). The very low probability of occurrence of tadpoles we observed at ponds on the natural section could be explained by a less intensive effort than that deployed for the larger study. The higher mean pond water pH (4.05) in the natural section, although statistically different from the pH in the mined (3.95) and

moderately disturbed (3.95) sections, was probably not biologically significant. Indeed, bog ponds in the natural section (having the highest pH) did not yield the greatest numbers of tadpoles and metamorphosed individuals. The pH of the bog ponds in all three sections was within the tolerance limit for green frog embryos and tadpoles, although very close to the lethal pH. Gosner and Black (1957) observed that fewer than 15% of green frog embryos reach hatching at a pH lower than 3.85, although Dale et al. (1985) have found tadpoles in water at a pH of 3.9. However, acid tolerance in green frogs, as in other amphibians, increases during development and varies within and between populations (Pierce 1985, Pierce and Wooten 1992).

Pond depth can increase the occurrence of frogs at ponds. Indeed, Laan and Verboom (1990) observed that amphibian species richness in old ponds within an agricultural landscape increased with pond depth (52.5 ± 31.3 cm, mean \pm SD). In our study, green frogs were not influenced by this pond variable. Despite their greater depth (i.e., 41.8 ± 19.1 cm, mean \pm SD), the ponds in the natural section (i.e., without ditches lowering the water level) did not yield more metamorphosed individuals or tadpoles than ponds in the other sections. The presence of drainage ditches possibly mitigated the effects of pond depth. Although resulting in lower water levels in the pond, the ditches containing water can complement the volume of water available to frogs.

The low occurrence of successful reproduction we observed for green frogs in bogs was similar to that reported for wood frogs (*Rana sylvatica* LeConte) (Karns 1992). This reinforces the notion of Bellis (1962), Schroeder (1976), and Mazerolle (2001), who proposed that amphibians use bogs as summering areas after completing breeding at ponds in nearby upland habitats. Alternately, it may indicate that bogs act as population sinks attracting breeders but inhibiting embryo and larvae development. In Chapter 1, I found that bogs are not productive amphibian breeding sites relative to upland ponds, and that bogs, just as adjacent upland habitats, can be used by amphibians during the summer periods, as metamorphosed individuals do not avoid *Sphagnum* substrates.

Management Implications

Drainage ditches are present in the mined sections and moderately disturbed sections. These ditches penetrate into ponds to lower water levels and could act as corridors

facilitating green frog movements. For instance, Reh and Seitz (1990) suggested that drainage ditches enhanced genetic mixing between populations of common frogs (*Rana temporaria* L.) in agricultural landscapes. Deprived of water during the summer, drainage ditches within the mined section offer little or no protection against desiccation, whereas trenches in the moderately disturbed section contain water and are surrounded by vegetation. However, the value of moderately disturbed sections is only temporary because they are an integral part of site preparation for peat mining and eventually will be mined.

Maintaining ponds within mined sections can effectively provide refugia for green frogs but not necessarily breeding habitat. Preserving vegetation around ponds would at least provide cover for individuals foraging around the pond. Semlitsch (1998) proposed preserving a 165-m buffer strip around upland ponds for pond-breeding salamanders. This also could be implemented for bog ponds, as it would be a great improvement to the common practice of mining the peat up to the edge of ponds, or draining and filling-in bog ponds.

Pond-breeding amphibians, including the green frog, typically use different landscape elements at different times of the year (Sinsch 1990, Pope et al. 2000). Thus, amphibians occurring at ponds within the mined section will have to move across mined surfaces to reach other required habitats. During dry conditions, the bare peat substrates surrounding ponds in the mined section form a desiccating environment that may reduce amphibian survival due to predation and dehydration. Although maintaining sufficiently large buffer zones (e.g., 165 m) around bog ponds within mined surfaces could increase pond use by amphibians, it is also possible that these areas become sinks over longer periods. Indeed, animals repeatedly failing to reach natural areas when moving across the peat surfaces separating ponds and upland habitats would eventually lead to population extinctions. In addition, regular circulation and harrowing with heavy machinery over mined surfaces (i.e., several times per day during dry periods) reduces further the probability that amphibians would reach ponds in peat fields. Establishing zones (e.g., vegetated corridors) that connect bog ponds with bog fragments and are not subject to mechanical circulation may alleviate peat mining effects on amphibians. Investigations on the use of vegetated corridors by amphibians are required and will provide additional information on which to formulate informed management decisions. Nonetheless,

preserving large buffer zones around ponds and vegetated corridors within peat fields will facilitate the restoration of mined sites by providing a source of dispersers for bog plants and bog-associated wildlife.

Our results show that ponds within mined sections can be used by green frogs, but they likely offer suboptimal habitat, as no green frogs called at ponds within the mined surface. Although frogs are more abundant and breed in ponds of the moderately disturbed section, the positive effect remains temporary, as these areas are part of site preparation for peat mining and will inevitably be mined. Establishing buffer zones around bog ponds within peat fields may or may not alleviate peat-mining effects on amphibians but, in the longer term, will provide a source of dispersers of bog plants and wildlife during the restoration phase.

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Chapitre 3

Landscape characteristics influence pond occupancy by frogs after accounting for detectability

MAZEROLLE^{1,2}, M. J., DESROCHERS^{1,2}, A., ROCHEFORT², L. En 2^{ième} révision. **Landscape characteristics influence pond occupancy by frogs after accounting for detectability.** *Ecological Applications*. ¹Centre de recherche en biologie forestière, Pavillon Abitibi-Price, Faculté de Foresterie et de Géomatique, Université Laval, Québec, Québec, Canada G1K 7P4. ²Groupe de recherche en écologie des tourbières, Pavillon Paul-Comtois, Université Laval, Québec, Québec, Canada G1K 7P4. *Ce chapitre est le fruit du travail du candidat. André Desrochers et Line Rochefort ont apporté des suggestions quant au design et à la préparation de ce chapitre.*

Résumé

Plusieurs chercheurs ont émis l'hypothèse que les caractéristiques du paysage, tels que la quantité et la proximité d'habitat, influencent la répartition spatiale des amphibiens. Par le fait même, ceci a généré plusieurs travaux sur les effets du paysage sur les patrons de présence d'amphibiens dans des parcelles d'habitat ou des étangs. La plupart ont conclu que le paysage est important. Néanmoins, nous avons identifié deux problèmes associés à ces études: le premier traite de leur application à d'autres types de paysage, étant donné que la plupart des études ont été effectuées en systèmes agricoles, tandis que le deuxième concerne la probabilité de détection et ses effets sur les conclusions de ces études. Nous avons testé l'hypothèse que les caractéristiques du paysage influencent les patrons de présence d'amphibiens aux étangs, après avoir tenu compte de la probabilité de détection, dans des paysages tourbeux soumis à l'extraction de la tourbe. Nous avons également montré les répercussions d'ignorer la détectabilité en comparant nos résultats à ceux obtenus avec des régressions logistiques conventionnelles. Les résultats indiquent que la présence des grenouilles augmente avec la quantité d'étangs à l'intérieur de rayons de 100, 250 et 1000 m, ainsi que la quantité de forêt à l'intérieur de 1000 m. Toutefois, le recouvrement forestier à 250 m diminue la probabilité de présence de grenouilles aux étangs. Les analyses ne tenant pas compte de la probabilité de détection tendent à surestimer l'influence des variables sur la présence. Notre étude appuie l'hypothèse que les caractéristiques du paysage influencent la répartition spatiale des amphibiens dans les étangs. Afin d'augmenter la qualité et le potentiel d'utilisation des modèles en

conservation, nous recommandons fortement l'estimation de la probabilité de détection pour tout inventaire effectué sur le terrain.

Abstract

Many investigators have hypothesized that landscape attributes such as the amount and proximity of habitat is 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 overestimating the influence of variables on frog occurrence. 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.

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 1980's 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., Andr en 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 Semlitsch 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 McPeck 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).

Table 1. Landscape characteristics influence the presence of pond-breeding amphibians at ponds. We only considered studies investigating both patch and landscape characteristics on amphibian presence, where the pond was considered as the patch.

Landscape type	Percent of taxa responding to			Total 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

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

[‡]Knapp et al. 2003, Bosch and Martínez-Solano 2003.

[¶]Houlahan and Findlay 2003.

[§]Bradford et al. 2003.

^{||}Mazerolle and Cormier 2003.

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. Non-detection 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, Chapman et al. 2003, Mazerolle 2001, 2003, this thesis, Chapter 1).

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 (Fig. 1). Peatlands are acidic wetlands limited to boreal countries, predominantly Canada and Russia, and extend over 4 million km² of the Earth's surface (Maltby and Proctor 1996). Through intensive draining for agriculture, forestry, or urbanisation, 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 million cubic meters in 1997 (Daigle et al. 2001).

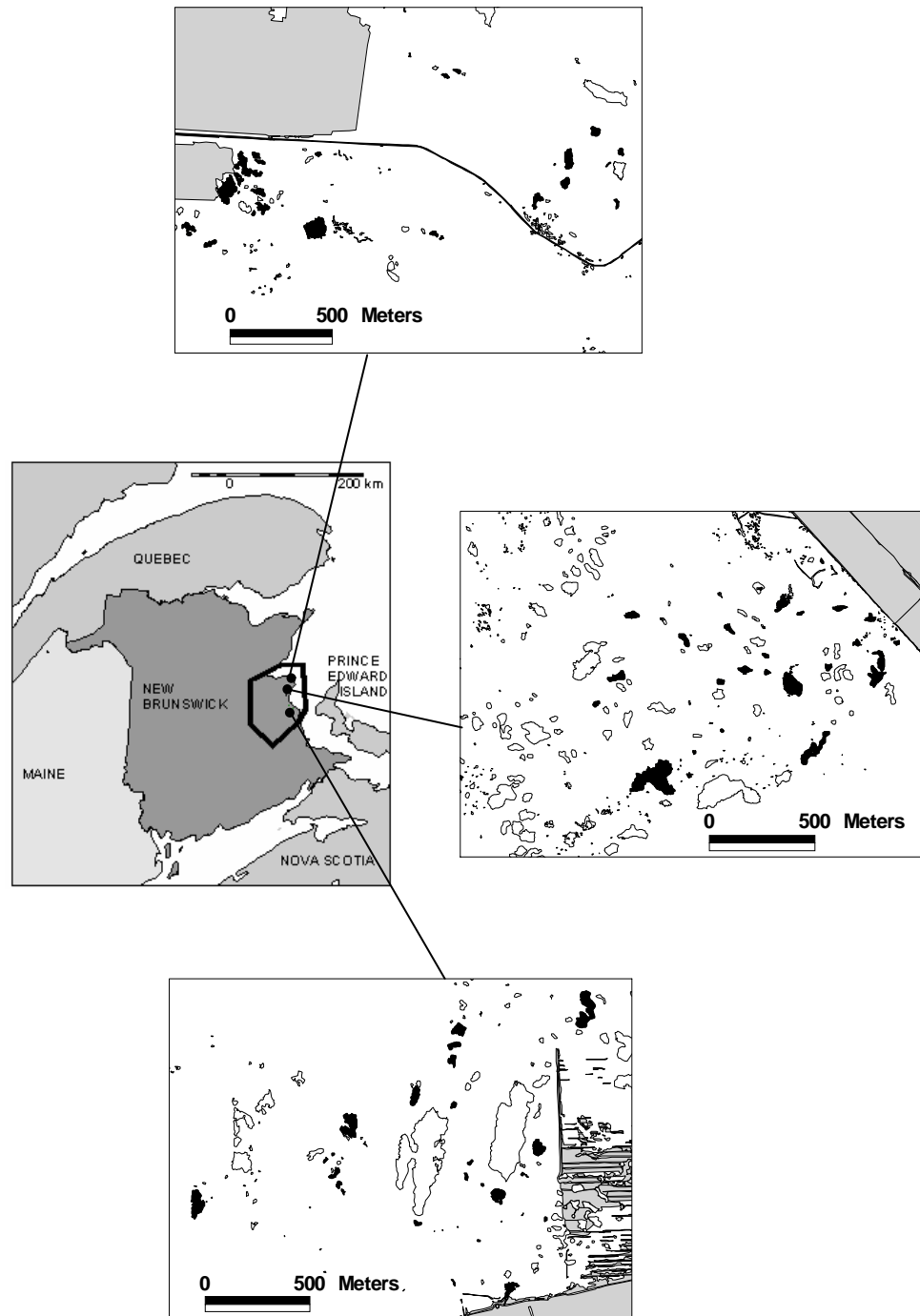


Figure 1. Location of bog ponds sampled in the three peatland landscapes under study in eastern New Brunswick for the study of green frog occurrence. Black polygons correspond to the 70 ponds sampled, empty polygons denote other bog ponds, whereas shaded areas indicate the surfaces undergoing peat mining.

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

Each of the three areas under study was 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 disturbance and had been mined for at least 5 years. Bog ponds were common in each peatland, and those located on the mined surfaces were not considered for this paper. In contrast to upland ponds, bog ponds are typically acidic (i.e., pH ca. 4.0) and devoid of fish (this thesis, Chapter 1). Each study year, we selected a subset of 12 ponds in each peat landscape through randomized stratified sampling across distance of ponds to the mined edge to ensure 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 for typical 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 x 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), 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 1600 and 2400, 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, Vitt et al. 1995, but see Tahvanainen and Tuomaala 2003). 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 x 1 m-quadrats centered on each call station (i.e., between 2-36 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 x 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, shrub layers 0.5-3 m, 30-50 cm, 10-30 cm, < 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 Table 2 for descriptive statistics of microhabitat variables.

Table 2. Descriptive statistics of microhabitat variables at bog ponds sampled within mined peatlands in eastern New Brunswick, Canada (n = 70 ponds).

Physical and chemical characteristics			Vegetation cover		
Variable	Unit	Mean \pm SD	Variable	Unit	Mean \pm SD
Pond perimeter	m	199.4 \pm 161.1	Tree layer > 3 m	%	0.1 \pm 0.6
Pond area	m ²	1823.2 \pm 2670.9	Shrub layer > 50 cm	%	1.8 \pm 5.1
Water depth	m	0.44 \pm 0.22	Shrub layer 30-50 cm	%	2.2 \pm 3.5
Water pH	pH	3.96 \pm 0.19	Shrub layer 10-30 cm	%	14.5 \pm 7.2
Water conductivity	μ S/cm	3.59 \pm 6.26	Shrub layer < 10 cm	%	8.6 \pm 6.5
Air temperature	$^{\circ}$ C	18.2 \pm 6.2	Herbaceous layer	%	10.3 \pm 5.2
			Moss layer	%	79.6 \pm 11.9
			Submerged	%	5.4 \pm 6.4
			vegetation		
			Emergent vegetation	%	8.8 \pm 6.9
			Floating vegetation	%	14.6 \pm 12.6

We used principal components analysis (PCA) to summarize the vegetation data with the first 4 axes, explaining a total of 76.6% of the variation (Table 3). The first axis was strongly correlated with the cover of tall shrubs and emergent vegetation, the second was an index of low shrubs and moss cover. Herbs and floating vegetation were summarized by the third axis, whereas the fourth axis represented submerged and floating vegetation. The factor loadings 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 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 less than 1 km within the landscape to reach breeding, summering, and hibernation habitats (Semlitsch and Bodie 2003, Dodd 1996). We then calculated the amount of forest habitat, pond habitat, and surfaces mined for peat, in the buffer areas surrounding each of the ponds we sampled. We also measured the distance of each pond to the nearest adjacent pond, forest patch, mined surface, and road. Table 4 summarizes the descriptive statistics for each landscape-scale variable.

Table 3. Factor loadings of principal components analysis (PCA) used to summarize vegetation structure data at bog ponds of eastern New Brunswick, Canada.

Variable	Factor loadings			
	PCA1	PCA2	PCA3	PCA4
Tree layer (> 3 m)†				
Shrub layer 0.5-3 m	0.708	-0.554	-0.147	0.192
Shrub layer 30-50 cm	0.853	-0.370	0.107	-0.003
Shrub layer 10-30 cm	0.754	0.401	0.207	0.109
Shrub layer < 10 cm	0.445	0.604	0.272	-0.114
Herbaceous layer	-0.064	0.299	-0.782	0.193
Moss layer	-0.422	0.649	0.293	0.169
Submerged vegetation	0.303	0.378	-0.396	0.604
Emergent vegetation	0.591	0.480	0.021	-0.260
Floating vegetation	0.154	0.197	-0.538	-0.711
Eigenvalue	2.642	1.892	1.295	1.065
Variance explained (%)	29.35	21.02	14.39	11.83

†Tree layer was not included in the analyses as only 2 ponds had tree cover on their perimeter.

Table 4. Descriptive statistics of landscape-scale variables around bog ponds sampled within mined peatlands in eastern New Brunswick, Canada (n = 70 ponds).

Disturbance characteristics		Adjacent habitat characteristics	
Variable	Mean \pm SD	Variable	Mean \pm SD
Distance to closest mined surface(m)	500.0 \pm 402.5	Distance to closest forest (m)	344.1 \pm 240.6
Distance to closest road (m)	690.3 \pm 411.6	Distance to closest pond (m)	26.9 \pm 26.3
% cover mined 100 m	2.3 \pm 6.4	% cover forest 100 m	2.6 \pm 8.3
% cover mined 250 m	6.9 \pm 11.9	% cover forest 250 m	2.5 \pm 6.4
% cover mined 500 m	11.0 \pm 14.8	% cover forest 500 m	3.4 \pm 5.7
% cover mined 1000 m	14.0 \pm 12.2	% cover forest 1000 m	7.5 \pm 6.3
		% cover pond 100 m	6.1 \pm 6.3
		% cover pond 250 m	7.3 \pm 6.3
		% cover pond 500 m	6.8 \pm 4.3
		% cover pond 1000 m	4.8 \pm 2.4

Statistical analyses

Because each pond was surveyed on 5 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-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).

We considered a set of candidate site-occupancy models consisting of microhabitat and landscape variables, either alone or combined, to determine to what extent landscape variables influence species occurrence (Table 5). We started with four microhabitat models likely to explain frog presence at the ponds: pond size, pond water chemistry, cover of shrubs and moss (PCA1 and PCA2), and cover of herbs and aquatic vegetation (PCA3 and

PCA4). 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 5). 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, all above-mentioned models were run with effort and air temperature on p , as well as with effort only. 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). Thus, we considered that systematically including a year covariable (i.e., 1999 vs 2000) was sufficient to account for additional spatial relationships, as each pond was sampled during a single year.

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 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). Please refer to Appendix 1 for detailed instructions on how to compute and interpret the results of the analysis of ecological data using this approach.

