EFFECTS OF PEAT MINING INTENSITY ON GREEN FROG (RANA CLAMITANS) OCCURRENCE IN BOG PONDS

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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.

Key Words: amphibian, tadpoles, reproduction, drainage trenches, peat mining, bog, peatland

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. 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 "harbors" 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. 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.

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 \pm 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 m² (range = 20-200m²) 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) 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 2000 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 $> 10^{\circ}$ 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 1953b). 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 (18 June 2000–1 July 2000, 19 July 2000–25 July 2000) to detect the presence of tadpoles. 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 m^2 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.

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

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, $\alpha = 0.10$).

¶ Data log-transformed before analysis.

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

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.

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 ± 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 dis-

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	
Mined Area	Moderately	Log of	Natural Log of
	Disturbed	Pond	Vegetation Cover 15 m
	Area	Perimeter	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.

turbed 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.

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).

Funnel trapping yielded too few tadpoles for adequate analysis. Tadpoles were only captured at four ponds, all within the moderately disturbed section. 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 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 (± Unconditional Standard Error)²

Pond Location ³		Natural	
Mined Area	Moderately	Log of	Natural Log of
	Disturbed	Pond	Vegetation Cover 15 m
	Area	Perimeter	from Pond (3–30 cm)
-2.7144	-0.1434	-0.5617	-0.6363
(1.4341)	(0.7602)	(0.5744)	(0.3265)

 \P 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.

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. Furthermore, the greater abundance of frogs in ponds of the moderately disturbed section probably stems from the presence of drainage ditches spaced at 30-m intervals, all containing water. Alternately, 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, 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 associated with the mined section variable (i.e., -2.7144), suggests that frogs were more likely to call in ponds within the natural section than the mined section. Ponds within mined areas could be considered unsuitable breeding habitat by male green frogs.

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).

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). We did not find a similar relationship for green frogs. 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. Further studies are required to determine whether the direction and timing

of amphibian movement between bogs and upland habitats are consistent with post-breeding movements from uplands to bogs.

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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LITERATURE CITED

- Adams, M. J., K. O. Richter, and W. P. Leonard. 1997. Surveying and monitoring amphibians using aquatic funnel traps. p. 47–54. *In* D. H. Olson, W. P. Leonard, and R. B. Bury (eds.) Sampling Amphibians in Lentic Habitats: Methods and Approaches for the Pacific Northwest. Northwest Fauna No. 4, Society for Northwestern Vertebrate Biology, Olympia, WA, USA.
- Anderson, D. R., K. P. Burnham, and W. L. Thompson. 2000. Null hypothesis testing: problems, prevalence, and an alternative. Journal of Wildlife Management 64:912–923.
- Barinaga, M. 1990. Where have all the froggies gone? Science 247: 1033–1034.
- Bellis, E. D. 1962. The influence of humidity on wood frog activity. American Midland Naturalist 68:139–148.
- Blaustein, A. R., D. B. Wake, and W. P. Sousa. 1994. Amphibian declines: judging stability, persistence, and susceptibility of populations to local and global extinctions. Conservation Biology 8: 60–71.
- Burnham, K. P. and D. R. Anderson. 1998. Model Selection and Inference: a Practical Information-Theoretic Approach. Springer-Verlag, New York, NY, USA.
- Crump, M. L. and N. J. Scott, Jr. 1994. Visual encounter surveys.

p. 84–92. *In* W. R. Heyer, M. A. Donnelly, R. W. McDiarmid, L.-A. Hayek, and M. S. Foster (eds.) Measuring and Monitoring Biological Diversity: Standard Methods for Amphibians. Smithsonian Institution Press, Washington, DC, USA.

