

*Research Article*

## **Drainage ditches facilitate frog movements in a hostile landscape**

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### **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 system consisting of ditch networks in bogs mined for peat in eastern New Brunswick, Canada, 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. Results indicate that drainage ditches containing water enable some movements between habitats isolated by peat mining, in contrast to peat surfaces, and suggest they function as amphibian movement corridors. Thus, such drainage ditches may mitigate the effects of peat extraction on amphibian populations. At the very least, these structures provide an alternative to hostile peat surfaces. This study highlights that small-scale corridors are potentially valuable in population dynamics.

### **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; Gibbs 1998). 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. 2004; 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.

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 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 to determine whether they could be used as corridors. 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). To my knowledge, this is the first time corridor survival is estimated *per se*, as most studies have addressed survival in isolated patches connected by corridors (e.g., Boudjemadi et al.

1999; Coffman et al. 2001; Lecomte et al. 2004). Indeed, mortality during dispersal is an important component of the study of corridors that has been overlooked (Hudgens and Haddad 2003).

## Methods

### *Study area and creation of ditches*

Work on frog breeding and movements in ditches was conducted in eight bogs mined for peat moss in eastern New Brunswick, Canada (Figure 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, 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; Poulin et al. 1999; Delage et al. 2000; Mazerolle 2003).

The bogs under study varied in area from 459 to 2315 ha ( $983.8 \pm 733.3$  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 surface vegetation had been removed to expose the peat layers and mining had begun (Figure 2). Two types of ditches occurred at the sites. Each peat mining site was surrounded by a large ditch (mean  $\pm$  SD,  $1.41 \pm 0.82$  m wide  $\times$   $1.07 \pm 0.35$  m deep, and several kilometers in length), hereafter, the main ditch. This trench diverted water to a sedimentation pond, and typically contained water year round. Smaller ditches (mean  $\pm$  SD,  $1.12 \pm 0.27$  m wide  $\times$   $0.80 \pm 0.24$  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 secondary ditches often dry up during the summer and have more peat deposited at their bottom from wind erosion than main ditches.

During peat mining, peat fields are furrowed 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

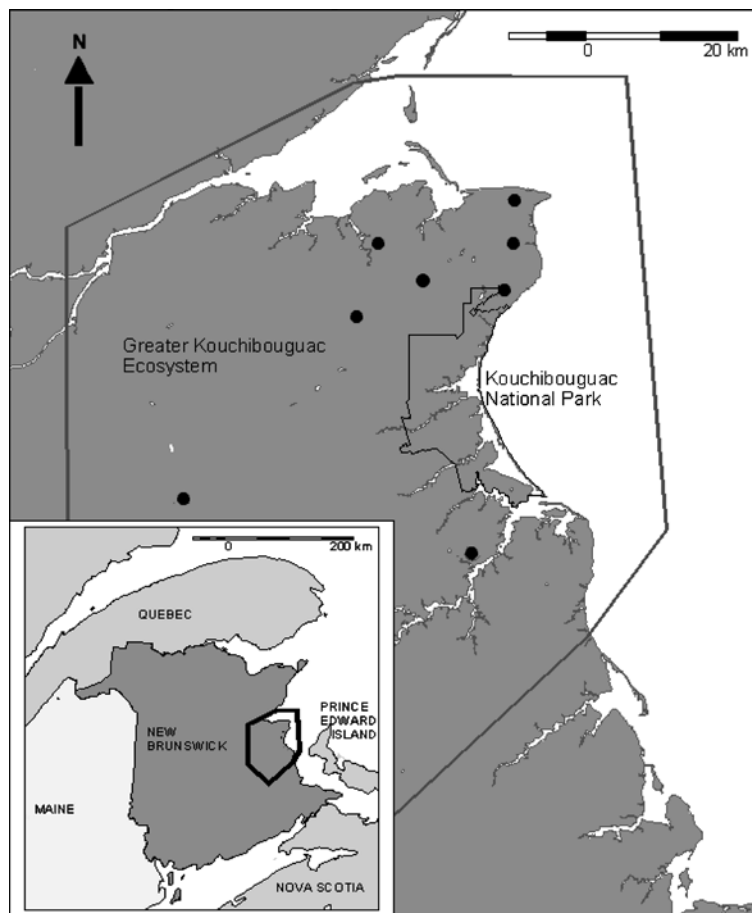


Figure 1. Location of bogs undergoing mining (circles) included in the study of amphibian use of drainage ditches in eastern New Brunswick, Canada.