Table 5. Set of candidate models considered to explain green frog occurrence at 70 bog ponds sampled either in 1999 or 2000 in mined peat landscapes. Terms in parentheses following ψ , the probability of occurrence, and p , the probability of detection given the presence of the species, indicate the variables included for each.

Model name	Model structure‡	Number of parameters‡
Pond-scale models		
Pond size	$\psi(\text{year perim depth}) p(\text{effort airtemp})$	7
Pond vegetation 1	$\psi(\text{year PCA1 PCA2}) p(\text{effort airtemp})$	7
Pond vegetation 2	$\psi(\text{year PCA3 PCA4}) p(\text{effort airtemp})$	7
Pond water	$\psi(\text{year pH cond}) p(\text{effort airtemp})$	7
Landscape-scale models		
Distance to adjacent habitat	$\psi(\text{distforest distpond}) p(\text{effort airtemp})$	7
Distance to disturbance	$\psi(\text{distroad distmined}) p(\text{effort airtemp})$	7
Percent cover of adjacent habitat†	$\psi(\text{forestcov watercov}) p(\text{effort airtemp})$	7
Percent cover of adjacent disturbance†	$\psi(\text{minedcov}) p(\text{effort airtemp})$	6
Combined models		
Pond and distance/cover of habitat	see models above	9
Pond and distance of disturbance	see models above	9
Pond and cover of disturbance	see models above	8

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

‡ Intercept parameters for ψ and p were included in all models. Alternate models were run with same parameters on ψ but without airtemp on p .

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 5). Here, however, each regression model had 2-3 parameters fewer than its site-occupancy counterpart, because logistic regressions did not account for the probability of detection (i.e., no parameter for either the intercept, effort, or air temperature). 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 $77.0 \pm 5.8\%$ (model-averaged estimate \pm unconditional SE) were occupied by green frogs, with a detection rate of $21.4 \pm 12.9\%$. 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 (Table 6). The “best” model given our set of candidate models consisted of pond vegetation structure and the percent cover of 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.

Based on model averaging, the probability of green frog occurrence increased strongly with the pond cover within 100, 250, and 1000 m (Table 6). 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 decreased the occurrence of frogs. Sampling effort strongly influenced the probability of detecting green frogs at the ponds during surveys, whereas air temperature did not have such an effect. There was very little evidence of an effect of the other microhabitat and landscape variables we considered in our study, as their

90% confidence intervals included 0.

Table 6. Highest ranked occupancy models of green frogs at ponds in peat landscapes undergoing peat mining. Models with Akaike weights < 0.05 are not shown for clarity.

Model name†	Number of parameters	Delta AIC _c	Akaike weight
Pond vegetation 2 and cover of habitat within 1000 m (effort on p)	8	0	0.52
Pond vegetation 2 and cover of habitat within 1000 m (effort and airtemp on p)	9	1.61	0.23
Pond vegetation 2 and cover of habitat within 500 m (effort on p)	8	3.63	0.09
Pond vegetation 2 and cover of habitat within 250 m (effort on p)	8	4.67	0.05
Cover of habitat within 100 m (effort on p)	6	4.71	0.05

Model-averaged estimates (\pm unconditional SE)‡

Parameters on ψ						Parameter on p
% pond cover 100 m	% pond cover 250 m	% pond cover 1000 m	% forest cover 250 m	% forest cover 1000 m		Effort
38.551	11.203	7.291	-5.112	4.218		0.782
(14.618)	(5.996)	(3.313)	(2.573)	(2.286)		(0.163)

†See table for model structure; AIC_c of highest ranking model = 288.08.

‡Parameters for which 0 is excluded from the 90% confidence interval are shown.

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 0.17-0.18) included pond vegetation structure, they suggested that the amount and proximity of mined surfaces strongly influenced frog presence (Table 7). Model-averaging revealed that out of the original variables considered, one pond and three landscape variables were important in explaining green frog occurrence. None of these variables were deemed important based on the site-occupancy analyses.

Table 7. Highest ranked logistic regression models of green frogs at ponds in bogs undergoing peat mining. Models with Akaike weights < 0.05 are not shown for clarity.

Model name†	Number of parameters	Delta AIC _c	Akaike weight
Pond vegetation 2 and cover of mined surface within 100 m	5	0	0.18
Cover of mined surface within 100 m	3	0.04	0.18
Pond vegetation 2 and distance to adjacent disturbance	6	0.15	0.17
Pond size and cover of mined surface within 100 m	5	1.62	0.08
Pond water and cover of mined surface within 100 m	5	2.14	0.06
Pond vegetation 2 and cover of habitat within 500 m	6	2.68	0.05

Model-averaged estimates (\pm unconditional SE)‡

Cover of floating and submerged vegetation (PCA4)	Distance to closest edge	Distance to mined road	Distance to % mined surface within 100 m
-0.687	-0.731	0.913	1.287
(0.374)	(0.355)	(0.399)	(0.752)

†See table for model structure; AIC_c of highest ranking model = 85.66.

‡Parameters for which 0 is excluded from the 90% confidence interval are shown.

DISCUSSION

Pond characteristics

Pond microhabitat variables did not influence the occurrence of green frogs at ponds. Although the importance of pond size on frog presence has been well documented for amphibians in other systems (e.g., Laan and Verboom 1990, Dickman 1987, 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 occurrence patterns of amphibians at ponds (e.g., Pope et al. 2000, Hecnar 1997, Hecnar and M'Closkey 1998), but not in our study. Indeed, neither water chemistry (pH and conductivity) nor vegetation structure influenced pond occupancy. This probably results from the low variability of pond water chemistry and vegetation 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. This is consistent with amphibian spatial patterns 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 larger 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. This may stem from a change of perception of the landscape by frogs across scales. Alternatively, it 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 on natural dispersal and movements of individuals, as well as their perceptual range at these scales, 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.

Given the physiology of amphibians, dry environments can impede their movements (Rothermel and Semlitsch 2002, Mazerolle and Desrochers submitted manuscript). The amount and proximity of peat mining did not influence pond occupancy by green frogs and was unexpected. Indeed, Mazerolle and Desrochers (submitted manuscript) 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. 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). Thus, the absence of a peat mining effect on pond occupancy suggests that frogs at ponds did not originate from areas beyond mined surfaces.

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. Wetland loss remains a serious concern in a variety of landscapes, as they are threatened by land use (Semlitsch and Bodie 1998, Gibbs 2000, Snodgrass et al. 2000). The need to preserve both large and small isolated wetlands has been raised by investigators (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, Johnson and Semlitsch 2003, Guerry and Hunter 2002, Gibbons 2003, Houlahan and Findlay 2003). Based on our data and the evidence from a number of amphibian studies (e.g., Vos and Stumpel 1995, Pope et al. 2000, Vos and Chardon 1998), 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.

Site-occupancy models vs logistic regressions

Many differences arose between the two modelling approaches. For instance, none 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 overestimated the influence of certain variables on frog occurrence at the ponds in our study system. Gu and Swihart (2004) also reported that non-detection produces biased logistic regression parameter estimates. 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, 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 analysing 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 occupancy of frogs at ponds increases with pond cover within 100, 250, and 1000 m (i.e., pond isolation), as well as high forest cover within 1000 m. At 250 m, however, forest cover decreases frog occurrence. We did not detect any effects of peat mining proximity or amount of mined surfaces on frog occurrence. Thus, preserving a complex of bog ponds and adjacent habitat should 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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Chapitre 4

Resistance to frog movements in a disturbed landscape

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Résumé

La capacité d'un animal à coloniser avec succès une parcelle dans le paysage dépend d'au moins deux composantes: sa capacité à détecter une parcelle et sa capacité à atteindre la parcelle. Par l'entremise d'une série d'expériences effectuées sur le terrain, nous avons comparé l'orientation initiale et le succès de retour de grenouilles vertes (*Rana clamitans melanota*) et de grenouilles léopards (*Rana pipiens*) déplacées sur des surfaces naturelles (i.e., avec couverture végétale) et arides (i.e., sans couverture végétale). Nous avons également évalué le choix de parcours pour des individus relocalisés, à savoir, un parcours court dépourvu de couverture végétale ou un parcours long avec couverture végétale. Finalement, nous avons quantifié la perte en eau et le comportement de grenouilles exposées à différents substrats qui résultent de perturbations anthropiques. Les grenouilles ont généralement évité les surfaces arides lors de leurs déplacements lorsqu'une surface naturelle était disponible. Bien que capables de s'orienter avec succès vers le site de capture (i.e., l'étang) lorsque relocalisées sur la surface aride, les grenouilles avaient une plus faible probabilité de retour que lorsque relocalisées à des distances semblables sur la surface naturelle. Les grenouilles sur les substrats associés à des perturbations anthropiques (i.e., terre ou tourbe) ont perdu près de deux fois plus d'eau que les individus sur le substrat témoin. Néanmoins, les plus grandes pertes en eau ont eu lieu sur la terre exposée sans écran (i.e., absence de couverture végétale). Nous concluons que les surfaces perturbées par les activités anthropiques qui résultent en une perte de couverture végétale et qui produisent des surfaces arides, tels que l'exploitation des tourbières ou l'agriculture, entravent les déplacements des grenouilles.

Abstract

The capacity of an animal to successfully recolonize a patch depends on at least two components: its ability to detect the patch and its ability to reach the patch. Through a series of field experiments, we compared the initial orientation and homing success of green frogs (*Rana clamitans melanota*) and leopard frogs (*Rana pipiens*) translocated across undisturbed (i.e., with cover) and barren surfaces (i.e., devoid of cover). We also assessed whether and to what extent individuals avoid crossing barren surfaces when presented with a choice against a longer, undisturbed, route. Finally, we assessed the water loss and behaviour of frogs exposed to different substrates resulting from anthropogenic disturbances. Frogs homing from a translocation site generally avoided barren surfaces when offered a choice between a long route on an undisturbed surface and a shortcut on a barren surface. Although able to orient towards the capture site (i.e., pond) when translocated on barren surfaces, frogs had a lower probability of homing successfully to the pond than when translocated at a similar distance on an undisturbed surface. Frogs on soil and peat substrates lost almost twice as much water as individuals on the control substrate, but the greatest losses were on soil without cover. We showed that anthropogenically disturbed areas that result in a loss of cover and produce barren surfaces, such as cutover peatlands and ploughed agricultural fields, disrupt the ability of frogs to reach habitat patches.

INTRODUCTION

Global amphibian declines have been reported during the last decades (Barinaga 1990, Vitt et al. 1990, Wyman 1990, Wake 1991, Houlihan et al. 2000). Although investigators denounce factors such as increased UV radiation, pathogens, or combinations thereof, habitat loss and fragmentation remain the most frequently mentioned agents believed responsible for these declines (Alford and Richards 1999, Johnson et al. 2002, Davidson et al. 2002). Indeed, it is well-established that habitat loss and fragmentation, through the establishment of roads or certain forestry and agricultural practices, reduce

amphibian abundance, species richness, or genetic diversity (e.g., deMaynadier and Hunter 1995, Hitchings and Beebee 1998, Vos and Chardon 1998, Koloszy and Swihart 1999, Joly et al. 2001, Scribner et al. 2001). However, evidence for the processes behind these patterns remains scarce (but see Rothermel and Semlitsch 2002, Johnston and Frid 2002, Chan-McLeod 2003).

One of the key processes behind population responses to habitat fragmentation is matrix-dependent mobility. Patch colonization is assumed to depend mainly on the distance between patches (Hanski and Gilpin 1991), but there is growing evidence that the quality of the matrix (e.g., cover, temperature, humidity) is important for animal movements (e.g., amphibians: Rothermel and Semlitsch 2002, Chan-McLeod 2003, mammals: Desrochers et al. 2003). The capacity of an animal to successfully recolonize a patch will depend on two major components. First, individuals must be able to detect the patch through their perceptual range (*sensu* Zollner and Lima 1997). Perceptual range can vary across species, distance, and weather conditions (Yeomans 1995, Zollner and Lima 1997, 1999, Gillis and Nams 1998), but its extent of variation across habitat types remains undetermined. Second, individuals must reach the patches that are detected, which relates to the permeability to the movement or landscape resistance (Ricketts 2001). Impediments to an animal's mobility include the matrix quality, the distance between patches, as well as increased predation and metabolic risks (Sjögren-Gulve 1994, Larsen and Boutin 1994, Rothermel and Semlitsch 2002, Turcotte and Desrochers 2003).

Pond-breeding amphibians use several habitats at different times of the year to complete their life cycles (Sinsch 1990, Pope et al. 2000). Amphibians can undertake migrations of a few kilometers, but most move less than 400 m during such movements (Dodd 1996, Semlitsch and Bodie 2003). In human-disturbed landscapes, reaching the breeding, summering, or overwintering habitats often implies crossing hostile environments that are dry or devoid of cover such as open agricultural fields, forest clearcuts, or peatlands mined for peat (Bury 1983, Chen et al. 1993, Wheeler and Shaw 1995, Price 1997). For amphibians, this can become a perilous endeavor. With their permeable skin, amphibians require moist environments, and few venture far from them (Sinsch 1990). Most species do not tolerate water losses exceeding 60% of their body water content (Thorson and Svihla

1943). Thus, amphibian movements over areas devoid of cover can be costly, not only because of increased predation risk but also because of physiological costs.

We addressed issues of patch detection and landscape resistance through a series of field experiments. We predicted that amphibian movements over anthropogenically-disturbed surfaces are more difficult than on natural surfaces. We evaluated the ability and the costs of moving over hostile areas for green frogs *Rana clamitans melanota* and leopard frogs *Rana pipiens*, two species commonly found in eastern North America (Wright and Wright 1949, Conant and Collins 1991). Although common in the study area, both species are sensitive to changes in the landscape resulting from urban development, forestry, agriculture, and peat mining activities (Bonin et al. 1997, Knutson et al. 1999, Koloszyvay and Swihart 1999, Mazerolle 2001, 2003, Woodford and Meyer 2003). In addition, these species exhibit strong site fidelity for their breeding and summering areas (Martof 1953, Dole 1968). Using frogs translocated from their summering habitat, we compared the initial orientation and homing success of the individuals moving across undisturbed and anthropogenically-disturbed surfaces. We also tested whether individuals avoid moving over a hostile surface, when given a choice against a safer but longer route. Finally, we determined the water loss and behaviour (e.g., burrowing, hiding, propped up above substrate) associated with the exposure to different types of substrates stemming from different anthropogenic disturbances. These data will provide useful parameters in the elaboration of predictive models of habitat disturbance in the landscape (e.g., spatially explicit models: Dunning et al. 1995, South 1999, Collingham and Huntley 2000).

MATERIALS AND METHODS

Study Area

All the experiments herein were conducted in eastern New Brunswick in the area surrounding Kouchibouguac National Park, New Brunswick, Canada. Mixed forest (*Picea mariana*, *Abies balsamea*, *Betula* spp., *Acer* spp.) and peatlands form most of the landscape. Intense forestry and peat mining activities are the main disturbances in the study area. These severely modify the landscape, leaving bare soil or bare peat, potential barriers to amphibian movements. Green frogs *Rana clamitans melanota* Rafinesque and leopard

frogs *Rana pipiens* Schreber are common in eastern New Brunswick and occur in various wetland habitats (Gorham 1970, McAlpine 1997).

Peat Mining

We conducted our study in a peatland-dominated landscape (i.e., bogs and fens). These acidic wetlands mostly occurring in northern countries (predominantly Canada and Russia) cover approximately 4 million km² worldwide (Maltby and Proctor 1996). However, they have undergone intensive draining for agriculture, forestry, and urbanisation and few remain unaltered in certain parts of Europe (Poulin and Pellerin 2001). Attention has recently been directed to the rapidly-growing peat mining industry which extracts large volumes of peat in Europe and eastern North America for use in horticulture or fuel (Wheeler and Shaw 1995, Lavoie and Rochefort 1996). For instance, global peat mining production reached 93.7 million cubic meters in 1997 (Daigle et al. 2001).

Peatlands disturbed by peat mining share several characteristics with agricultural fields and lands under certain forestry practices and thus may serve as model systems. During peat mining, the vegetation is removed, vast networks of ditches are established, surfaces are levelled, devoid of live vegetation, and dry (see details in Mazerolle 2003). Due to the precarious status of peatlands in many parts of the world, the known negative impacts on the fauna and flora (Poulin et al. 1999; Delage et al. 2000, Mazerolle 2003), and the drastic contrast between mined and undisturbed surfaces, we used these systems for our landscape-scale experiments.

Orientation and Homing Success

In order to test the detection ability of frogs and landscape resistance, we conducted orientation and homing experiments on barren and undisturbed surfaces. We selected a pond (perimeter = 105 m) in an undisturbed portion of Pointe-Sapin Bog in eastern New Brunswick, Canada (46°57'N, 64°52'W). The pond is 70 m from the edge of barren peat, and is used mostly as summering habitat by green frogs and leopard frogs (Mazerolle unpublished data). In late April 2000, we erected a continuous aluminum drift-fence (40 cm height above ground, 20 cm below) on the pond's perimeter ca. 2 m from the water's edge.

We placed 11.4-L pitfall traps at 5-m intervals on both sides of the fence (see Mazerolle 2003 for trap design), for a total of 24 traps on each side. Traps were opened from 5 May 2000 to 29 August 2000, and 28 May 2001 to 30 August 2001, when amphibians frequented the site. During the same trapping periods, we placed 7 minnow traps (see Mazerolle and Cormier 2003 for minnow trap details) to increase the trapping effort and capture individuals already within the fenced area. Traps were visited in the evening: every day during the peak of the season, and every other day afterwards. At the end of summer, pitfall traps were closed with tight-fitting lids, minnow traps were withdrawn, and parts of the fence removed to allow individuals to move freely in the pond area between trapping periods.

Green frogs and leopard frogs captured at the pond were measured and marked for individual recognition based on the Donnelly system (Donnelly et al. 1994). Each individual was then placed for 10 min. in a release device modified from Yeomans (1995) before starting the experiments. The device consisted in an opaque 2-L container fitted with a lid. We cut a pivoting trap door on the side of the container on which a string was tied. This allowed the investigator to open the door from behind without being seen by frogs.

Amphibians were put in the release device at the pond and translocated from the pond according to the following treatments. Each individual was assigned randomly to a distance treatment (i.e., 35 or 70 m from the pond). Because the pond is 70 m from the barren surface, all 35-m translocations were on the undisturbed surface. For the 70-m translocations, we determined randomly whether the individual would be placed on the barren or undisturbed surface (i.e., surface type treatment). The 70-m translocation on barren peat was 1 m into the peat field, across a large drainage ditch. Previous experimentations ($n = 21$ frogs) on the barren surfaces indicated that green frogs and leopard frogs maintained their orientation towards the pond of capture, regardless of the proximity of a ditch (Mazerolle unpublished).