- Dale, J. M., B. Freedman, and J. Kerekes. 1985. Acidity and associated water chemistry of amphibian habitats in Nova Scotia. Canadian Journal of Zoology 63:97–105.
- Day, R. W. and G. P. Quinn. 1989. Comparisons of treatments after an analysis of variance in ecology. Ecological Monographs 59: 433–463.
- Diggle, P. J., K.-Y. Liang, and S. L. Zeger. 1994. Analysis of Longitudinal Data. Oxford University Press, Oxford, UK.
- Gibbs, J. P. 1993. Importance of small wetlands for the persistence of local populations of wetland-associated animals. Wetlands 13: 25–31.
- Gosner, K. L. and I. H. Black. 1957. The effects of acidity on the development and hatching of New Jersey frogs. Ecology 38:256– 262.
- Hagan, J. M., W. M. Vander Haegen, and P. S. McKinley. 1996. The early development of forest fragmentation effects on birds. Conservation Biology 10:188–202.
- Heyer, W. R., M. A. Donnelly, R. W. McDiarmid, L.-A. Hayek, and M. S. Foster. 1994. Measuring and Monitoring Biological Diversity: Standard Methods for Amphibians. Smithsonian Institution Press, Washington, DC, USA.
- Karns, D. R. 1992. Effects of acidic bog habitats on amphibian reproduction in a northern Minnesota peatland. Journal of Herpetology 26:401–412.
- Laan, R. and B. Verboom. 1990. Effects of pool size and isolation on amphibian communities. Biological Conservation 54:251–262.
- Lawton, J. H. 1996. Bog-plodging and sustainable development. Oikos 76:209–210.
- Martof, B. S. 1953a. Home range and movements of the green frog, *Rana clamitans*. Ecology 34:529–543.
- Martof, B. S. 1953*b*. Territoriality in the green frog, *Rana clamitans*. Ecology 34:165–174.
- Mazerolle, M. J. 1999. Amphibians in fragmented peat bogs: abundance, activity, movements and size. M. Sc. Thesis. Dalhousie University, Halifax, Nova Scotia, Canada.
- Mazerolle, M. J. 2001. Amphibian activity, movement patterns, and body size in fragmented peat bogs. Journal of Herpetology 35: 13–20.
- Mazerolle, M. J. 2003. Detrimental effects of peat mining on amphibian abundance and species richness in bogs. Biological Conservation 113:215–223.
- Oseen, K. L. and R. J. Wassersug. 2002. Environmental factors influencing calling in sympatric anurans. Oecologia 133:616–625.
- Pan, W. 2001. Akaike's information criterion in generalized estimating equations. Biometrics 57:120–125.
- Pierce, B. A. 1985. Acid tolerance in amphibians. BioScience 35: 239–243.
- Pierce, B. A. and D. K. Wooten. 1992. Genetic variation in tolerance of amphibians to low pH. Journal of Herpetology 26:422–429.
- Pope, S. E., L. Fahrig, and H. G. Merriam. 2000. Landscape complementation and metapopulation effects on leopard frog populations. Ecology 81:2498–2508.
- Poulin, M. and S. Pellerin. 2001. La conservation des tourbières: le contexte international, canadien et québécois. p. 503–518. *In* S. Payette and L. Rochefort (eds.) Écologie des Tourbières du Québec-Labrador: une Perspective Nord-Américaine. Presses de l'Université Laval, Québec, Québec, Canada.
- Reh, W. and A. Seitz. 1990. The influence of land use on the genetic structure of populations of the common frog *Rana temporaria*. Biological Conservation 54:239–249.
- Rubec, C. 1996. The status of peatland resources in Canada. p. 243– 252. In E. Lappalainen (ed.) Global Peat Resources. International Peat Society, Jyskä, Finland.
- Schmiegelow, F. K. A., Machtans, C. S., and S. J. Hannon. 1997. Are boreal birds resilient to forest fragmentation? An experimental study of short-term community responses. Ecology 78:1914–1932.
- Schroeder, E. E. 1976. Dispersal and movement of newly transformed green frogs, *Rana clamitans*. American Midland Naturalist 95:471–474.

- Scott, N. J., Jr. and B. D. Woodward. 1994. Surveys at breeding sites. p.118–125. *In* W. R. Heyer, M. A. Donnelly, R. W. Mc-Diarmid, L.-A. Hayek, and M. S. Foster (eds.) Measuring and Monitoring Biological Diversity: Standard Methods for Amphibians. Smithsonian Institution Press, Washington, DC, USA.
- Semlitsch, R. D. 1998. Biological delineation of terrestrial buffer zones for pond-breeding salamanders. Conservation Biology 12: 1113–1119.
- Sinsch, U. 1988. Seasonal changes in the migratory behaviour of the toad *Bufo bufo*: direction and magnitude of movements. Oecologia 76:390–398.
- Sinsch, U. 1990. Migration and orientation in anuran amphibians. Ethology, Ecology and Evolution 2:65–79.
- Stokes, M. E., Davis, C. S., and G. G. Koch. 2001. Categorical Data Analysis Using the SAS System. SAS Institute, Inc., Cary, NC, USA.
- Vitt, D. H. 1994. An overview of factors that influence the development of Canadian peatlands. Memoirs of the Entomological Society of Canada 169:7–20.
- Vitt, L. J., J. P. Caldwell, H. M. Wilbur, and D. C. Smith. 1990. Amphibians as harbingers of decay. BioScience 40:418.
- Wake, D. B. 1991. Declining amphibian populations. Science 253: 860.

- Wells, E. D. and H. E. Hirvonen. 1988. Terres humides atlantiques du Canada. p. 249–303. *In* Groupe de Travail National sur les Terres Humides (ed.). Terres Humides du Canada. Série de la Classification Écologique du Territoire, Numéro 24. Service Canadien de la Faune, Environment Canada, Polyscience Publications Inc., Montréal, Québec, Canada.
- Wheeler, B. D. and S. C. Shaw. 1995. Restoration of damaged peatlands. HMSO, London, UK.
- Wright, A. H. and A. A. Wright. 1949. Handbook of Frogs and Toads of the United States and Canada. Cornell University Press, Ithaca, NY, USA.
- Wyman, R. L. 1990. What's happening to the amphibians? Conservation Biology 4:350–352.
- Zar, J. H. 1984. Biostatistical Analysis. Prentice Hall, Englewood Cliffs, NJ, USA.
- Zimmerman, B. L. 1994. Audio strip transects. p. 92–97. In W. R. Heyer, M. A. Donnelly, R. W. McDiarmid, L.-A. Hayek, and M. S. Foster (eds.) Measuring and Monitoring Biological Diversity: Standard Methods for Amphibians. Smithsonian Institution Press, Washington, DC, USA.
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