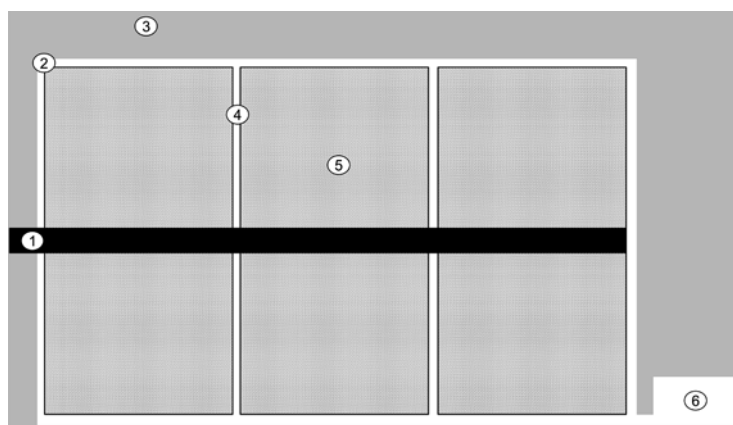


Figure 2. Typical configuration of peat mining sites in eastern Canada. 1, access road; 2, main drainage ditch; 3, unmined bog remnant; 4, secondary ditch; 5, peat mining field; 6, sedimentation pond.

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.

#### *Surveys on peat fields*

To provide a baseline to compare against the results of ditch surveys, I sampled peat fields during 2001 within four bogs undergoing peat mining to detect amphibians occurring on these surfaces. Surveys were conducted at night between 2200 and 0230, 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 five 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 likely few 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 and 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:  $\leq 5$  cm, high peat:  $> 5$  cm) were measured. 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.

I used logistic regressions to model the probability of green frog presence in the 100-m ditch transects (Hosmer and Lemeshow 1989; McCullagh and Nelder 1989). 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 four levels). I fitted a series of plausible models including the variables ditch type (i.e., main versus secondary), air temperature, wind (i.e., no/low wind versus 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<sub>c</sub>), 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).

#### *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. I conducted the work at eight 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 (Figure 2). Typically, the main ditch allows the water to drain out of the bog into sedimentation ponds before exiting into a water

course. Because amphibians usually move less than 1 km during migrations (Semlitsch and Bodie 2003), I believed that a scale of 300 m would likely yield differences in amphibian movements without being logistically difficult to sample efficiently on several occasions.

I 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 precipitation. At the start of a survey, we recorded air temperature, wind, and the percentage of cloud cover.

I used normal regressions (id link) 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 frog size (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.,  $\leq 22$  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 nine 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 ( $\phi$ ) 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 ( $\phi$ ) 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 ( $\hat{c}$ ) was close to one (i.e., observed  $\hat{c}/\text{mean of bootstrapped } \hat{c} = 1.175$ ) 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).

## Results

### *Surveys on peat fields*

No amphibians were detected on peat surfaces during the 8 km of transects surveyed at night on

Table 1. Highest-ranked logistic regression models (according to AIC<sub>c</sub>) and model-averaged estimates explaining green frog occurrence in 100-m stretches of main and secondary ditches within seven mined bogs of eastern New Brunswick, Canada.

Model	Parameters	Delta AIC <sub>c</sub> <sup>a</sup>	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 <sup>b</sup>	Ditch type <sup>c</sup>	Air	Wind	Cloud		
Period 1	Period 2	Period 3				
<b>-2.1405</b>	-0.8946	-0.5074	<b>1.7189</b>	0.0363	-0.2552	<b>-0.0246</b>
<b>(0.7669)</b>	(0.5384)	(0.5351)	<b>(0.4762)</b>	(0.0570)	(0.4658)	<b>(0.0089)</b>

A total of 280 sections of 100 m were retained for analysis. Only models with delta AIC<sub>c</sub> < 4.0 are shown for brevity. Estimates in bold indicate that 0 is excluded from 95% confidence interval and that variable influences frog presence in ditches.

<sup>a</sup>AIC<sub>c</sub> of highest-ranked model = 184.04.

<sup>b</sup>Surveys conducted on four periods (late May–early August); Period 4 used as reference level.

<sup>c</sup>Secondary ditch used as reference level.

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.