We randomly allocated the orientation of the opening of the release device relative to the pond (towards or opposite). At the start of each trial, the investigator opened the trap door and retreated at least 10 m from the frog. The investigator crouched down during the trials, and remained behind the frog to minimize disturbance. We recorded the initial

orientation of the frog (i.e., first frog movement 1-m from the release area) relative to the pond. That is, we calculated the minimum angular deviation between the orientation of the pond and the frog (i.e., smallest angle between orientation of the frog and that of the pond). Small pieces of flagging tape were placed flush to the ground 1-m around the release device to provide points of reference. The observations were terminated when the frog reached the perimeter delimited by the pieces of tape (i.e., 1 m from the release device), or after 30 min.

We conducted the translocations after 1800 to reduce the disturbance from the peat-mining activities, and to facilitate frog movements, as individuals are usually most active later in the day and evening (Oseen and Wassersug 2002). Air temperature, wind velocity (i.e., low wind or moderate to strong wind), and percent cloud cover were recorded during each trial. Frogs were used only once in the experiment. Translocated frogs recaptured at the pond, either in pitfall traps or minnow traps, were noted to have successfully homed to the pond.

We used linear and logistic regressions to model the log of the angular deviation of frog orientation and the probability of homing successfully to the pond, respectively. For both analyses, the basic model consisted of the intercept, and the explanatory variables year, opening orientation of the release device, and species. We fitted a series of plausible models including the variables surface type (i.e., barren vs undisturbed), the species x surface type interaction, distance (i.e., 35 m vs 70 m), body size (snout-vent length), air temperature, wind (i.e., no/low wind vs high wind), and percent of cloud cover. Model fit was evaluated with the most complex model. We evaluated the strength of evidence for each model based on the second-order Akaike Information Criterion (AIC_c), following Burnham and Anderson (2002). Estimates and standard errors for the parameters of interest were obtained with model-averaging techniques (Anderson et al. 2000, Burnham and Anderson 2002). Please refer to Appendix 1 for detailed instructions on how to compute and interpret the results of the analysis of ecological data using this approach.

Avoidance of Barren Substrates

As an additional measure of landscape resistance, we tested whether translocated frogs avoid venturing onto barren surfaces when given a choice between a short route on a

barren surface and a longer route on an undisturbed surface. In June 2001, we created a testing arena simulating both natural bog vegetation and barren peat surfaces, on an abandoned part of Pointe-Sapin Bog, bordered by a small rectangular pond (Fig. 1). The arena was delimited by a fence 45 cm high made of cloth used in landscaping. Using spades, we collected the surface vegetation (i.e., *Sphagnum* moss, ericaceous shrubs, herbs) including the roots and peat from the first 10 cm below the surface of an adjacent undisturbed bog remnant. We then arranged the blocks of vegetation into two perpendicular corridors (2.25 x 12 m and 2.25 x 20) in the arena. The blocks of vegetation were packed tightly against one another to reduce dehydration and watered every 48 hours. The rest of the arena was covered with 10 cm of loose peat found on the barren surface of peat fields.

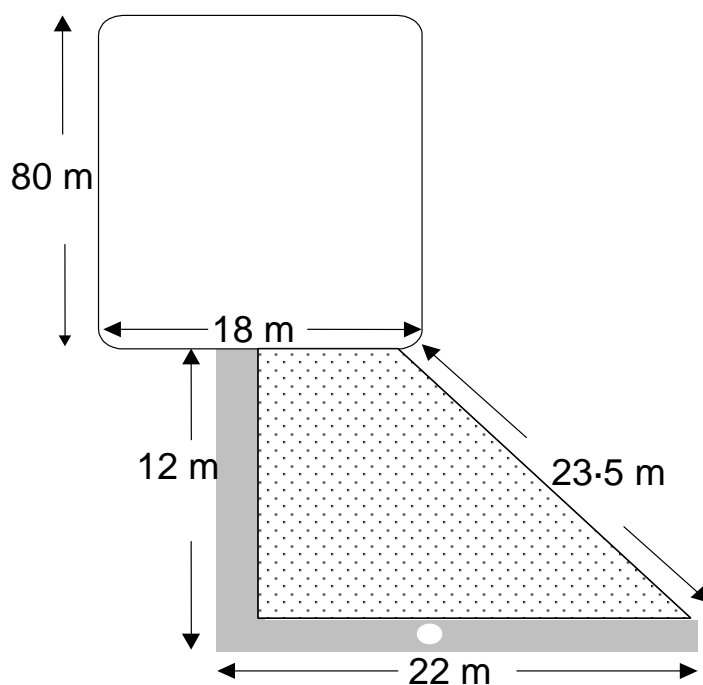


Figure 1. Test arena used to determine avoidance of barren peat by amphibians (not drawn to scale). The circle denotes the point of release of frogs, the shaded surface corresponds to the vegetated corridor, whereas the dotted surface represents barren peat.

We captured green frogs and leopard frogs with dipnets in the pond and the vicinity for our experiment. Each individual was measured to snout-vent length immediately after capture, marked, and placed in a release device (described above). The release device was placed on the corridor 13 m from the pond, with the trap door either facing the pond (i.e., the risky shortcut) or the end of the corridor (i.e., the safe detour). The assignment of the treatment was completely randomized. Following a 10-min. acclimation period, the trap door was opened and we began the observations. The trial was terminated either after 30 min., or when the individual reached the pond, during which we noted whether the frog moved over the peat or not. Trials were conducted after 1800, between 29 June and 13 August 2001 under similar meteorological conditions, (i.e., on days without precipitations). We recorded air temperature, wind velocity, and cloud cover.

We evaluated the effect of frog size, species, air temperature, wind velocity, cloud cover on the probability of choosing the barren substrate with logistic regressions. All models included the intercept and the orientation of the release device. Each model was ranked based on the AIC_c. The estimates and standard errors for the parameters of interest were then computed with model-averaging techniques.

Dehydration

We quantified the physiological costs (i.e., dehydration) of frogs moving in matrices within landscapes differing in human disturbance, and used dehydration rates as another measure of landscape resistance. We captured a total of 126 green frogs for the experiments described below during mornings at several breeding ponds in the study area. Individuals were temporarily housed in plastic containers with water for no more than 24 h before starting the experiments. Each was used only once. After the experimental trial, the individual was marked by clipping a single digit and released at its point of capture at the end of the day. We conducted the experiments between 20 June and 15 August 2002, under similar meteorological conditions, between 1200 and 1800. Before the start of each trial, each frog was carefully cleaned to remove any particles on the skin and blotted dry with a paper towel. We gently pressed on the abdomen of the frog to empty the bladder. The frog was then weighed to the nearest 0.1 g using a portable electronic scale (Acculab,

Huntingdon, PA, USA). Following the initial weighing, the frog was placed in a plastic container (54.5 x 22 x 39 cm in depth) which had a layer of 5 cm of one of three substrates. We estimated the water loss associated to the passage of frogs over two hostile environments (i.e., substrates) of anthropogenic origin commonly encountered in the study area. We used a bare soil substrate (sifted sandy soil) to simulate conditions encountered during movements over areas remaining after certain agricultural or forestry practices, whereas a bare peat substrate (loose peat) was used to simulate movements over bogs undergoing peat mining. A third substrate, consisting of a living carpet of moist *Sphagnum* spp. moss taken from a peat bog in the study area acted as a control treatment. These substrates were likely to be encountered by frogs during migrations in the study area. During the experimental trials, a single frog was introduced in each container. The allocation of individuals to treatments was completely randomized.

The dehydration experiment was conducted outside in open mowed fields devoid of any vegetative cover > 1 cm. We covered each container with a nylon window screening fastened with clothespins on the outer rim of the container to prevent the escape of frogs during the trials. Half of the total number of containers was placed under an opaque tarpaulin ca. 1 m above the containers (shade treatment) to simulate the cover provided by a dense vegetation cover whereas the other half was not shaded. Each frog was submitted to a dehydration period of 2 h, and was weighed at 0, 1, and 2 h as described above. We calculated the change in mass at each hour relative to body mass at the previous hour. We selected a period of 2 h to minimize stress to frogs and believed that this would approximate the time of exposure of frogs when moving over substrates. Preliminary trials under the same conditions yielded dehydration rates below the vital limits of ca. 34% of body mass lost recorded for the species by Thorson (1955) and Schmid (1965). Consequently, we refer to frogs having undergone the 2-h dehydration period as acutely-dehydrated frogs.

Researchers have reported that certain species adopt specialized behaviours, such as burrowing in the soil or retreating to cavities, to reduce water losses under dry conditions (Bentley 1966, Katz 1989, Schwarzkopf and Alford 1996, Prather and Briggler 2001, Rohr and Madison 2003). We recorded the behaviour of the frogs in the containers at the end of the first and second hours of the trials. Frogs were approached slowly to avoid modifying

their behaviour and position. We characterized five types of behaviour: 1) hidden in cavity (hidden in a small depression in substrate, but not buried), 2) buried (partially or completely buried in substrate), 3) crouched (head and body against substrate), 4) head up (head is above substrate but rest of body against substrate), and 5) propped up (head and body above substrate, front legs extended). We only considered the first three as behaviours minimizing the surface exposed to evaporative water loss (i.e., an attempt to reduce dehydration).

The air temperature, the percentage of cloud cover, and the wind intensity (low/no wind or moderate to strong wind) were recorded during the dehydration trials. We took three samples of the substrate at the start of the trial for each frog of the experiment. The substrate samples were later dried in an oven at 200°C to determine their percent water content.

We analyzed the change in mass (i.e., mass lost or gained) with regression models using Generalized Estimating Equations (GEE's) (Diggle et al. 1994, Stokes et al. 2000, Horton and Lipsitz 1999) from the GENMOD procedure in SAS 8.01 (SAS Institute Inc. 1993). GEE's are an extension of generalized linear models and are specially adapted for repeated measures (e.g., successively measuring mass in the same individual at 3 different periods), yielding robust estimates of parameters and standard errors. We used a normal regression for repeated measures to evaluate the effects of shade, substrate type, wind speed, cloud cover, and air temperature, on the mass (square-root transformed) lost each hour to dehydration. We expected a curved response of mass loss with the size of frogs, because small frogs have a greater surface to volume ratio than large frogs and thus, lose water faster (Thorson 1955, Schmid 1965). Thus, we included initial frog mass (i.e., before dehydration) and initial frog mass squared in the model. We also added the "shade x substrate type" interaction. Similarly, we evaluated the effect of the same variables mentioned above (except initial frog mass squared) on the frogs' probability of minimizing their body surface exposed during dehydration with a logistic regression for repeated measures. We built a set of plausible candidate models and assessed the strength of evidence for each with the AIC_c to calculate model-averaged parameters and unconditional standard errors.

Table 1. Highest-ranked linear regression models (i.e., $\Delta AIC_c \geq 0.10$) and estimates explaining the initial orientation (i.e., angular deviation) of frogs across undisturbed and disturbed surfaces ($n = 76$ individuals). Estimates in bold indicate that 0 is excluded from 95% confidence interval and that variable influences frog orientation. Interaction terms did not influence frog orientation and are not shown for brevity.

Model	Number of parameters	Delta AIC_c	Akaike weight
year opening species airtemp wind cloud surface	8	0	0.35
year opening species surface	5	0.92	0.22
year opening species svl surface	6	1.89	0.14

Model-averaged parameters (\pm unconditional SE)						
Species	SVL	Distance	Surface	Airtemp	Wind	Cloud
(green vs leopard frog)	vs	(35 vs 70 m)	(barren vs natural)	vs		
-0.168	-0.153	0.209	-2.540	-0.033	0.496	0.003
(0.357)	(0.129)	(0.311)	(0.292)	(0.021)	(0.283)	(0.003)

RESULTS

Orientation and Homing Success

Regardless of the species, frogs translocated on barren peat tended to orient accurately toward the pond, as opposed to the individuals relocated on undisturbed surfaces (Table 1). The average angular deviation \pm SD of frogs translocated on the undisturbed surface at 35 and 70 m was $86.2 \pm 52.9^\circ$ and $86.9 \pm 54.7^\circ$, respectively, whereas that of frogs 70 m on the barren surface was $20.1 \pm 41.3^\circ$. Frog orientation did not vary across distance, species, frog size, air temperature, wind velocity, or cloud cover. Large frogs were more likely to home successfully than smaller frogs. The effect of surface type on frog homing success, was less marked, but suggested that individuals translocated on the barren surface were less likely to successfully home to the pond than those translocated on the

undisturbed surface (Table 2). Indeed, the 95% confidence interval for the variable barely included 0, as indicated by the lower confidence limit (i.e., 0.0383). The probability of homing was independent of distance, species, air temperature, wind velocity, and cloud cover.

Table 2. Highest-ranked logistic regression models (i.e., $\Delta AIC_c \geq 0.10$) and estimates explaining the probability of homing across undisturbed and disturbed bog surfaces ($n = 84$ individuals). Estimates in bold indicate that 0 is excluded from 95% confidence interval and that variable influences frog homing success. Interaction terms did not influence homing and are not shown for brevity.

Model	Number of parameters	Delta AIC_c	Akaike weight
year opening species svl distance surface	7	0	0.26
year opening species svl surface	6	1.04	0.15
year opening species distance surface	6	1.64	0.11
year opening species svl	5	1.95	0.10

Model-averaged parameters (\pm unconditional SE)						
Species	SVL	Distance	Surface	Airtemp	Wind	Cloud
(green vs leopard frogs)		(35 vs 70 m)	(barren vs natural)			
0.364	0.528	-1.044	-1.386	-0.072	-1.144	-0.012
(0.746)	(0.269)	(0.663)	(0.7265)	(0.056)	(0.665)	(0.008)

Avoidance of Barren Substrates

During the selection experiment, the probability of frogs moving across the peat did not vary across frog size, species, or weather conditions (Table 3). Based on a log-linear

model of the frequency of frogs on both substrates, more frogs tended to avoid the barren substrate than venture on it (18 frogs vs 7 frogs, respectively; type 3 likelihood-ratio statistic = 7.10, $df = 1$, $P = 0.0077$). Those that proceeded across peat moved on average (\pm SD) 8.6 ± 7.6 m over this surface.

Table 3. Highest-ranked logistic regression models (i.e., $\Delta AIC_c \geq 0.10$) and estimates explaining the probability of frogs jumping on the barren peat surface when given a choice between short route on barren peat surface and longer route on the undisturbed surface ($n = 25$ individuals). The 95% confidence intervals for all the estimates included 0, indicating that the probability of frogs jumping on peat was independent of the variables in the model.

Model	Number of parameters	Delta AIC_c	Akaike weight
Opening species	3	0	0.27
Opening svl species	4	0.89	0.17
Opening svl	3	1.03	0.16

Model-averaged parameters (\pm unconditional SE)				
Species	SVL	Airtemp	Wind	Cloud
(green vs leopard frogs)				
-1.460	0.671	-0.087	-0.628	0.011
(1.083)	(0.655)	(0.128)	(1.042)	(0.015)

Dehydration

At the end of the 2-h dehydration period, green frogs lost almost twice as less water on the *Sphagnum* substrate than on either the soil or peat substrates (Fig. 2). The *Sphagnum*, soil, and peat substrates had a water content of $91.3 \pm 1.1\%$ (mean \pm SE), 10.1

$\pm 0.5\%$, and $63.1 \pm 1.1\%$, respectively. The mass lost by green frogs was greatest on the soil out of the shade (shade x substrate interaction, Fig. 2, Table 4). We detected a curved response of water loss with the frog mass before dehydration. Weather conditions also influenced frog dehydration. Although water loss decreased with cloud cover and was greatest under windy conditions, it was independent of air temperature.

During the first and second hours of dehydration, 53% of frogs exhibited postures minimizing their body surface to evaporative water loss. When out of the shade, green frogs tended to minimize the body surface exposed to evaporative water loss (Table 5). The small frogs reduced the surface exposed to evaporation more often than larger individuals. Substrate type, air temperature, wind speed, and cloud cover did not influence frog behaviour.

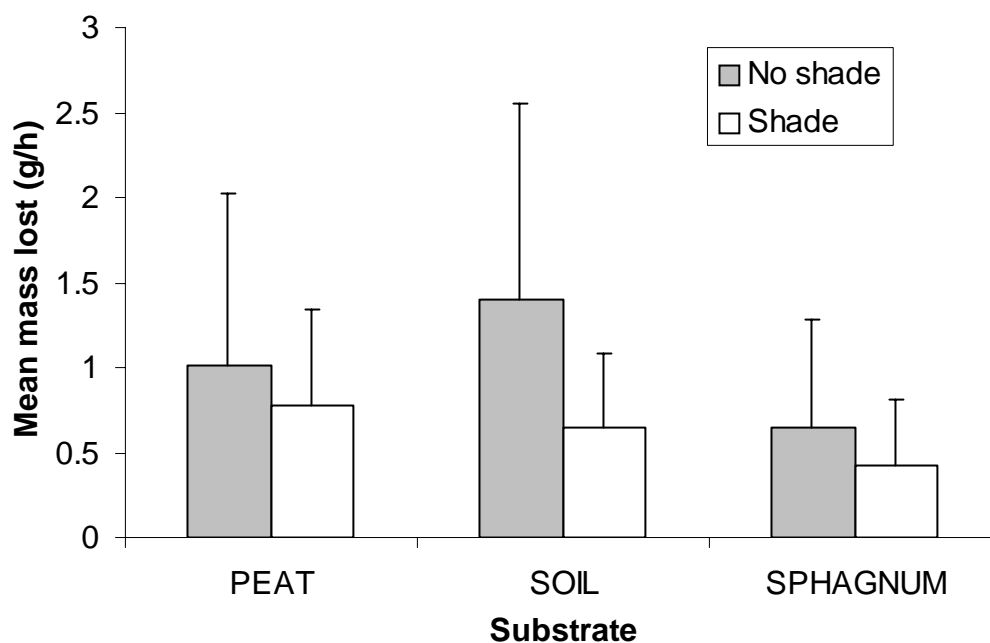


Figure 2. Mean mass lost in water (g) per hour for green frogs exposed to three different substrates and shade treatments. The bars represent 1 SD around the mean.

Table 4. Highest-ranked normal regression models for repeated measures (i.e., Delta $AIC_c \geq 0.10$) and estimates explaining the mass in water lost (square-root transformed) during dehydration of green frogs on different substrates ($n = 121$ frogs). Mass: body mass before dehydration; Mass2: square of the body mass before dehydration. Shade and *Sphagnum* were the reference levels for shade and substrate treatments, respectively. Estimates in bold indicate that 0 is excluded from 95% confidence interval and that variable influences frog mass lost.

Model	Number of parameters	Delta AIC_c	Akaike weight
Shade substrate mass mass2 airtemp wind cloud shade x substrate	11	0	0.96

Model-averaged parameters (\pm unconditional SE)

Interaction		Initial mass	Initial mass squared	Airtemp	Wind	Cloud
Shade x Peat	Shade x Soil					
0.134 (0.114)	0.395 (0.129)	0.064 (0.007)	-0.001 (0.0002)	0.008 (0.006)	0.211 (0.052)	-0.003 (0.001)

Table 5. Highest-ranked logistic regression models for repeated measures (i.e., $\Delta AIC_c \geq 0.10$) and estimates explaining the probability of frogs to minimize the surface exposed to evaporative water loss on different substrates ($n = 118$ frogs). Mass: body mass before dehydration. Shade and *Sphagnum* were the reference levels for shade and substrate treatments, respectively. Estimates in bold indicate that 0 is excluded from 95% confidence interval and that variable influences frog behaviour. Interaction terms did not influence frog behaviour and are not shown for brevity.

Model	Number of parameters	Delta AIC_c	Akaike weight
Shade mass	3	0	0.27
Shade substrate mass airtemp shade x substrate	8	1.38	0.14
Shade substrate mass airtemp	6	1.50	0.13
Shade substrate mass shade x substrate	7	1.84	0.11
Shade substrate mass	5	1.85	0.11

Model-averaged parameters (\pm unconditional SE)						
Shade	Substrate		Initial mass	Airtemp	Wind	Cloud
	Peat	Soil				
1.0662	0.432	0.301	-0.054	0.057	-0.001	0.203
(0.475)	(0.469)	(0.513)	(0.012)	(0.042)	(0.436)	(0.299)

DISCUSSION

The results of the homing, barren surface avoidance, and dehydration experiments consistently indicate that barren surfaces devoid of cover, following anthropogenic disturbances such as ploughing or in this case, peat mining, are resistant to amphibian movements. Green frogs and leopard frogs avoided barren surfaces when offered a choice between moving on the undisturbed and barren surfaces. For the first time, we provide

evidence that patterns of abundance in hostile environments are the result of amphibian behaviour and physiology. Indeed, in previous studies exclusively based on trap rates in different environments, researchers concluded that amphibians avoid open habitats without substantial evidence. For instance, deMaynadier and Hunter (1999) and Rothermel and Semlitsch (2002) reported that juvenile wood frogs, American toads, and spotted salamanders avoid open-canopy habitats as fewer individuals were captured in traps in these habitats. Similarly, Gibbs (1998) reported that certain adult amphibians also seem to avoid other environments devoid of cover, such as forest-road edges. These results likely stem from the effects of dehydration observed in dry environments such as clearcuts, mined bogs, or open fields (Bury 1983, Chen et al. 1993, Wheeler and Shaw 1995, Price 1997).

For the first time, we contrasted amphibian dehydration rates and behaviour between substrates associated to different degrees of human disturbance and actually encountered in the field by individuals. We found that green frogs lost the most water on the soil substrate out of the shade. Consequently, cover such as that provided by vegetation can greatly reduce amphibian dehydration rates on dry substrates. Vegetative cover probably reduces evaporative water loss, by providing shade and shelter from the wind. Frogs out of the shade had a stronger tendency to minimize their body surface, whereas the substrate type did not influence their behaviour. Such behaviours to minimize water loss are consistent with other reports of a more fundamental nature than our study (Thorson and Svihla 1943, Packer 1963, Dole 1967, Parris 1998), and may be an efficient mean of reducing water losses in natural environments. However, in regularly disturbed environments, such as mined peat fields (i.e., harrowed several times a day), these behaviours inevitably lead to death or serious injury for animals seeking refuge in the substrate. In other cases, amphibians may refrain altogether from burrowing in substrates associated with human disturbances, even under dry conditions (Jansen, Summers and Delis 2001). These results generally suggest that surfaces devoid of cover jeopardize the survival of individuals attempting to cross them, and constitute barriers to frog movements.

Frogs translocated on the barren surface were less likely to home to the pond than those translocated on the natural surface. This suggests that barren surfaces impede frog movements. Habitat loss and fragmentation are known to disrupt the movements of certain taxa, either directly, by lack of cover (amphibians: Rothermel and Semlitsch 2002,

Johnston and Frid 2002; birds: St. Clair et al. 1998, Bélisle et al. 2001, Bélisle and Desrochers 2002; mammals: Diffendorfer et al. 1995; reptiles: Stanley 1998); or, less intuitively, by restricting movement activity to optimal weather conditions (Mazerolle 2001, Johnston and Frid 2002, Chan-McLeod 2003). Furthermore, individuals are susceptible to predation during movements (Larsen and Boutin 1994, Bonnet et al. 1999) and are presumably obvious to predators in areas without cover. This might also have decreased the homing probability of frogs translocated on barren surfaces, though predators were rarely seen on mined surfaces. Nonetheless, based on our homing experiment, for routes of equal distances, we should expect individuals moving under cover to have the best chances of reaching a distant habitat patch.

Small frogs had a particularly low probability of homing successfully. This may be the result of a higher evaporative water loss than in large individuals, such as that observed in our dehydration experiment. Weather conditions limit the activity patterns of amphibians (e.g., Mazerolle 2001, Johnston and Frid 2002, Chan-McLeod 2003), as well as their potential to move across the landscape (Prest and Pough 1989). For instance, Prest and Pough (1989) observed that the most dehydrated *Bufo americanus* toads travel farthest at intermediate temperatures. This relationship is potentially greater for small individuals and requires further investigation. Regardless, it is essential to assess the distance thresholds below which amphibians cross both hostile and favourable environments successfully. This will yield pond isolation measures based on amphibian movements and physiology, and considerably improve predictive models of amphibian pond recolonization in complex landscapes.

Frogs translocated on barren peat oriented and moved toward the pond on the undisturbed surface, whereas those translocated on the undisturbed surface did not have a specific orientation. This may stem from an urgency to flee the hostile conditions on the peat, whereas moisture and cover are high on the undisturbed bog surface and render it suitable for foraging. At the distances we tested, substrate type did not influence the frogs' perceptual range. Small mammals are generally capable of orienting relative to forest habitat, when relocated in fields less than 30 m from the forest edge (Zollner and Lima 1997, Gillis and Nams 1998). Schooley and Wiens (2003) also recently reported directional movements of an arthropod in an unsuitable matrix. In our experiments, frogs were 70 m

from the pond when translocated on the barren surface, but the undisturbed surface was ca. 3 m from the point of release. We are conscious that this may have helped frog orientation, but maintain that comparison with individuals translocated on the undisturbed surface is warranted. Indeed, additional translocations at greater distances into mined surfaces yielded similar results (Mazerolle unpublished).

Amphibians and Landscape Resistance

Based on the behaviours we observed in our experiments, anthropogenically-disturbed areas devoid of cover and especially those that offer dry substrates, such as barren peat, agricultural land, or recently cut stands, increase the resistance of the landscape to amphibian movements. Indeed, our results provide substantial evidence for the mechanisms yielding the low abundances of amphibians in cut forests or mined peat bogs (e.g., deMaynadier and Hunter 1995, Grialou et al. 2000, Mazerolle 2003). These patterns are likely the result, as we report here, of lack of moisture followed by direct mortality (from desiccation or predation), emigration, or subsequent avoidance of such areas by amphibians.

We have shown for the first time that frogs can successfully orient in disturbed environments, and when a choice is given, avoid them. Although certain individuals do venture on hostile surfaces, their chance of moving successfully over such areas is lower than for those moving on undisturbed surfaces. Small individuals are least likely to home successfully. This has direct implications for connectivity and the persistence of amphibians in the landscape. Furthermore, our data also yield important movement parameters (i.e., orientation and probability of homing successfully) to ameliorate simulation models and strengthen predictions on the effects of habitat disturbance in the landscape on amphibian populations (e.g., spatially explicit models: Dunning et al. 1995, South 1999, Collingham and Huntley 2000).

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Chapitre 5

Drainage ditches facilitate frog movements in a hostile landscape

Mazerolle, M. J. En 2^{ième} révision. **Drainage ditches facilitate frog movements in a hostile landscape.** Landscape Ecology. Centre de recherche en biologie forestière, Pavillon Abitibi-Price, Faculté de Foresterie et de Géomatique, Université Laval, Québec, Québec, Canada G1K 7P4 et Groupe de recherche en écologie des tourbières, Pavillon Paul-Comtois, Université Laval, Québec, Québec, Canada G1K 7P4.

Résumé

Les canaux de drainage sont fréquents dans les paysages influencés par l'agriculture, certaines pratiques forestières et les activités d'extraction de la tourbe. Néanmoins, la valeur de ces structures linéaires comme corridors de dispersion des animaux n'a pas été évaluée. Les amphibiens se reproduisant en étang peuvent rencontrer des milieux hostiles lors de leurs déplacements entre les sites de reproduction, d'estivage et d'hibernation, et pourraient potentiellement bénéficier de canaux de drainage dans le paysage. Dans un système modèle constitué de réseaux de canaux de drainage dans des tourbières exploitées pour la tourbe dans l'est du Nouveau-Brunswick, j'ai quantifié la reproduction, la survie et les mouvements de grenouilles vertes (*Rana clamitans melanota*) dans des canaux de drainage, et j'ai également échantillonné des surfaces exploitées. Les grenouilles se sont rarement aventurées sur les surfaces exploitées mais la plupart des individus ont fréquenté les canaux de drainage contenant de l'eau, particulièrement à la fin de l'été. Bien que les grenouilles ne se soient pas reproduites dans les canaux de drainage, leur taux de survie dans ces structures fut élevé (88%). Les canaux de drainage n'ont pas entravé les déplacements des grenouilles. En effet, les grenouilles se sont déplacées indépendamment de la direction du courant et ont été en mesure d'escalader les parois des canaux. Les résultats suggèrent que les canaux de drainage contenant de l'eau agissent comme corridors et facilitent les mouvements des amphibiens à l'intérieur de tourbières exploitées. Dans un contexte d'extraction de tourbe, les canaux de drainage contenant de l'eau pourraient réduire les effets de l'exploitation de la tourbe sur les populations des amphibiens. À tout le moins, ces structures offrent une alternative aux surfaces de tourbe hostiles.

Abstract

Ditches are common in landscapes influenced by agricultural, forestry, and peat mining activities, and their value as corridors remains unassessed. Pond-breeding amphibians can encounter hostile environments when moving between breeding, summering, or hibernation sites, and are likely to benefit from the presence of ditches in the landscape. Within a model system consisting of ditch networks in bogs mined for peat in eastern New Brunswick, I quantified the breeding, survival, and movements of green frogs (*Rana clamitans melanota*) in drainage ditches and also surveyed peat fields. Frogs rarely ventured on peat fields and most individuals frequented drainage ditches containing water, particularly in late summer. Though frogs did not breed in ditches, their survival rate in ditches was high (88%). Ditches did not hinder frog movements, as frogs moved independently of the current and climbed readily out of these structures. Results suggest that drainage ditches containing water act as amphibian movement corridors within mined bogs, facilitating movements through these hostile environments. In the context of peat mining, drainage ditches containing water may mitigate the effects of peat extraction on amphibian populations. At the very least, these structure provide an alternative to hostile peat surfaces.

INTRODUCTION

Habitat loss and fragmentation through anthropogenic activities increase the isolation of patches, which can disrupt demographic processes such as emigration and immigration, and consequently, lead to the isolation of animal populations (Mader 1984, Tiebout and Anderson 1997, Hitchings and Beebee 1998, Roland et al. 2000, Joly et al. 2001). These disturbances are sometimes accompanied by the creation of new structures which may further threaten the viability of animal populations. For instance, the creation of roads in an already fragmented forest or agricultural landscape can raise the risk of mortality of individuals or increase the resistance of the landscape to their movements (Fahrig et al. 1995, Reijnen et al. 1995, Forman and Alexander 1998, Gibbs 1998, Forman

et al. 2003). In some cases, however, the effect of certain artificially-created structures on animal populations is less straightforward. Drainage ditches are such an example.

Drainage ditches originate from various human disturbances (e.g., agriculture, forestry, peat mining) but may mitigate habitat loss and fragmentation by acting as corridors for animal movements. Though the use of ditches has been investigated in different taxa (e.g., fish: Masters et al. 2002; invertebrates: Coulson et al. 1990, DeMers 1993; Painter 1999, Armitage et al. 2003, Williams et al. 2003; small mammals: Mauritzen et al. 1999), most studies have been limited to occurrence data and conducted in agricultural landscapes (but see DeMers 1993, Mauritzen et al. 1999). Thus, the actual processes (i.e., movements) in these structures remain obscure, and consequently, so is the role of ditches in population dynamics (i.e., source, corridors, or sinks).

Based on the vast literature on the effectiveness of corridors (reviewed in Simberloff et al. 1992, Beier and Noss 1998), it is reasonable to assume that ditches functioning as corridors should consist of habitat of moderate quality. Indeed, corridors of low quality can constitute sinks, whereas those of high quality can supply breeding habitat without necessarily promoting the exchange of individuals between habitat patches (Henein and Merriam 1990, Merriam 1991, Andreassen et al. 1996). Nonetheless, this will depend on habitat characteristics and the requirements of the species intended to use them (e.g., Ruefenacht and Knight 1995, Andreassen et al. 1996, Tischendorf and Wissel 1997).

Pond-breeding amphibians develop in water, require moisture after metamorphosis, move across the landscape to reach their breeding, summering, and hibernating sites during the year, and are sensitive to habitat loss and fragmentation (e.g., Sinsch 1990, Pope et al. 2000, Johnston and Frid 2002, Pilliod et al. 2002). Thus, they are likely to benefit from the presence of ditches. In a model system consisting of vast networks of ditches in bogs undergoing peat mining, I tested the hypotheses that ditches are breeding sites and that they do not hinder frog survival or movements. In effect, I evaluated two demographic parameters (reproduction and survival) of frogs in ditches, and monitored the movement patterns of marked individuals in these structures. I focused on the green frog (*Rana clamitans melanota*), a species sensitive to disturbances in the landscape resulting from urban development, forestry, agriculture, and peat mining activities (Bonin et al. 1997,

Knutson et al. 1999, Koloszvary and Swihart 1999, Mazerolle 2001, 2003, Woodford and Meyer 2003).

METHODS

Study Area and Creation of Ditches

Work on frog breeding and movements in ditches was conducted in 8 bogs mined for peat moss in eastern New Brunswick, Canada (Fig. 1). Peat mining, especially important in eastern Canada and Europe (Poulin and Pellerin 2001), is typically conducted over large surfaces (i.e., several hundred hectares). It radically modifies peatland habitats, through habitat loss *per se*, but also with the establishment of large networks of drainage ditches. Thus, the peat surfaces become dry, devoid of cover, and constitute hostile environments for several plant and animal species (Wheeler and Shaw 1995, Delage et al. 2000, Poulin et al. 1999, Campbell et al. 2002, Mazerolle 2003).

The bogs under study varied in area from 459 to 2315 ha (984 ± 733 ha, mean \pm SD), with an average of $27.3 \pm 18.3\%$ of their surface mined. The sites had all been mined for at least 5 years, and were still undergoing mining during the study. Each site was drained by a network of ditches excavated a few years before the actual bog mining had begun (Fig. 2). The surface vegetation had also been removed to reveal the peat layers. Each mining site was surrounded by a large ditch (on average, 1.41 m wide x 1.07 m deep, and several kilometers in length), hereafter, the main ditch. This ditch discharged water to a sedimentation pond. Smaller ditches (on average, 1.12 m wide x 78.00 m deep, and usually several hundred meters in length) were dug perpendicular to the main ditch and were spaced at 30-m intervals, hereafter, the secondary ditches. The sides of ditches were vertical. During peat mining, peat fields are harrowed to break the surface peat into small fragments, left to dry, and then collected by tractor-pulled vacuums. The peat layers below are sequentially tilled and the peat collected until either the mineral soil is reached or woody debris become too numerous and hinder heavy machinery activity. Peat deposition, mostly through wind erosion, often occurred in the ditches and these were cleared by peat mining companies to facilitate drainage. These sites and mining techniques are typical of peat mining activities in eastern Canada.

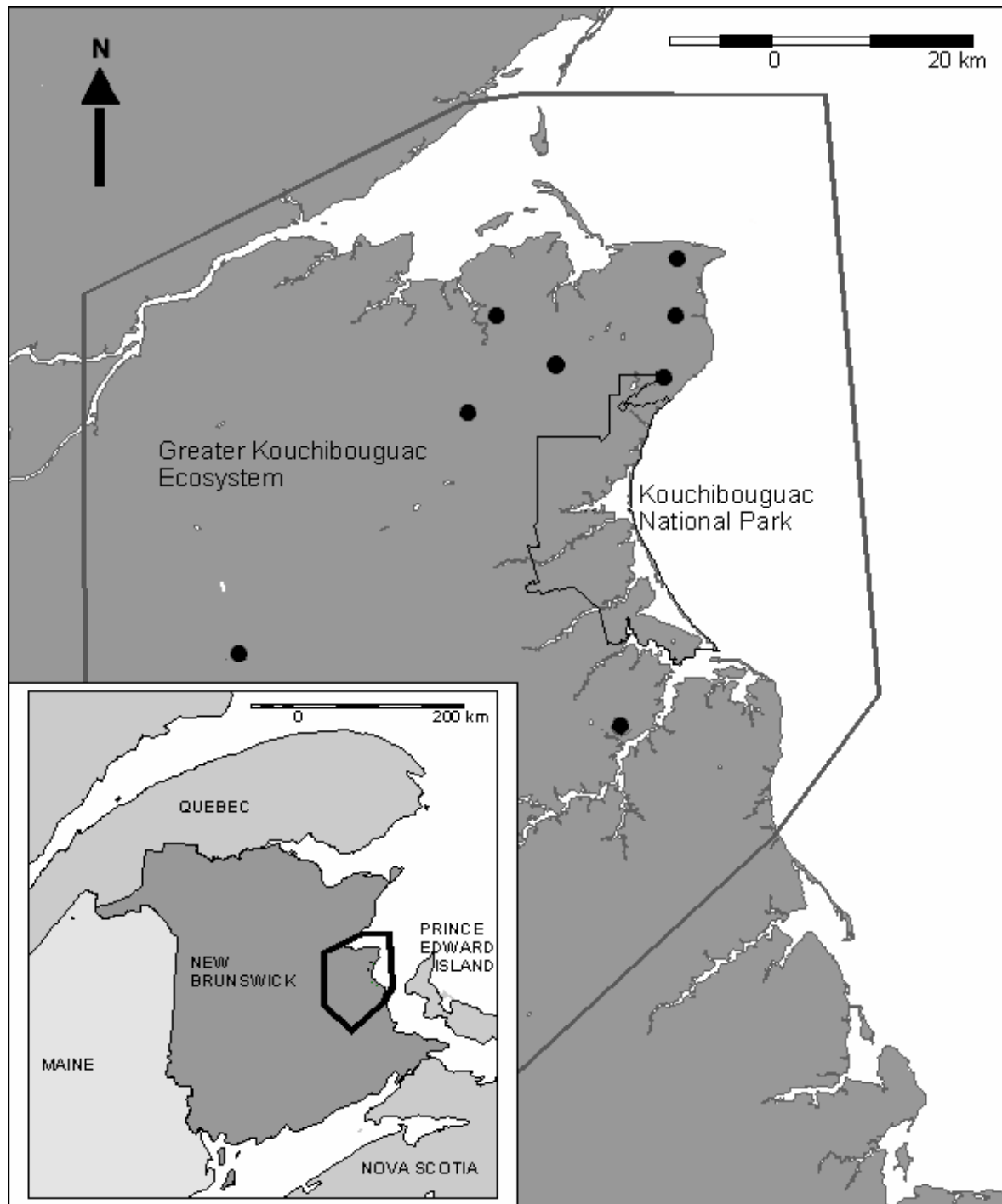


Figure 1. Location of bogs undergoing mining (circles) included in the study of amphibian use of drainage ditches in eastern New Brunswick, Canada.