#### 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  $3.86 \pm 10.01$  green frogs were observed per km of main ditches surveyed, whereas  $0.64 \pm 2.99$  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.

#### 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 (Figure 3). Individuals moved an average net distance of  $34.1 \pm 44.8$  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 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).

Across the two sites included in the analysis, the average probability of surviving between two capture visits 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).

#### 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 in these structures was high. Furthermore, frogs could move freely within ditches. Overall, data suggest that ditches containing

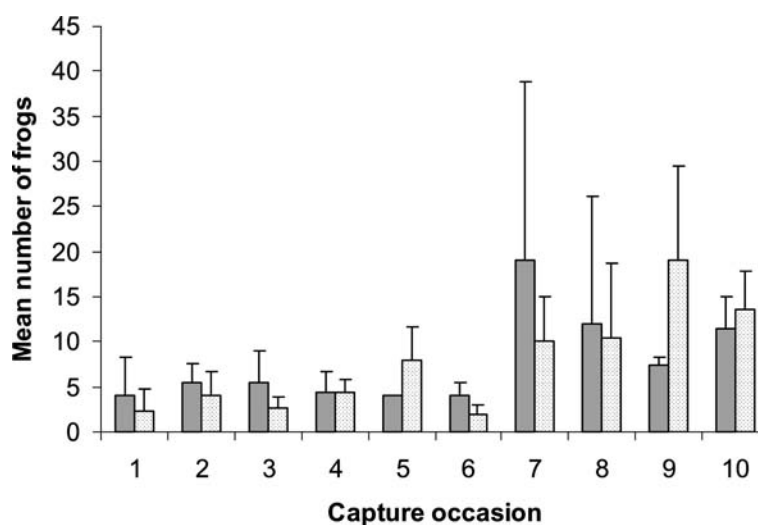


Figure 3. Mean number of green frogs captured in 300-m sections of ditches sampled repeatedly on 10 occasions during 2000 (grey) and 2001 (white). Error bars indicate 1 SD around each mean for the five sites with the most captures. Sampling occasions 1–6 correspond to breeding period (mid June to late July), whereas occasions 7–10 correspond to post-breeding period (early to late August).

Table 2. Highest-ranked linear regression models (according to  $AIC_c$ ) and model-averaged estimates explaining green frog movements in 300-m stretches of main ditches within five mined bogs of eastern New Brunswick, Canada ( $n = 95$  frogs).

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	
year site(year) firstcapture svl	8	3.42	0.04	
year site(year) ndays direction	7	3.50	0.04	
year site(year) firstcapture	7	3.57	0.03	
year site(year) svl ndays direction	8	3.71	0.03	
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
(0.4257)	(0.3571)	(0.1470)	(0.8335)	(0.2887)
				0.1853
				(0.3008)

Direction denotes direction of frog movement (i.e., with or against current); ndays indicates number of days between first and last capture (i.e.,  $\leq 22$  days or  $> 22$  days); firstcapture indicates date of first capture (i.e., June, July, or August). Only models with delta  $AIC_c < 4.0$  are shown for brevity. Variables did not influence frog movement in ditches (i.e., 95% confidence interval included 0 for all parameter estimates).

<sup>a</sup> $AIC_c$  of highest-ranked model = 323.09.

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 versus 4.00: Gorham et al. 1984; Vitt 1994; Joensuu et al. 2002; this study), because of

Table 3. Highest-ranked capture–recapture models and model-averaged estimates evaluating the effect of period (during or after breeding) and SVL on green frog survival and capture rates in 300-m sections of drainage ditches within two mined bogs of eastern New Brunswick, Canada.

Model	Parameters <sup>a</sup>	Delta QAIC <sub>c</sub> <sup>b</sup>	Akaike weight
$\phi_{\text{site+period}}, p_{\text{site+period}}$	6	0	0.30
$\phi_{\text{site+period}}, p_{\text{site}}$	3	1.02	0.18
$\phi_{\text{site+period+svl}}, p_{\text{site+period}}$	7	1.80	0.12
$\phi_{\text{site+period}}, p_{\text{site+period+svl}}$	7	2.08	0.10
$\phi_{\text{site+period+svl}}, p_{\text{site}}$	4	3.07	0.06
$\phi_{\text{site+period}}, p_{\text{site+svl}}$	4	3.08	0.06
$\phi_{\text{site+period+svl}}, p_{\text{site+period+svl}}$	8	3.98	0.04
Model-averaged parameter estimates ( $\pm$ unconditional SE)			
Effect on survival probability		Effect on capture probability	
Period	SVL	Period	SVL
–2.2011	0.1579	<b>1.0283</b>	0.0306
(1.5547)	(0.3814)	<b>(0.4440)</b>	(0.1843)

Capture–recapture model notation follows Lebreton et al. (1992). Analyses are based on the capture histories of 123 individuals over nine capture events. Only models with QAIC<sub>c</sub> < 4.0 are shown for brevity. Estimates in bold indicate that 0 is excluded from 95% confidence interval and that variable influences frog survival or capture rates.