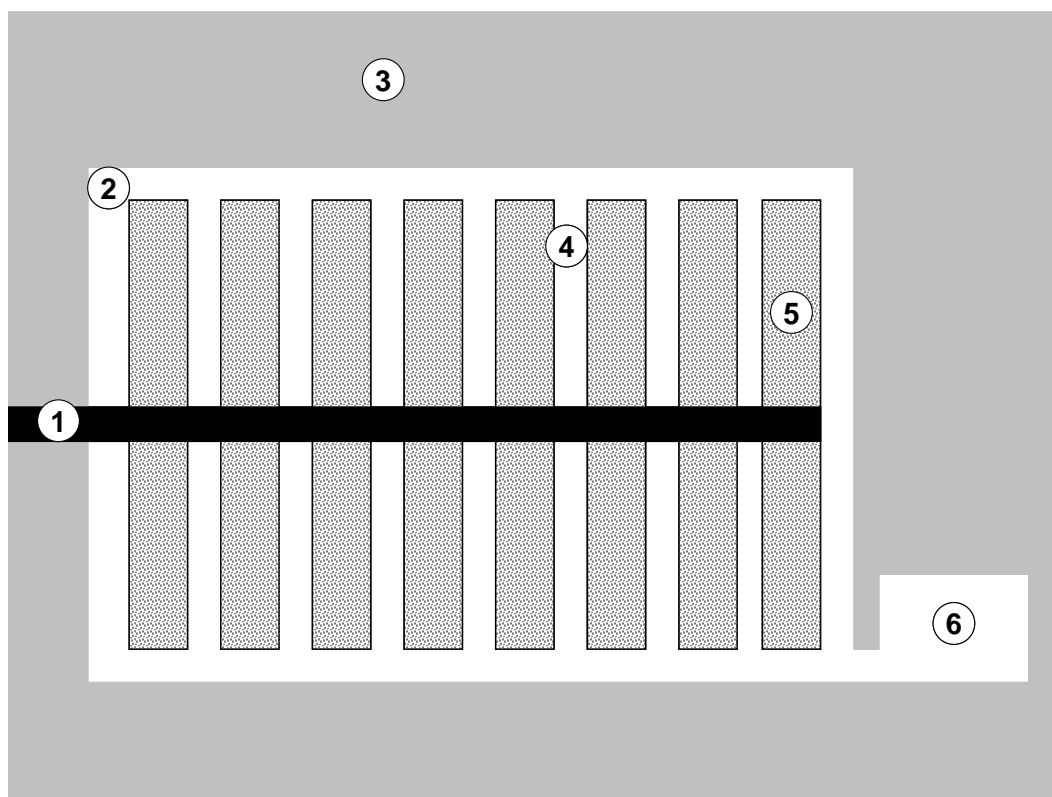


Figure 2. Typical configuration of peat mining sites in eastern Canada. 1, access road; 2, main drainage ditch; 3, unmined bog remnant; 4, secondary ditch; 5, peat mining field; 6, sedimentation pond.

Surveys on Peat Fields

To provide a baseline to compare against the results of ditch surveys, I sampled peat fields during 2001 within 4 bogs undergoing peat mining to detect amphibians occurring on these surfaces. Surveys were conducted at night between 22:00 and 2:30, when frogs were most likely to be active (Wright and Wright 1949, Oseen and Wassersug 2002). I sampled each bog on four occasions between 8 June and 8 August. During each nocturnal survey, I selected randomly 5 peat fields and established a 100-m transect in each, for a total of 500 m sampled every night. From a random starting point on each peat field, I walked along a 100-m transect following a zigzag pattern (i.e., each part of the transect was oriented 45°

relative to the ditches on either side of peat fields). Every time I reached the edge of a peat field, I changed direction (i.e., 90° relative to the previous orientation). This ensured a uniform coverage of the field. I used a headlamp to scan a 2-m wide area along the transect for amphibians. Because peat fields are devoid of any cover, it is unlikely amphibians within the transect were missed. I computed the number of individuals observed per m of transect surveyed. At the end of the field season, a total of 2 km of peat fields had been searched in each bog.

Ditches as Breeding Sites

To assess breeding and the occurrence of amphibians in ditches, I conducted visual and call surveys along drainage ditches within the eight bogs described above: four bogs were surveyed in 2000, and four others in 2001. Surveys were conducted during four periods in each bog between 1730-0100 from late May to early August of each year. On each survey, five transects of 100 m were randomly selected in the main and secondary ditches for a total of 1 km of ditches surveyed per night. The presence of egg masses, calling males, and the number of individuals observed in each transect were recorded. At four randomly selected points on each 100-m transect, the bottom of the ditch was scooped four times with a dipnet to assess the presence of tadpoles. At these four points, ditch width and depth, as well as water depth, and amount of loose peat debris on the bottom (i.e., no peat: 0 cm, low peat: ≤ 5 cm, high peat: > 5 cm), were measured at four randomly selected points on each 100-m transect. In addition, I evaluated the percent water coverage for each 100-m transect. Air temperature, wind velocity (i.e., no/low wind, high wind), and percent cloud cover, were recorded at the beginning of each 100-m section of transect.

High correlations between ditch characteristics (e.g., depth, width) and ditch type (main vs secondary) precluded the inclusion of such ditch characteristics in the analyses. I first determined the difference in physical characteristics between 100-m sections of main and secondary ditches with a logistic regression model which included the intercept, ditch depth, ditch width, percent of water, and amount of loose peat debris (McCullagh and Nelder 1989, Hosmer and Lemeshow 1989). Ditch type (i.e., main or secondary) was used as the response variable.

I used logistic regressions to model the probability of green frog presence in the 100-m ditch transects. The basic model consisted of the intercept, and the explanatory variables year, site nested within year, and period of survey (i.e., categorical variable with 4 levels). I fitted a series of plausible models including the variables ditch type (i.e., main vs secondary), air temperature, wind (i.e., no/low wind vs high wind), and percent of cloud cover. Model fit was evaluated with the most complex model. I evaluated the strength of evidence for each model based on the second-order Akaike Information Criterion (AIC_c), following Burnham and Anderson (2002). Estimates and standard errors for the parameters of interest were obtained with model averaging techniques (Anderson et al. 2000, Burnham and Anderson 2002). Please refer to Appendix 1 for detailed instructions on how to compute and interpret the results of the analysis of ecological data using this approach.

Ditches Directing Movements and Survival

To quantify the extent to which ditches hinder or facilitate the movements of green frogs (i.e., determining if movements are in the direction of current flow), I used a capture-mark-recapture approach. We conducted the work at 8 bog sites undergoing peat mining (i.e., same sites as described above), with four bogs in 2000, and four other bogs in 2001. At each site, I selected the last 300-m stretch of the main ditch that led to the output of the site (Fig. 2). Typically, the main ditch allows the water to drain out of the bog into sedimentation ponds before exiting into a water course.

We sampled the 300-m stretch of main ditch at each site on 10 occasions at regular intervals of ca. 10 days. These surveys were conducted between 13 June and 25 August of each year. During a sampling visit, the investigator moved into the ditch and started the survey from the downstream portion of the 300-m stretch of ditch. A second investigator measured the distance covered along the top of the ditch with a measuring wheel and noted the position of each individual observed in the ditch. Frogs were captured with a dipnet, identified, measured to snout-vent length (SVL), marked with an individual toe-clip based on the Donnelly system (Donnelly et al. 1994) to minimize the number of digits amputated, and then released at the point of capture. Surveys were conducted between late morning and late afternoon on days without precipitations. At the start of a survey, we recorded air temperature, wind, and the percentage of cloud cover.

I used regressions with a normal error structure to assess the distance moved by recaptured frogs in main ditches. The net distance moved by each individual was computed as the difference between the position at its first and last capture (i.e., relative to the farthest point downstream of the 300-m section of ditch). The natural logarithm of the net distance moved by each green frog in the main drainage ditches was modeled as a function of size (snout-vent length, SVL), the net direction of movement (i.e., with or against water flow), the date of first capture (i.e., June, July, or August), the number of days between the first and last capture (i.e., ≤ 22 days, or > 22 days), and the interaction between SVL and direction. Each plausible model was ranked based on the AIC_c . The intercept and the variables year and site nested within year were included in all models. I used model averaging to obtain estimates and standard errors of the parameters of interest (Burnham and Anderson 2002).

I conducted capture-recapture analyses based on the Cormack-Jolly-Seber model for open populations (Pollock et al. 1990, Lebreton et al. 1992) to estimate the survival of green frogs in ditches. Pollock et al. (1990), Lebreton et al. (1992), and Schmidt and Anholt (1999) provide detailed accounts of the framework and interpretation of capture-recapture analyses. Due to the sparseness of the data, I restricted the analyses to the two sites with the highest green frog captures and the last 9 capture events (out of 10). One site was sampled in 2000, and the other in 2001 (see above). Because the year and site variables were confounded, I did not seek to assess differences in frog survival across sites. Thus, I systematically included the effect of the site variable on the probabilities of green frog survival (ϕ) and capture (p) in all the candidate models, and restricted the interpretation to overall survival trends in ditches after accounting for the site variable. The general model consisted of the additive effects of site, period (i.e., during breeding: mid June to late July; or after breeding: early to late August), and SVL on the probabilities of survival (ϕ) and capture (p).

Standard goodness of fit tests (tests 2 and 3, test for transience) implemented in program U-Care version 2.0 (Choquet et al. 2003) did not suggest systematic departures from model assumptions. Similarly, bootstrap goodness of fit testing of the general model ($n = 1000$ simulations) did not indicate systematic departures from model assumptions ($P = 0.19$ of observing a deviance in the simulated data set as large or greater than the deviance

of the general model). There was also little evidence of overdispersion in the data, as the inflation factor (*c-hat*) was close to one (i.e., observed *c-hat*/mean of bootstrapped *c-hat* = 1.175) and suggested good model fit. All models were subsequently corrected for overdispersion with the estimate of the inflation factor (Burnham and Anderson 2002), and ranked according to the QAIC_c (i.e., AIC_c corrected for overdispersion). Model averaging techniques were used to obtain estimates and standard errors for the parameters of interest. Capture-recapture analyses were performed with version 2.1 of the program MARK (White and Burnham 1999).

Climbing out of Ditches

To quantify the ability of frogs to climb out of ditches (i.e., assessing if movements out of ditches are possible), I conducted an experiment in a section of main ditch within the Baie-Sainte-Anne Bog undergoing peat mining (46°59'N, 64°59'W). This bog site was not included in the study assessing frog movements or breeding in ditches. A section of ditch of 2.6 m x 0.85 m x 2 m (length x width x depth) was first selected and divided, with three sheets of agglomerate plywood, into two test ditches 1.3 m in length (Fig. 3). In one of the test ditches, a sheet of plywood was placed horizontally 1 m from the top of the ditch, to create a test ditch 1 m in depth. Similarly, I added a sheet of plywood on the other side of the median partition 0.5 m from the top to form the 0.5 m test ditch. All pieces of plywood were previously cut to fit snugly with the sides of the ditch. I also glued loose peat (i.e., dry peat occurring on the bog surface during mining) on all sides of the sheets of plywood in order to match the nature and texture of the substrate of the ditch.

Forty-two green frogs (mean snout-vent length \pm 1 SD: 5.64 \pm 1.17 cm) were captured at a pond < 200 m from the experimental site. Given the strong homing behavior of the species to breeding and summering sites (Oldham 1967), I assumed that individuals were motivated to return to the capture site. During each trial, a single individual was placed at the bottom of one of the test ditches and observed for a period of 1 h. If the individual reached the top and exited the ditch before the time was elapsed, the trial was considered successful. Individuals were used only once. Following each trial, the individual was measured to snout-vent length, marked, and immediately released at the point of capture. Peat samples were taken at the first and last trials of each day to determine peat

water content in each section. The experimental trials were conducted on 11, 12, 13, 14, and 16 August 2001 between 1200 and 2000 under similar meteorological conditions.

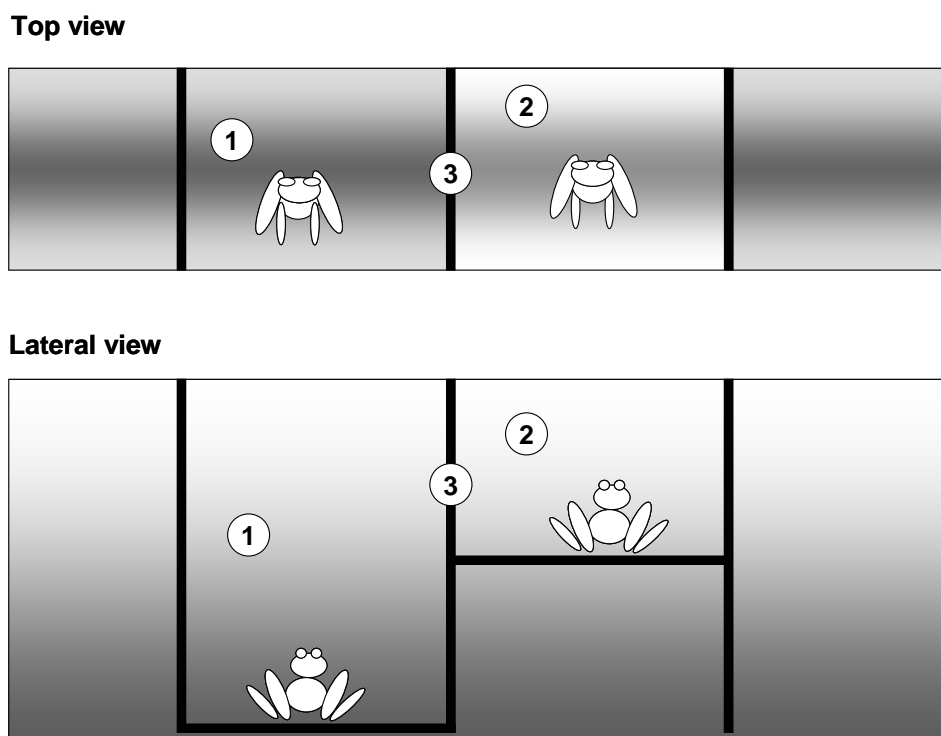


Figure 3. Design of a section of drainage ditch used to evaluate the probability of escape of green frogs (top and lateral view). 1, deep test ditch (1 m); 2, shallow test ditch (0.5 m); 3, median partition. Thick lines denote the pieces of plywood delimiting the two test ditches, on which peat was glued to match the texture of the sides and bottom of the ditches.

I evaluated the probability of escape of 42 green frogs placed in the sections of ditches of either 0.50 or 1 m deep with a candidate set of plausible logistic regression models. All models included the intercept. Each model was ranked based on the AIC_c . The

estimates and standard errors for the parameters of interest were then computed with model averaging techniques.

RESULTS

Surveys on Peat Fields

No amphibians were detected on peat surfaces during the 8 km of transects surveyed at night on peat fields. However, five green frogs and a single wood frog (*Rana sylvatica*) were accidentally encountered on peat fields when conducting ditch surveys, generally found within 1 m of the ditches.

Ditch Characteristics

As indicated by the logistic regression analysis of ditch type as a function of ditch characteristics, main ditches were wider (type 3 likelihood-ratio statistic = 6.35, $df = 1$, $P = 0.012$), deeper (type 3 likelihood-ratio statistic = 18.97, $df = 1$, $P < 0.001$), and had less loose peat deposited at their bottom (type 3 likelihood-ratio statistic = 13.54, $df = 2$, $P = 0.001$) than secondary ditches. Main ditches also tended to have slightly more water than secondary ditches (type 3 likelihood-ratio statistic = 3.26, $P = 0.071$). The model discriminated efficiently between main and secondary ditches, as revealed by the classification table with 67 % of the observations classified correctly.

Ditches as Breeding Sites

Even though green frogs were present, no calling males, egg masses, or tadpoles were detected in the 16 km of ditches of each type. Similarly, I did not observe reproductive activity from any other species of amphibians in ditches surveyed. An average (mean \pm 1 SD) of 3.86 ± 10.01 green frogs were observed per km of main ditches surveyed, whereas 0.64 ± 2.99 frogs occurred per km of secondary ditches. One site was excluded from the analyses, because no green frogs were found during the surveys at that locality. Green frogs were more likely to occur in main ditches than in secondary ditches (Table 1). Furthermore, frogs were found in ditches later in the season (i.e., after mid June).

Individuals were most often seen under conditions of low cloud coverage, whereas air temperature and wind velocity did not influence the detection of frogs.

Table 1. Logistic regression models (ranked according to AIC_c) and model-averaged estimates explaining green frog occurrence in 100-m stretches of main and secondary ditches within 7 mined bogs of eastern New Brunswick, Canada. A total of 280 sections of 100 m were retained for analysis. Estimates in bold indicate that 0 is excluded from 95% confidence interval and that variable influences frog presence in ditches. Models with Aikaike weights < 0.05 are not shown for brevity.

Model	Parameters	Delta AIC_c^a	Akaike weight
Year site(year) period ditchtype cloud	12	0	0.49
Year site(year) period ditchtype air cloud	13	1.74	0.21
Year site(year) period ditchtype wind cloud	13	1.79	0.20
Year site(year) period ditchtype air wind cloud	14	3.80	0.07

Model-averaged parameters (\pm unconditional SE)						
Period ^b			Ditch type ^c	Air	Wind	Cloud
Period 1	Period 2	Period 3				
-2.1405	-0.8946	-0.5074	1.7189	0.0363	-0.2552	-0.0246
(0.7669)	(0.5384)	(0.5351)	(0.4762)	(0.0570)	(0.4658)	(0.0089)

^a AIC_c of highest-ranked model = 184.04.

^bSurveys conducted on 4 periods (May - August); Period 4 used as reference level.

^cSecondary ditch used as reference level.

Ditches Directing Movements and Survival

A total of 243 green frogs were individually marked, and 41% of these were recaptured at least once. Most captures occurred in August, following the breeding period (Fig. 4). Individuals moved an average net distance of 34.1 ± 44.8 m (mean \pm SD) within the 300-m sections of ditches during the study period. Three of the eight sites were excluded from the analyses due to low captures, for a total of 95 recaptured individuals remaining in the movement analyses. None of the variables included in the models influenced the net distance moved by green frogs. Indeed, the net distance was independent of the current, the size of the individuals, the date of first capture, and the number of days between the first and last capture (Table 2).

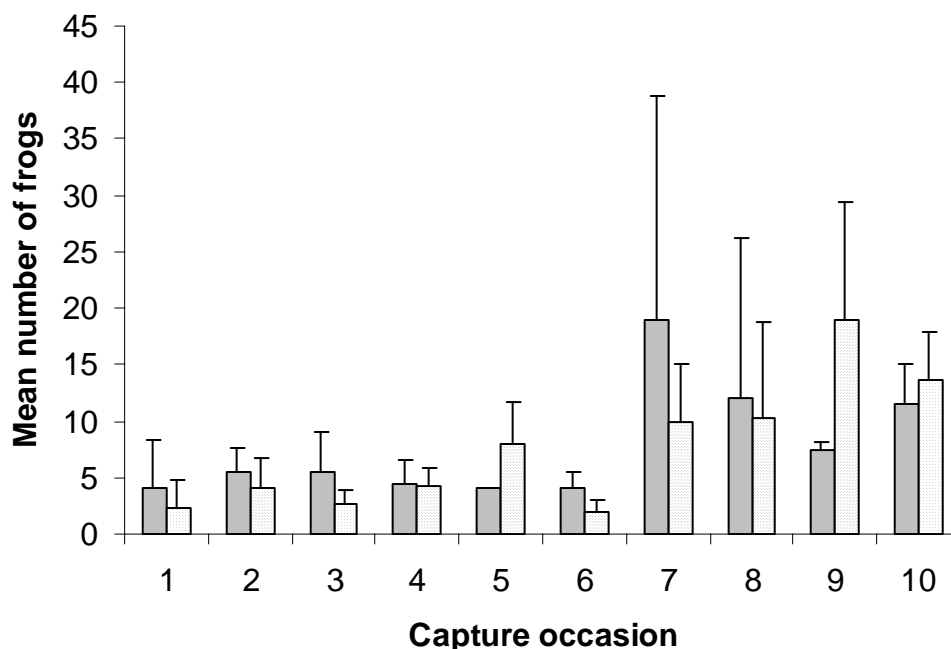


Figure 4. Mean number of green frogs captured in 300-m sections of ditches sampled repeatedly on 10 occasions during 2000 (grey) and 2001 (white). Error bars indicate 1 SD around each mean for the 5 sites with the most captures. Sampling occasions 1-6 correspond to breeding period (mid June to late July), whereas occasions 7-10 correspond to post-breeding period (early to late August).

Table 2. Linear regression models (ranked according to AIC_c) and model-averaged estimates explaining green frog movements in 300-m stretches of main ditches within 5 mined bogs of eastern New Brunswick, Canada ($n = 95$ frogs). Direction denotes direction of frog movement (i.e., with or against current); ndays indicates number of days between first and last capture (i.e., ≤ 22 days or > 22 days); firstcapture indicates date of first capture (i.e., June, July, or August). The variables did not influence frog movement in ditches (i.e., 95% confidence interval included 0 for all parameter estimates). Models with Aikaike weights < 0.05 are not shown for brevity.

Model	Parameters	Delta AIC _c ^a	Akaike weight
year site(year) svl	6	0	0.20
year site(year)	5	0.34	0.17
year site(year) direction	6	1.36	0.10
year site(year) svl direction	7	1.71	0.09
year site(year) svl ndays	7	2.01	0.07
year site(year) ndays	6	2.52	0.06
year site(year) svl direction svl*direction	8	2.82	0.05

Model-averaged parameters (\pm unconditional standard error)					
Date of first capture		SVL	Direction	SVL*Direction	Ndays
June	July				
0.4647	0.1133	0.2330	0.1333	-0.3308	0.1853
(0.4257)	(0.3571)	(0.1470)	(0.8335)	(0.2887)	(0.3008)

^aAIC_c of highest-ranked model = 323.09.

Across the two sites included in the analysis, the average probability of survival in the 300-m sections of ditches was 0.88 with unconditional SE ranging between 0.01 and 0.15, whereas the average probability of capture was 0.26 with unconditional SE between 0.06 and 0.11. Green frog survival did not differ between periods (i.e., during or after breeding) and was not influenced by frog size (Table 3). However, the probability of capture increased following the breeding period, but did not vary with frog size (Table 3).

Table 3. Capture-recapture models and model-averaged estimates evaluating the effect of period (during or after breeding) and SVL on green frog survival (ϕ) and capture rates (p) in 300-m sections of drainage ditches within two mined bogs of eastern New Brunswick, Canada. Capture-recapture model notation follows Lebreton et al. (1992). Analyses are based on the capture histories of 123 individuals over 9 capture events. Models with Aikake weights < 0.05 are not shown for brevity.

Model	Parameters ^a	Delta QAIC _c ^b	Akaike weight
$\phi_{\text{site} + \text{period}}, p_{\text{site} + \text{period}}$	6	0	0.30
$\phi_{\text{site} + \text{period}}, p_{\text{site}}$	3	1.02	0.18
$\phi_{\text{site} + \text{period} + \text{svl}}, p_{\text{site} + \text{period}}$	7	1.80	0.12
$\phi_{\text{site} + \text{period}}, p_{\text{site} + \text{period} + \text{svl}}$	7	2.08	0.10
$\phi_{\text{site} + \text{period} + \text{svl}}, p_{\text{site}}$	4	3.07	0.06
$\phi_{\text{site} + \text{period}}, p_{\text{site} + \text{svl}}$	4	3.08	0.06

Model-averaged parameter estimates (\pm unconditional SE)

Effect on survival probability		Effect on capture probability	
Period	SVL	Period	SVL
-2.2011	0.1579	1.0283	0.0306
(1.5547)	(0.3814)	(0.4440)	(0.1843)

^a Number of identifiable parameters based on model structure and sparseness of data; estimate of overdispersion (i.e., \hat{c} = 1.175) included in parameter count.

^b QAIC_c of highest-ranked model = 352.47.

Climbing out of Ditches

Although a number of individuals successfully climbed the steep surface and managed to get out of the ditch, green frogs were more likely to escape from the shallow ditches (0.5 m) than the deep (1 m) ones (Table 4). Neither frog size nor the percent water content of the peat at the bottom of the ditch influenced the probability of frogs of escaping.

Table 4. Logistic regression models (ranked according to AIC_c) and model-averaged estimates explaining the probability of green frogs climbing out of drainage ditches of different depths during experimental trials ($n = 42$ frogs). Estimates in bold indicate that 0 is excluded from 95% confidence interval and that the variable influences the escape of frogs from ditches. Models with Aikake weights < 0.05 are not shown for brevity.

Model	Parameters	Delta AIC_c^a	Akaike weight
Ditchdepth	2	0	0.52
Ditchdepth peathumidity	3	2.25	0.17
Svl ditchdepth	3	2.32	0.16
Svl ditchdepth svl*ditch	4	4.68	0.05
Svl ditchdepth peathumidity	4	4.70	0.05

Model-averaged parameters (\pm unconditional SE)			
SVL	Ditch depth (0.5 m vs 1 m)	Peat humidity	SVL*ditch
-0.0890 (0.5027)	3.0359 (1.5226)	-0.0063 (0.0418)	0.3080 (1.1028)

^a AIC_c of highest-ranked model = 41.41.

DISCUSSION

The results indicate that green frogs rarely moved on peat, and most individuals occurred in ditches with water. Though no reproduction occurred in ditches, frog survival was high. Furthermore, frogs could move freely within and out of ditches. Overall, data suggest that ditches containing water facilitate frog movements within mined bogs in contrast to peat surfaces.

Ditches were not viable sites for green frog reproduction. This was rather unexpected, as green frog tadpoles have a high tolerance to low pH (LC 50 of pH 3.36: Freda and Taylor 1992, see also Dale et al. 1985). Indeed, the water in ditches was considerably less acidic than bog water (i.e., pH ca. 5.00 vs 4.00: Vitt 1994, Gorham et al.

1984, Joensuu et al. 2002; this study), because of contact with the mineral layer. High amounts of peat debris at the bottom of the ditches in combination with peat suspended in the water column could explain the absence of tadpoles in these structures. Sedimentation decreases periphyton productivity (Power 1990), which is the primary food source of grazing anuran tadpoles (Duellman and Trueb 1994), and reduces habitat quality. Accordingly, Gillespie (2002) observed that tadpole growth and development are considerably reduced by increasing sediment loads in streams. This eventually decreases the larval abundance in streams (Corn and Bury 1989, Welsh and Ollivier 1998). In addition, most frogs occurred in ditches later in the season during breeding and post-breeding movements in the study area. This is consistent with previous reports of increasing frog abundance in both natural and disturbed bog habitats in late summer (Mazerolle 2001), and further suggests that frogs do not breed in ditches within mined bogs.

Green frogs were more likely to occur in main ditches than secondary ditches. This was not surprising as main ditches contain water throughout the summer, whereas secondary ditches dry up. In addition, the great amount of peat debris in secondary ditches probably rendered them less inviting to frogs than main ditches. Regardless, results suggest that few individuals venture deep into mined peat bogs (i.e., secondary ditches) and most stay along the perimeter of the mined surface (i.e., main ditches). The few individuals occurring on mined surfaces also supports the hypothesis that amphibians remain in ditches and do not venture far from these structures.

Ditches Directing Movements and Survival

Frogs in the main ditches moved independently of the current, regardless of their size. The net distance covered by recaptured frogs in ditches was generally low and did not vary across periods. At first glance, one could argue that the high probabilities of survival in conjunction with low net distance suggests that individuals did not undergo great movements in the ditches during the study. In fact, Mauritzen et al. (1999) reported that ditches promoted back and forth movements of marked root voles, *Microtus oeconomus*, rather than unidirectional movements. Nonetheless, 59% of marked frogs in my study were never recaptured, which reduced capture rates and decreased the precision of survival

estimates. This might indicate that sampling visits in my study were spaced too far apart and that most frogs exited the 300-m sections before being recaptured. Thus, although certain individuals elected to remain in the ditches (i.e., reflected by the low net distance of recaptured frogs), many others continued to other habitats.

The lack of cover in the ditches surveyed herein did not deter frogs, and their high survival rates in these structures was rather surprising. It is likely that most of the individuals never recaptured emigrated out of the 300-m sections of ditches rather than died. In fact, no terrestrial or avian predators were observed during diurnal and nocturnal surveys at the sites. Thus, I hypothesize that the complement of frog survival in the 300-m sections is frog emigration (i.e., $1 - \text{probability of survival}$) from these sections, rather than local mortality. Indeed, sampling was conducted for 10 weeks at each site, well below frog life expectancy. Future studies investigating the rate of emigration in ditches separating two distinct habitats, based on a multi-state design (e.g., Coffman et al. 2001, Béchet et al. 2003), are required to address formally this issue.

Climbing out of Ditches

Green frogs can escape from large ditches, but they do so less often than when in shallow ditches. The 1-h observation period might have been too short for most individuals to escape from the large ditches. Based on the frogs that attempted to scale the sides (i.e., 62% of individuals), frogs had climbed on average 54 cm at the end of the trial in the 1-m ditch (vs 39 cm in the shallow ditch). Furthermore, during the repetitive sampling of the 300-m sections of ditches, several marked frogs were recaptured after being observed jumping from the top of the ditches (ca. 2 m) into the water. Other researchers have noted impressive climbing abilities in green frogs (Martof 1953) and California red-legged frogs, *Rana aurora draytonii* (Bulger et al. 2003, Rathbun et al. 1997). This suggests that frogs take more time to climb out of deep ditches, but eventually manage to venture out of these structures.

Landscape Resistance to Movements

Habitat fragmentation of anthropogenic origin, from activities such as forestry or agriculture, decrease the permeability of the landscape to amphibian movements (Joly et al.

2001, Rothermel and Semlitsch 2002). Similarly, peat surfaces undergoing mining, dry and devoid of cover, render venturing into peat fields very perilous for these organisms. Mazerolle (this thesis, Chapter 4) reported that individuals on peat lost on average 10.5 % of their initial mass in water within 2 hours. The regular circulation of machinery used to harrow and collect the peat also adds to the disturbance of these sites. Thus, amphibian movements on peat fields *per se* seem rare, as no amphibians were detected on peat surfaces during nocturnal surveys. At any rate, main ditches containing water are less hazardous than these surfaces, and reduce the risk of dehydration in mined bogs.

Ditches as Corridors

Results suggest that main ditches containing water facilitate amphibian movements through mined bogs. Indeed, individuals rarely occurred on the peat fields. In support of this hypothesis, Mazerolle and Desrochers (this thesis, Chapter 4) showed that frog homing success is lower on peat surfaces than on undisturbed habitat, and that when given a choice, frogs prefer natural bog vegetation over peat surfaces. Furthermore, Mazerolle and Cormier (2003) recorded higher green frog abundances in bog ponds intersected by ditches than in ponds without ditches. Similarly, Reh and Seitz (1990) reported positive effects of ditches on the genetic diversity of the frog *Rana temporaria* in agricultural landscapes. Recent investigations have convincingly shown that the presence of corridors linking patches together can increase densities and movement rates of individuals (microtine rodents: Coffman et al. 2001; butterflies: Haddad 1999, Haddad and Baum 1999). Nonetheless, the presence of linear habitats, such as hedgerows or ditches, does not equate into their use by amphibians as corridors in all possible landscape types, and are not substitutes for the disappearance of areas permeable to amphibian movement (Joly et al. 2001).

Factors such as the severity of the landscape matrix or corridor width can determine whether individuals of a species use it or not (Andreassen et al. 1996, Rosenberg et al. 1998). Based on the results of the present study, the creation of ditches emulating the characteristics of main ditches (i.e., wide, deep, and containing water) within the mined area (as opposed to confining these large ditches to the site perimeter), can promote the movements of individuals across these hostile environments. Nonetheless, the preservation of undisturbed and proximal breeding, summering, and hibernation habitats should not be

overlooked, as they are important components for the management of pond-breeding amphibians (see review in Semlitsch 2000, Richter et al. 2001).

Conclusion

Main ditches (i.e., wide and deep ditches containing water) seem to offer habitat of an intermediate quality to green frogs within bogs mined for peat moss. The peat surface harbors very harsh conditions, whereas ditches containing water provide shelter from desiccation. Ditches do not offer breeding habitat (i.e., no breeding attempts occurred and most frogs arrived in ditches following the breeding period), and do not constitute population sources, as all individuals were immigrants. Nonetheless, frog survival in these structures is high, which suggests ditches provide temporary habitat for individuals moving in the landscape. Furthermore, ditches do not hinder frog movements (i.e., individuals moved independently of current flow). In fact, high rates of emigration and immigration seem to occur in main ditches, as several frogs were never recaptured. Frogs could also climb relatively easily from these structures despite their steep faces. Based on this evidence, ditches seem to facilitate movements through mined bogs to upland habitats, as corridors, but may also act as summering habitat.

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- Woodford, J. E., and M. W. Meyer. 2003. Impact of lakeshore development on green frog abundance. *Biological Conservation* **110**:277-284.

Conclusion générale

Trois objectifs principaux ont été poursuivis dans cette thèse. Dans les cinq chapitres qui constituent la présente étude, j'ai évalué l'utilisation des tourbières par les amphibiens, déterminé les effets de l'exploitation des tourbières sur la fréquentation des étangs de tourbières par les amphibiens, et exploré quantitativement les contraintes aux mouvements des amphibiens dans ces milieux perturbés. Ces travaux ont été motivés par le manque d'études comportementales effectuées dans un contexte de conservation, et avaient pour but d'inférer à partir de ces études à petites échelles, sur les patrons à plus grande échelle (*sensu* Sutherland 1998, Morales et Ellner 2002). Bien qu'ayant répondu à quelques-unes de ces lacunes de façon innovatrice, cette thèse soulève encore plusieurs questions quant à la pérennité des amphibiens dans les paysages perturbés par l'humain.

L'utilisation des tourbières par les amphibiens

Dans le premier chapitre de la thèse, je visais à comparer l'utilisation des tourbières et des milieux non tourbeux environnants par les amphibiens. Tout d'abord, j'ai montré que les bogs (tourbières ombrotrophes) sont des milieux peu propices à la reproduction d'amphibiens, par rapport aux milieux moins acides présents dans les environs. Néanmoins, les grenouilles vertes (*Rana clamitans melanota*) adultes et juvéniles n'évitent pas les substrats associés aux bogs et utilisent les bogs pendant la saison estivale au même titre que les milieux forestiers à la périphérie des tourbières. Ces amphibiens peuvent donc exploiter des milieux dont l'acidité s'approche de leurs limites physiologiques. En effet, les tourbières, malgré leur acidité, offrent une abondance d'arthropodes (Danks et Rosenberg 1987, Larson et House 1990) ainsi que des refuges humides contre la dessiccation et la prédation pouvant être utilisés par les amphibiens. D'ailleurs, les petits mammifères fréquentent en abondance ces habitats et y creusent des galeries (Mazerolle et al. 2001). Les galeries de petits mammifères établies dans divers habitats non tourbeux sont fréquentées par plusieurs espèces d'amphibiens (p. ex., Jehle et Arntzen 2000, Regosin et al. 2003). Donc, on devrait s'attendre à ce que ces structures, particulièrement dans les zones plus sèches des tourbières, abritent des amphibiens pendant leur saison d'activité et qu'elles

agissent comme sites d'hibernation pour certaines espèces. D'ailleurs, l'utilisation des sites d'hibernation aquatiques ou terrestres par les amphibiens demeure un aspect peu étudié de l'écologie de ces organismes et serait un aspect intéressant à étudier dans différents milieux.