<sup>a</sup>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.

<sup>b</sup>QAIC<sub>c</sub> of highest-ranked model = 352.47.

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 (e.g., unconditional SE of 0.09 and 0.15). 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 temporarily in the ditches (i.e., reflected by the low average net distance of recaptured frogs), many others continued to other habitats, and the high frog survival rates in the ditches further support such a hypothesis.

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, and only a single frog was found dead during surveys in main and secondary ditches. Thus, I hypothesize that the complement of frog survival in the 300-m sections is frog emigration (i.e., 1 – 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.

#### *Ditches as corridors*

Hudgens and Haddad (2003) highlight that on a short time scale (i.e., immediately following a disturbance) the presence of a corridor is most beneficial for species experiencing low survival during dispersal through an unsuitable matrix environment. For instance, an environment can become unsuitable and hinder animal movements as a result of high predation risk (Sakai and Noon 1997; Bonnet et al. 1999), of metabolic risks due to harsh conditions (e.g., desiccation: Rothermel and Semlitsch 2002; Mazerolle and Desrochers submitted; stress: Newcomb Homan et al. 2003), or of a simple aversion of animals to venture over it (Bélisle and Desrochers 2002; Rothermel and Semlitsch 2002; Chan-McLeod 2003; Mazerolle and Desrochers submitted). Regardless, these phenomena reduce the effective migration between isolated patches of habitat. In these situations, corridors provide benefit merely by increasing movements between patches (Hudgens and Haddad 2003).

In the context of peatlands undergoing mining, peat surfaces which are dry, devoid of cover, and under regular disturbance from the circulation of machinery, are barriers to amphibian movements. Indeed, no individuals were observed on peat fields during nocturnal surveys as opposed to ditches. Previous experiments have shown that frog homing success is lower on peat surfaces than on undisturbed habitat, and when given a choice, frogs prefer natural bog vegetation over peat surfaces (Mazerolle and Desrochers submitted). Mazerolle and Desrochers (submitted) also reported that individuals on peat lost approximately twice as much water (i.e., 10.5% of their initial mass in water after 2 hours) as those on natural bog surfaces. In addition, Mazerolle and Cormier (2003) recorded higher green frog abundances in bog ponds intersected by ditches than in ponds without ditches. Thus, ditches enable some movements between habitats isolated by peat mining, in contrast to peat surfaces, and seemingly function as corridors.

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). At any rate, main ditches containing water are less hazardous than peat surfaces, and reduce the risk of dehydration in mined bogs.

### Conclusion

Main ditches (i.e., wide and deep ditches containing water) seem to offer a compromise between high and low quality habitat for green frogs within bogs mined for peat moss. Peat surfaces harbor very harsh conditions, whereas ditches containing water provide shelter from desiccation. Ditches do not offer breeding habitat, as no breeding attempts occurred and most frogs arrived in ditches following the breeding period. 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. Based on this and previous evidence, ditches could facilitate movements between bog remnants in mined bogs (or remnants and upland habitats), functioning as corridors that allow migrations in this disturbed landscape type. This study shows that small-scale corridors can be potentially valuable in population dynamics, although such corridors are not the standard in conservation biology which focuses largely on top carnivores.