Les résultats soulignent également les variations géographiques de la tolérance des individus d'une même espèce à l'acidité. Ceci devient évident lors de comparaisons avec des études antérieures effectuées dans d'autres régions. Par exemple, Vatnick et al. (1999) ont observé un taux de mortalité de 72% de grenouilles léopards (*Rana pipiens*) adultes à des pH de 5,5 et remarquèrent que les grenouilles vertes (*Rana clamitans*) et grenouilles léopards évitaient les substrats acides (4,0 et 5,5), bien que peu d'individus aient été testés. Lors de mes travaux dans les tourbières, des têtards, des juvéniles, ainsi que des adultes des deux espèces ci-mentionnées ont été capturés dans des étangs de tourbières avec pH de 4,0. En Europe, Räsänen et al. (2003) ont récemment montré les variations géographiques de tolérance à l'acidité de la grenouille *Rana arvalis*. Néanmoins, il serait intéressant de tester la tolérance des grenouilles trouvées à la fois dans des régions avec et sans tourbières sur l'étendue du continent nord-américain. On pourrait s'attendre à ce que les individus des populations des régions avec tourbières soient plus tolérants à l'acidité que les régions sans tourbières, mais cette relation devrait également varier selon un gradient Ouest - Est (c'est-à-dire, en fonction des précipitations acides amenées par les vents dominants surtout dans l'Est du continent). La grenouille des bois (*Rana sylvatica*) serait une candidate idéale pour une telle étude, étant donné sa grande aire de répartition sur le continent, ainsi que les similarités écologiques qu'elle partage avec certaines espèces européennes (p. ex., *Rana temporaria*). De plus, de tels travaux permettraient d'évaluer, pour la première fois, la présence des amphibiens dans les tourbières du continent.

Effets de l'exploitation des tourbières sur la reproduction et les déplacements des amphibiens

La presque totalité de mon doctorat traite des effets de l'exploitation des tourbières sur les mouvements et la reproduction des amphibiens. Sa raison d'être découle des résultats de mes travaux antérieurs (à l'Université de Dalhousie, N.-É.), pendant lesquels

j'avais constaté que la richesse en espèces et l'abondance des amphibiens dans les sites de tourbières adjacents aux surfaces exploitées étaient inférieures à celles des sites en tourbières naturelles (Mazerolle 2003). J'avais également observé que l'activité des amphibiens dans les sites perturbés par l'exploitation était confinée aux conditions météorologiques optimales, alors qu'elle était moins limitée par ces facteurs dans les sites naturels (Mazerolle 2001). Ces travaux ont motivé l'élaboration de ce doctorat pendant lequel j'ai visé à identifier les mécanismes expliquant ces patrons d'abondance et d'activité dans les tourbières perturbées.

Les travaux qui figurent dans la présente thèse indiquent que l'extraction de la tourbe influence l'utilisation des étangs de tourbières par les amphibiens, et confirment que la présence d'habitats complémentaires peut atténuer les effets de l'exploitation. De plus, les expériences sur les mouvements montrent clairement que les surfaces exploitées sont hostiles aux déplacements des amphibiens. En effet, les taux de déshydratation sur les surfaces exploitées sont supérieurs à ceux des surfaces naturelles. De plus, la probabilité de retour des individus relocalisés sur les surfaces exploitées est plus faible que celle des individus relocalisés sur des surfaces naturelles. Étant donné que les amphibiens se reproduisent peu dans les tourbières par rapport aux milieux non tourbeux, il est peu probable que la reproduction dans les étangs soit un facteur déterminant des patrons des populations d'amphibiens en tourbières perturbées. Il est beaucoup plus probable que les patrons d'abondance et de richesse en espèces d'amphibiens sur les tourbières adjacentes aux surfaces exploitées résultent surtout des contraintes imposées par ces surfaces aux déplacements des amphibiens.

Les amphibiens qui se reproduisent dans les étangs se déplacent entre les sites d'hibernation, de reproduction et d'estivage, des éléments généralement distincts du paysage (Pope et al. 2000, Pilliod et al. 2002, Semlitsch et Bodie 2003, Gibbons 2003). Chacun de ces éléments est essentiel au cycle vital des amphibiens et doit être considéré dans la gestion et la conservation des populations de ces organismes (Semlitsch 1998, Gibbons 2003, Semlitsch et Bodie 2003). Néanmoins, le maintien de ces éléments du paysage ne suffit pas. En effet, la présence de perturbations d'origine humaine (p. ex., routes, milieu arides résultant de coupe forestière) sectionnant les routes de migrations peut s'avérer problématique.

À court terme, de telles perturbations peuvent augmenter les taux de mortalité (Fahrig et al. 1995, Mazerolle 2004) et amenuiser les effectifs de populations d'amphibiens qui fluctuent déjà grandement de façon naturelle (Pechmann et al. 1991, Houlihan et al. 2000, Green 2003). À long terme, elles peuvent résulter en l'extinction de populations. Dans le cas de parcelles isolées par des milieux hostiles, on peut imaginer que la probabilité de recolonisation sera faible. Mes travaux montrent justement que les surfaces arides résultant de l'extraction de la tourbe entravent les déplacements des amphibiens. Il s'ensuivra une réduction de la connectivité fonctionnelle *sensu* Taylor et al. (1993) entre les parcelles séparées par les surfaces de tourbe, c'est-à-dire que le taux d'échange d'individus se déplaçant d'une parcelle à une autre sera plus faible. L'extraction de la tourbe peut donc menacer la pérennité des populations dans le paysage à l'échelle locale. Étant donné que les amphibiens se déplacent entre plusieurs habitats pendant une même saison, les impacts ne se limitent pas aux tourbières mais s'étendent aux milieux adjacents.

La présente étude est parmi les premières à cibler directement les déplacements des amphibiens dans des milieux perturbés par l'humain (voir aussi Vos 1999, Rothermel et Semlitsch 2002, Johnston et Frid 2002, Chan-McLeod 2003), et la toute première à l'effectuer dans des tourbières. En effet, on commence à s'intéresser directement aux mouvements de ces organismes dans le paysage. Toutefois, il reste encore à évaluer les déplacements (i.e., orientation et probabilité de retour) en différents milieux perturbés, tels que les champs agricoles, les routes et les milieux forestiers. De plus, ils s'avérerait nécessaire d'étudier des espèces additionnelles d'amphibiens avec des modes de développement différents (p. ex., les salamandres avec un développement totalement terrestre).

Pendant mes expériences avec les grenouilles vertes (*Rana clamitans*) et les grenouilles léopards (*Rana pipiens*), j'ai utilisé le comportement de retour (découlant de la fidélité aux étangs) comme motivation de déplacement. Il serait également utile d'évaluer s'il existe des différences entre les déplacements de ce genre et ceux d'individus en phases de dispersion ou de migration. Ultiment, les données sur la capacité des amphibiens à franchir différents milieux permettront de « paramétriser » des modèles de populations qui font directement référence à l'espace (« spatialement explicites »; Dunning et al. 1995, South 1999, Collingham et Huntley 2000, Rustigian et al. 2003). Nous serons donc en

mesure d'améliorer les modèles de simulation et de fortifier les prédictions des effets de perte d'habitat dans le paysage sur les populations d'amphibiens. En outre, il est absolument nécessaire d'étudier simultanément plusieurs processus, tels que les mouvements et leurs impacts sur les patrons d'abondance des amphibiens. Les approches de capture-marquage-recapture (Nichols 1992) sont très prometteuses en ce sens. De telles études, contrairement aux travaux visant soit les processus ou les patrons, permettront finalement de valider nos prédictions sur la pérennité des organismes dans les milieux modifiés par l'humain.

Dans le cadre de cette thèse, j'ai étudié l'utilisation des canaux de drainage par les amphibiens, alors qu'aucun travail du genre n'avait été effectué sur ces organismes, malgré l'abondance des canaux dans les paysages forestiers et agricoles. Pour la première fois, j'ai évalué la survie des amphibiens dans de telles structures. J'ai montré que dans les canaux, particulièrement ceux contenant de l'eau à la périphérie des tourbières exploitées, le taux d'accroissement dû à la reproduction est nul: les individus sont tous immigrants et la mortalité y est faible. Donc, les canaux de drainage ne constituent pas des sources (*sensu* Pulliam 1988), c'est-à-dire, des habitats avec des taux d'accroissement de population supérieurs à 1. En effet, aucune tentative et signes de reproduction n'ont été observés dans ces structures. Néanmoins, la survie des individus dans les canaux était élevée, ce qui suggère que les canaux n'agissent pas comme puits de population d'amphibiens pendant l'été, c'est-à-dire des habitats qui subissent une diminution de l'effectif de population. Par ailleurs, les canaux n'entravent pas les déplacements des individus. Ces structures pourraient donc agir comme corridors en facilitant les mouvements des amphibiens à l'intérieur de tourbières exploitées.

Bien qu'ayant utilisé des techniques de marquage-capture-recapture dans l'évaluation des déplacements des amphibiens dans les canaux, il demeure que mes résultats relèvent d'observations et non de manipulations. Il serait souhaitable d'effectuer des expériences contrôlées afin d'évaluer les paramètres démographiques, tels que la survie, l'immigration et l'émigration entre des sites séparés par des surfaces perturbées, reliés ou non par des canaux de drainage. De plus, il s'avérerait également important d'évaluer les taux de prédation dont souffrent des individus se déplaçant dans les canaux de

drainage, sur les surfaces de tourbes et sur les surfaces naturelles, afin de quantifier convenablement les risques associés à se déplacer sur ces différentes surfaces.

La perte des tourbières est-elle réellement problématique pour la pérennité des populations d'amphibiens?

Au cours des dernières années, j'ai abordé plusieurs aspects de l'écologie des amphibiens dans les tourbières dans un contexte d'extraction de la tourbe. À travers les résultats qui transpirent de ma thèse, certains individus pourraient critiquer la valeur des tourbières pour les amphibiens et le bien fondé de s'acharner à protéger les tourbières pour ces organismes menant une vie à la fois terrestre et aquatique. En effet, on pourrait poser la question: "Si les amphibiens s'y reproduisent rarement, ces milieux sont-ils réellement importants pour ces organismes?" ou encore, "La disparition de toutes les tourbières d'une région influencera-t-elle les populations d'amphibiens?" À ces critiques, je rappelle que les amphibiens requièrent des éléments distincts du paysage au cours d'une même année (i.e., habitats d'hibernation, de reproduction et habitat d'estivage) et qu'ils sont fidèles à ces sites au cours de leur existence (e.g., Martof 1953, Dole 1968, Pope et al. 2000). Il s'ensuit que si l'un de ces habitats disparaît, cela réduira la probabilité de survie des individus, et dans certains cas, la pérennité de la population. Donc, la disparition de sites d'estivage est en elle-même problématique, tout comme celle des sites d'hibernation.

Bien qu'aucune espèce spécialiste des tourbières n'ait été retrouvée lors de mes travaux dans l'Est du Nouveau-Brunswick, on a documenté la présence de la salamandre à quatre doigts (*Hemidactylium scutatum*), une spécialiste de mousses dont la sphaigne, à 100 km au sud de mon aire d'étude (Woodley et Rosen 1988). Son comportement cryptique en plus de sa petite taille la rendent difficile à recenser, ce qui explique en partie son statut d'espèce rare ou en péril au Nouveau-Brunswick et au Québec (McAlpine 1997, Bider et Matte 1994). La salamandre à quatre doigts est plutôt limitée dans ses déplacements et existe en populations disjointes (Bleakney et Cook 1957, Denman 1961, Sharbel 1991) et on suppose que la disparition de tourbières aura un effet négatif sur l'espèce, bien qu'on connaisse encore mal sa distribution dans les milieux tourbeux. Des travaux dans différents types de tourbières et visant en particulier la salamandre à quatre doigts sont d'ailleurs nécessaires afin de préciser le statut des populations de cette espèce.

On peut pousser encore plus loin la critique de la valeur des tourbières pour les amphibiens. Par exemple, étant donné que les amphibiens de mon aire d'étude n'utilisent pas exclusivement les tourbières comme site d'estivage, on pourrait argumenter que les amphibiens substitueront simplement les tourbières disparues par les autres milieux qui y sont adjacents. Toutefois, les résultats de mes travaux portant sur les déplacements suggèrent autrement (Chapitre 4). En effet, les surfaces de tourbes dénudées de végétation vivante entravent les déplacements des individus, ce qui rendrait plusieurs milieux inaccessibles. À court terme, l'apparition de surfaces exploitées dans le paysage peut séparer deux habitats utilisés par les amphibiens, il en résulte que des habitats deviennent inaccessibles. À plus long terme (i.e., sur plusieurs générations), ceci peut résulter en l'isolement des populations séparées par des surfaces exploitées. Ainsi, des sites soumis à des extinctions locales de populations ne pourront être recolonisés. Il demeure qu'il faut démontrer de façon convaincante que la présence de canaux de drainage peut pallier à ce problème. Le problème est très similaire dans les systèmes forestiers et agricoles, qui présentent des surfaces hostiles pour les amphibiens.

Recommandations en aménagement des tourbières

Finalement, au niveau de l'aménagement, mes résultats suggèrent que le maintien d'habitats aquatiques et terrestres dans un rayon allant jusqu'à 1000 m autour d'un étang favorisera l'utilisation des étangs de tourbières par les amphibiens et pourra minimiser les effets de l'exploitation sur ces organismes. Étant donné que le nombre de sites d'extraction de tourbe abandonnés augmentera dans les années à venir, on commence déjà à s'interroger quant au retour des amphibiens dans ces milieux. On pourrait adopter certaines mesures afin de faciliter la recolonisation des tourbières abandonnées, et particulièrement des sites présentement en restauration. En se basant sur les données de mes travaux, certaines conditions devraient favoriser la colonisation par les amphibiens des sites restaurés. Par exemple, la proximité des populations à l'extérieur des tourbières, la présence de canaux bloqués afin de retenir l'eau et de maintenir le site humide, le maintien de points d'eau sur le site dans des rayons de 100 à 1000 m autour d'un étang donné sur le site restauré, ainsi que le maintien d'une grande quantité de forêt à 1000 m, sont tous des éléments pouvant favoriser la colonisation des sites par certaines espèces d'amphibiens.

Conclusion

Dans les cinq chapitres qui constituent la présente étude, j'ai abordé différents aspects de l'écologie des amphibiens en tourbières naturelles et perturbées par l'exploitation. Globalement, les études indiquent que l'exploitation des tourbières génère des conditions qui peuvent entraver les mouvements des amphibiens sur les surfaces exploitées. Le maintien d'un ensemble de milieux humides et terrestres (i.e., constituant les habitats de reproduction, d'estivage et d'hibernation des amphibiens) à proximité des exploitations de tourbières réduira les effets de cette activité sur ce groupe d'animaux. La réalisation d'expériences contrôlées à l'échelle du paysage ainsi que l'avènement de méthodes de télémétrie moins dispendieuses et mieux adaptées aux petits organismes amèneront des éléments essentiels à la prédiction de la pérennité et la conservation des populations des amphibiens en milieux perturbés par les activités anthropiques.

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APPENDIX 1:

Making sense out of Akaike's Information Criterion (AIC): its use and interpretation in model selection and inference from ecological data

Making sense out of Akaike's Information Criterion (AIC): its use and interpretation in model selection and inference from ecological data

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Abstract

A large component of ecology consists of observational studies where the goal is to explain a pattern, such as the number of individuals in a patch, with a series of explanatory (i.e., independent) variables. To do so, ecologists have long relied on hypothesis testing to include or exclude variables in models, although the conclusions often depend on the approach used (e.g., forward, backward, stepwise). In the mid 1970's, the advent of methods based on information theory, also known as information-theoretic approaches, has changed the way we look at model selection and inference. A few decades later, measures of information, such as the Akaike information criteria (AIC) and associated measures of model uncertainty, have begun to surface in the ecological disciplines. Though still underutilized, these approaches provide a new framework on which to base both model selection and inference from ecological data, and are far superior to traditional hypothesis testing. In this paper, I illustrate the use of such approaches as well as the interpretation of results analysed in this framework. Hypothesis-testing is still useful in controlled experiments with very few parameters, but attention should strive away from mere declarations of significance and instead focus on the estimation of the effect and its precision. However, information-theoretic approaches, given their ease of use and interpretation, as well as their flexibility, should be readily adopted by ecologists in any exploratory data analysis, especially in issues of model selection.

Key words: data analysis; effect; hypothesis testing; model averaging; model selection; regression; precision.

OUT WITH THE OLD?

When conducting statistical analyses, we often strive to estimate the effect (magnitude) of a given variable on a response variable and its precision. In certain instances, our objective is to go beyond and assess whether the effect is sufficiently important to include the parameter in the model in order to make predictions, an issue of model selection. This is often the case in observational studies, where a number of variables are believed to explain a given ecological process or pattern. Whereas classical techniques such as tests of null hypotheses are well-suited for manipulative experiments, their widespread use and abuse to tackle issues such as parameter estimation and model selection only reflects the slow migration of superior techniques from the distant world of statistics into ecological disciplines. Indeed, hypothesis testing is problematic as it indirectly addresses these issues (i.e., the effect is or is not significant), and it does not perform particularly well in model selection (e.g., variables selected by forward, backward, or stepwise approaches). Though this is debated by some (Robinson and Wainer 2002), better approaches do exist (Anderson et al. 2000, 2001, Guthery et al. 2001, Johnson 1999, 2002).

One such approach, developed in the early 1970's, rests on Akaike's information criterion (AIC) and its associated measures. This framework is also known as the information-theoretic approach, as it has arisen from information theory, a field encompassing a number of methods and theories pivotal to many of the sciences. Because information theory *per se* goes beyond the scope of the present paper, the reader should consult Kullback and Leibler (1951), Cover and Thomas (1991), and Burnham and Anderson (2002) for further discussions on the issue. In ecology, the AIC and its related measures were first applied almost exclusively in the context of model selection in capture-recapture analyses (Lebreton et al. 1992, Anderson et al. 1994), but have gained popularity since the last decade in more general situations (Johnson and Omland 2004). This trend becomes apparent by noting the number of published papers having adopted this approach in the leading ecological journals such as *Ecology*, *Ecological Applications*, *Oikos*, *Journal*

of Wildlife Management, and Journal of Applied Ecology. However, some fields such as herpetology, still seem reticent to use these techniques. In this paper, I illustrate with simple examples, the use and interpretation of results of herpetological data using information-theoretic approaches.

FIRST THINGS FIRST

As pointed out by Burnham and Anderson (2001), three principles regulate our ability to make inferences in the sciences: 1) simplicity and parsimony, 2) several working hypotheses, and 3) strength of evidence. Simplicity and parsimony is a concept based on Occam's razor, which suggests that the simplest explanation is probably the most likely. This is a quality often strived for in science. Parsimony is particularly evident in issues of model building, where the investigator must make a compromise between model bias and variance. Here, bias corresponds to the difference between the estimated value and true unknown value of a parameter, whereas variance reflects the precision of these estimates; a common measure of precision is the SE of the estimate. Thus, a model with too many variables will have low precision whereas a model with too few variables will be biased (Burnham and Anderson 2002). The principle of multiple working hypotheses consists in testing a hypothesis from one experiment, then according to the results, formulating a new hypothesis to test with a new experiment (Chamberlin 1965). In model selection, this translates into testing, for the data at hand, a series of plausible models specified before conducting the analyses. Following the analyses, we then require an indication of which model is the best among those we considered and a measure of the strength of evidence for each model. Information-theoretic approaches adhere in part to all three principles, which makes them quite attractive.

MINIMIZING THE LOSS OF INFORMATION

Before engaging in the construction of a model (e.g., a linear regression model or any generalized linear model), we must accept that there are no true models. Indeed, models only approximate reality. The question then is to find which model would best approximate reality given the data we have recorded. In other words, we are trying to minimize the loss of information. Kullback and Leibler (1951) addressed such issues and developed a measure, the Kullback-Leibler information, to represent the information lost

when approximating reality (i.e., a good model minimizes the loss of information). A few decades later, Akaike (1973 cited by Burnham and Anderson 2001) proposed using Kullback-Leibler information for model selection. He established a relationship between the maximum likelihood, which is an estimation method used in many statistical analyses, and the Kullback-Leibler information. In essence, he developed an information criterion to estimate the Kullback-Leibler information, Akaike's information criterion (AIC), which he defined as

$$\text{AIC} = -2(\log\text{-likelihood}) + 2K,$$

where K is the number of estimated parameters included in the model (i.e., number of variables + the intercept). The log-likelihood of the model given the data, is readily available in statistical output, and reflects the overall fit of the model (smaller values indicate worse fit).

In cases where analyses are based on more conventional least squares regression for normally distributed errors, one can compute readily the AIC with the following formula (where arbitrary constants have been deleted)

$$\text{AIC} = n \log(\hat{\sigma}^2) + 2K,$$

where $\hat{\sigma}^2 = \frac{\text{Residual Sum of Squares}}{n}$

and n is the sample size. It is important to note here that because the variance is estimated, it must be included in the count of parameters (K).

The AIC penalizes for the addition of parameters, and thus selects a model that fits well but has a minimum number of parameters (i.e., simplicity and parsimony). For small sample sizes (i.e., $n/K < \sim 40$), the second-order Akaike Information Criterion (AIC_c) should be used instead

$$AIC_c = -2(\log\text{-likelihood}) + 2K + \frac{2K(K+1)}{(n-K-1)}$$

where n is the sample size. As sample size increases, the last term of the AIC_c approaches zero, and the AIC_c tends to yield the same conclusions as the AIC (Burnham and Anderson 2002).

MODEL SELECTION

In itself, the value of the AIC for a given data set has no meaning. It becomes interesting when it is compared to the AIC of a series of models specified a priori, the model with the lowest AIC being the « best » model among all models specified for the data at hand. If only poor models are considered, the AIC will select the best of the poor models. This highlights the importance of spending time to determine the set of candidate models based on previous investigations, as well as judgement and a knowledge of the system under study. After having specified the set of plausible models to explain the data and before conducting the analyses (e.g., linear regression), one should assess the fit of the global model, defined as the most complex model of the set. We generally assume that if the global model fits, simpler models also fit because they originate from the global model (Burnham and Anderson 2002, Cooch and White 2001).

Once the appropriate transformations have been conducted (if warranted) and the global model fits the data, one can run each of the models and compute the AIC (or AIC_c). The models can then be ranked from best to worse (i.e., low to high AIC values). One should ensure that the same data set is used for each model, i.e., the same observations must be used for each analysis. Missing values for only certain variables in the data set can also lead to variations in the number of observations. Furthermore, the same response variable (y) must be used for all models (i.e., it must be identical across models, consistently with or without transformation). Nonetheless, one may specify different link functions or distributions to compare different types of models (e.g., normal, Poisson, logistic; see McCullagh and Nelder 1989).

COMPARING MODELS

Two measures associated with the AIC can be used to compare models: the delta AIC and Akaike weights. These are easy to compute, as calculations remain the same regardless of whether the AIC or AIC_c is used, and also have the advantage of being easy to interpret. The simplest, the delta AIC (Δ_i), is a measure of each model relative to the best model, and is calculated as

$$\text{Delta AIC} = \Delta_i = AIC_i - \min \text{AIC}$$

where AIC_i is the AIC value for model i , and $\min \text{AIC}$ is the AIC value of the « best » model. As a rule of thumb, a $\Delta_i < 2$ suggests substantial evidence for the model, values between 3 and 7 indicate that the model has considerably less support, whereas a $\Delta_i > 10$ indicates that the model is very unlikely (Burnham and Anderson 2002).

Akaike weights (w_i) provide another measure of the strength of evidence for each model, and represent the ratio of delta AIC (Δ_i) values for each model relative to the whole set of R candidate models:

$$\text{Akaike weight} = w_i = \frac{\exp(-\Delta_i/2)}{\sum_{r=1}^R \exp(-\Delta_r/2)}$$

In effect, we are simply changing the scale of the Δ_i 's to compare them on a scale of 1 (i.e., so that the sum of the w_i equals 1). The interpretation of Akaike weights (w_i) is straightforward: they indicate the probability that the model is the best among the whole set of candidate models. For instance, an Akaike weight of 0.75 for a model, indicates that given the data, it has a 75% chance of being the best one among those considered in the set of candidate models. In addition, one can compare the Akaike weights of the « best » model and competing models to determine to what extent it is better than another. These are termed evidence ratios and are calculated as

$$\text{Evidence ratio} = \frac{w_j}{w_i}$$

where model j is compared against model i . For example, an evidence ratio of

$$\frac{w_j}{w_i} = \frac{0.55}{0.40} = 1.375$$

would indicate that model j is only 1.375 more likely than model i to be the best, given the set of R candidate models and the data. This suggests that the rank of model j might change if we were to take a series of independent samples of identical size (Burnham and Anderson 2002). In other words, there would be a high degree of uncertainty regarding the best model. Akaike weights are also useful to give a measure of the relative importance of a variable: one simply sums the w_i of the models including the variable and compares it to those that do not. However, a better approach is to obtain a model-averaged estimate for the variable across all models (see *multimodel inference* below).

AIC vs Ho

The AIC is not a hypothesis test, does not have an α -value and does not use notions of significance. Instead, the AIC focuses on the strength of evidence (i.e., Δ_i and w_i), and gives a measure of uncertainty for each model. In contrast, conventional model selection approaches such as backward, forward, or stepwise selection procedures are generally based on hypothesis tests, where at a certain P -value, a variable is included or excluded (Zar 1984, Hosmer and Lemeshow 1989, Afifi and Clark 1996, Kleinbaum et al. 1998). These techniques often yield different conclusions depending on the order in which the models are computed, whereas the AIC approach yields consistent results and is independent of the order in which the models are computed (Anderson et al. 2000, 2001, Burnham and Anderson 2002).

AN EXAMPLE

Now, let's illustrate the use of the AIC_c in a real data set. In this example, we use the mass lost in water following dehydration of 126 green frogs (*Rana clamitans melanota*) on three different substrates (i.e., *Sphagnum* moss, soil, or peat) in or out of the shade (21 frogs for each combination of treatments). The initial mass in grams before dehydration was measured, as well as the snout-vent length of the individuals. The mass lost in water after 2 h was modeled with a linear regression fitted with maximum likelihood. Note that least-squares regression can also be used to compute AIC with a simple formula (see above). Before the analyses, 5 cases with missing data were deleted (to avoid variations in the number of observations used in the analyses), and a logarithmic transformation (base e) was applied to the dependent variable to homogenize variances. For the purpose of this example, I chose a set of 7 ($R = 7$) candidate models (Table 1). The global model (model 1) suggested good fit, based on visual inspection of the residuals plotted against the predicted values.

The results in Table 1 indicate that model 4 is the best given the set of 7 candidate models with an Akaike weight of 0.61. However, model 1, which includes the additional variable initial mass, follows it rather closely. Indeed, model 1 has a Δ_i of 0.95 and an Akaike weight of 0.38. Thus, model 1 is only 1.61 times more likely to be the best model than model 4 (evidence ratio = $0.61/0.38$), and reveals a relatively high amount of uncertainty regarding the best model. Thus, both models are equally likely, whereas the other models in the set of candidate models are very unlikely (i.e., $\Delta_i > 10$). This reveals a common problem: when no single model is clearly the best, we cannot base predictions on the model ranked in first place. Fortunately, as highlighted in the next section, there are ways to address the issue.

Table 1. Akaike's second-order information criterion (AIC_c) of the regression models of mass lost by frogs after 2 h across three substrate types in or out of the shade. A total of 121 observations were retained for analysis.

Model*	Model ID	Log-likelihood	Number of parameters (K)	AIC_c	Delta AIC_c (Δ_i)	Akaike weight (w_i)
Shade subtype imass SVL	1	-3.54	6	19.81	0.95	0.38
Shade subtype imass	2	-9.30	5	29.12	10.25	0.00
Shade imass SVL	3	-16.74	4	41.82	22.96	0.00
Shade subtype SVL	4	-4.17	5	18.86	0.00	0.61
Shade imass	5	-22.60	3	51.40	32.54	0.00
Subtype imass SVL	6	-13.52	5	37.56	18.69	0.00
Substrate initmass	7	-17.99	4	44.33	25.47	0.00

*Subtype: categorical variable with 3 levels (*Sphagnum* used as reference level); shade: categorical variable with 2 levels (i.e., no shade vs shade); SVL: snout-vent length (cm); imass: initial mass (g) of frogs before experiment.

WHEN SEVERAL MODELS COMPETE FOR FIRST PLACE: MULTIMODEL INFERENCE

As noted above, in some instances, the « best » model may have competitors for the top rank (i.e., $\Delta_i < 2$, or equivalently, evidence ratios < 2.7). A solution to this problem is to base the inference on the entire set of models, an approach termed multimodel inference or model averaging. Indeed, instead of relying solely on the estimates of the best model, we compute a weighted average of the estimates based on model uncertainty (i.e., the Akaike weights). In essence, we are using all the information available from the entire set of models to make inference and it is a very elegant way of tackling the problem.

For a given parameter, the first step consists in rearranging the AIC table with the models containing the parameter of interest. Delta AIC and Akaike weights are then recomputed for this subset of the models. To conduct model averaging, the estimate of the parameter for each model is then weighted by the Akaike weights, as follows

$$\text{Model-averaged estimate} = \hat{\theta} = \sum_{i=1}^R w_i \hat{\theta}_i$$

where $\hat{\theta}_i$ denotes the estimate for model i .

Similarly, we can also compute the precision (SE) of the model-averaged estimate, termed as the unconditional SE (i.e., a SE not restricted to a single “best” model)

$$\text{Unconditional SE} = \sum_{i=1}^R w_i \sqrt{\hat{\text{var}}(\hat{\theta}_i | g_i) + (\hat{\theta}_i - \hat{\theta})^2}$$

where $\hat{\text{var}}(\hat{\theta}_i | g_i)$ represents the variance of the estimate $\hat{\theta}_i$ given model g_i . Note that $\text{var}(\hat{\theta}_i | g_i)$ equates to squaring the SE of $\hat{\theta}_i$. Returning to our example with dehydrated frogs, we can easily compute the model-averaged estimate. Table 2 illustrates this approach for the effect of the shade variable.

In many cases, model averaging reduces bias and increases precision, which are very desirable properties (Burham and Anderson 2002). Once the model-averaged estimates and SE are calculated, we can use confidence intervals to assess the magnitude of the effect. For a 95% confidence interval,

$$\text{Upper 95\% confidence limit} = \text{estimate} + (1.96)\text{SE}$$

and

$$\text{Lower 95\% confidence limit} = \text{estimate} - (1.96)\text{SE}$$

We conclude that the estimate is different from 0 (i.e., there is an effect) when the confidence interval excludes 0. In our dehydrated frog example, the 95% confidence interval for the model-averaged estimate of shade would be (0.1233, 0.3019). The confidence interval excludes 0 and indicates that frogs out of the shade lost more water than those in the shade.

Table 2. Akaike's second-order information criterion (AIC_c) and associated measures recomputed to obtain the model-averaging estimate and precision (i.e., unconditional SE) of the shade variable, based on normal regression models of mass lost by frogs after 2 h across three substrate types in or out of the shade. Analyses are based on 121 observations.

Model*	Model ID	AIC_c	Delta AIC_c (Δ_i)	Akaike weight (w_i)	Regression estimate of shade	SE of estimate of shade
Shade subtype imass SVL	1	19.81	0.95	0.38	0.2114	0.0454
Shade subtype imass	2	29.12	10.25	0.00	0.2057	0.0476
Shade imass SVL	3	41.82	22.96	0.00	0.2104	0.0506
Shade subtype SVL	4	18.86	0.00	0.61	0.2134	0.0456
Shade imass	5	51.40	32.54	0.00	0.2035	0.0531
Model-averaged estimate					0.2126	
Unconditional SE						0.0455

*Subtype: categorical variable with 3 levels (*Sphagnum* used as reference level); shade: categorical variable with 2 levels (i.e., no shade vs shade); SVL: snout-vent length (cm); imass: initial mass (g) of frogs before experiment.

SPECIAL ISSUES WITH COUNT DATA

Discrete data (i.e., data occurring as integers) such as the number of individuals in a trap can be modeled using Poisson regression (McCullagh and Nelder 1989, Agresti 1996). However, it is common to encounter overdispersion in such data. In other words, data vary more than expected from data following a Poisson distribution (McCullagh and Nelder 1989). Poisson-distributed data have a mean equal to the variance (i.e., $\mu = \sigma^2$), whereas overdispersion occurs when the mean exceeds the variance (i.e., $\mu > \sigma^2$). Overdispersion may arise due to biological phenomenon such as aggregation, or may be a sign of inadequacy of a model. To detect whether overdispersion occurs in a data set subjected to

Poisson regression, we can estimate the dispersion parameter, $c\text{-hat}$, with the ratio of the deviance over the residual degrees of freedom (McCullagh and Nelder 1989),

$$c\text{-hat} = \frac{\text{Residual deviance}}{\text{Residual df}}$$

If $c\text{-hat} = 1$, then no overdispersion occurs. If $c\text{-hat}$ exceeds 1, then there is indication of overdispersion; values < 1 may suggest underdispersion but often hint inadequate model structure. Regardless, a model with $c\text{-hat} \ll 1$ or $c\text{-hat} \gg 4$ suggests that a Poisson model is probably not adequate. Alternatively, a negative binomial model could be used to account for overdispersion (McCullagh and Nelder 1989). We can account for overdispersion in the AIC as follows,

$$\text{QAIC} = \frac{-2(\log\text{-likelihood}) + 2K}{c\text{-hat}}$$

Similarly, the AIC_c can also be adjusted for overdispersion:

$$\text{QAIC}_c = \frac{\text{QAIC} + \frac{2K(K+1)}{n-K-1}}{c\text{-hat}}$$

Note that $c\text{-hat}$ is an additional parameter to estimate. Thus, it must be included in the count of parameters. As the estimated $c\text{-hat}$ will vary from model to model, it is advised to use the $c\text{-hat}$ of the global model (i.e., the most complex model) and use it consistently for the other models. The logic being that the most complex model will yield the best estimate for $c\text{-hat}$. Refer to Burnham and Anderson (2002) for further issues in overdispersion, especially regarding model averaging and estimating $c\text{-hat}$ when no global model exists.

ADVANTAGES AND LIMITATIONS OF AIC

The AIC provides an objective way of determining which model among a set of models is most parsimonious, as we do not rely on α . It is rigorous, founded on solid

statistical principles (i.e., maximum likelihood), yet easy to calculate and interpret. Indeed, all elements can be obtained from most statistical analysis software, such as SAS, R, S-PLUS, or SPSS. In addition, the measures associated with the AIC, such as delta AIC and Akaike weights, supply information on the strength of evidence for each model. Thus, the concept of significance becomes superfluous with the AIC. Anderson et al. (2001) suggest using it to solve conflicts in the applied sciences. The greatest strength of the AIC is its potential in model selection (i.e., variable selection), because it is independent of the order in which models are computed. In the case where there are many models ranked highly based on the AIC, we can incorporate model uncertainty to obtain robust and precise estimates, and confidence intervals.

Nonetheless, the AIC approach is not a panacea. For instance, a model is only good as the data which have generated it. In addition, the conclusions will depend on the set of candidate models specified before the analyses are conducted: we will never know if a better model exists unless it is specified in the candidate set. To the great joy of ANOVA aficionados, in certain cases, it is still preferable to use hypothesis testing instead of the AIC. This is particularly true for controlled experiments, randomized, and replicated with few independent variables. Indeed, using the AIC for a three-way ANOVA, or whenever only few models, say 1-3, appear in the candidate set will not be more instructive than hypothesis tests. However, even in these cases, investigators should routinely report the estimate and SE of the parameters they have estimated as they are much more instructive than *P*-values and simple declarations of « significant » or « not significant ». The presentation of estimates and associated SE greatly improves the value of a study, and it becomes especially useful for investigators subsequently conducting meta-analyses.

A FLASH IN THE PAN OR HERE TO STAY?

In conclusion, the information-theoretic approach revolving around the AIC shows great promise for various applications in ecology, conservation biology, behavioral ecology, and physiology. Its strength is particularly in model selection, for situations generated by observational studies conducted in the field, where regressions are sought to model a given pattern or process as a function of a number of independent variables. As it

is rather straightforward in computation and interpretation, the AIC is a useful tool that should be seriously considered by biologists faced with the task of analysing empirical data.

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