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### References

- Anderson D.R., Burnham K.P. and Thompson W.L. 2000. Null hypothesis testing: problems, prevalence, and an alternative. *J. Wildlife Manage.* 64: 912–923.
- Andreassen H.P., Halle S. and Ims R.A. 1996. Optimal width of movement corridors for root voles: not too narrow and not too wide. *J. Appl. Ecol.* 33: 63–70.
- Armitage P.D., Szoszkiewicz K., Blackburn J.H. and Nesbitt I. 2003. Ditch communities: a major contributor to floodplain biodiversity. *Aqua. Conserv. Mar. Freshwater Ecosyst.* 13: 165–185.
- Béchet A., Giroux J.-F., Gauthier G., Nichols J.D. and Hines J.E. 2003. Spring hunting changes regional movements of migrating greater snow geese. *J. Appl. Ecol.* 40: 553–564.
- Beier P. and Noss R.F. 1998. Do habitat corridors provide connectivity? *Conserv. Biol.* 12: 1241–1252.
- Bélisle M. and Desrochers A. 2002. Gap-crossing decisions by forest birds: an empirical basis for parameterizing spatially-explicit, individual-based models. *Landscape Ecol.* 17: 219–231.
- Bonin J., Desgranges J.-L., Rodrigue J. and Ouellet M. 1997. Anuran species richness in agricultural landscapes of Québec: foreseeing long-term results of road call surveys. In: Green D.M. (ed.), *Amphibians in Decline: Canadian Studies of a Global Problem*, Society for the Study of Amphibians and Reptiles. Saint Louis, Missouri, USA, pp. 141–149.
- Bonnet X., Naulleau G. and Shine R. 1999. The dangers of leaving home: dispersal and mortality in snakes. *Biol. Conserv.* 89: 39–50.
- Boudjemadi K., Lecomte J. and Clobert J. 1999. Influence of connectivity on demography and dispersal in two contrasting habitats: an experimental approach. *J. Animal Ecol.* 68: 1207–1224.
- Burnham K.P. and Anderson D.R. 2002. *Model Selection and Multimodel Inference: A Practical Information-theoretic Approach*. Springer-Verlag, New York, USA.
- Chan-McLeod A.C.A. 2003. Factors affecting the permeability of clearcuts to red-legged frogs. *J. Wildlife Manage.* 67: 663–671.
- Choquet R., Reboulet A.M., Pradel R., Gimenez O. and Lebreton J.D. 2003. U-Care User's Guide, Version 2.0. Mimeographed Document. CEFE/CNRS, Montpellier, France (<ftp://ftp.cefe.cnrs-mop.fr/biom/Soft-CR/>).
- Coffman C.J., Nichols J.D. and Pollock K.H. 2001. Population dynamics of *Microtus pennsylvanicus* in corridor-linked patches. *Oikos* 93: 3–21.
- Corn P.S. and Bury R.B. 1989. Logging in western Oregon: responses of headwater habitats and stream amphibians. *Forest Ecol. Manage.* 29: 39–57.
- Coulson J.C., Butterfield J.E.L. and Henderson E. 1990. The effect of open drainage ditches on the plant and invertebrate communities of moorland and on the decomposition of peat. *J. Appl. Ecol.* 27: 549–561.
- Dale J.M., Freedman B. and Kerekes J. 1985. Acidity and associated water chemistry of amphibian habitats in Nova Scotia. *Can. J. Zool.* 63: 97–105.
- Delage V., Fortin M.-J. and Desrochers A. 2000. Effets de lisière et d'isolement des habitats d'oiseaux chanteurs dans les tourbières exploitées. *Écoscience* 7: 149–156.

- DeMers M.N. 1993. Roadside ditches as corridors for range expansion of the western harvester ant (*Pogonomyrmex occidentalis* Cresson). *Landscape Ecol.* 8: 93–102.
- Donnelly M.A., Guyer C., Juterbock J.E. and Alford R.A. 1994. Techniques for marking amphibians. In: Heyer W.R., Donnelly M.A., McDiarmid R.W., Hayek L.-A.C. and Foster M.S. (eds), *Measuring and Monitoring Biological Diversity: Standard Methods for Amphibians*. Smithsonian Institution Press, Washington DC, USA, pp. 277–284.
- Duellman W.E. and Trueb L. 1994. *Biology of Amphibians*. John Hopkins University Press, Baltimore, Maryland, USA.
- Fahrig L., Pedlar J.H., Pope S.E., Taylor P.D. and Wegner J.F. 1995. Effect of road traffic on amphibian density. *Biol. Conserv.* 73: 177–182.
- Freda J. and Taylor D.H. 1992. Behavioral response of amphibian larvae to acidic water. *J. Herpetol.* 26: 429–433.
- Gibbs J.P. 1998. Amphibian movements in response to forest edges, roads, and streambeds in southern New England. *J. Wildlife Manage.* 62: 584–589.
- Gillespie G.R. 2002. Impacts of sediment loads, tadpole density, and food type on the growth and development of tadpoles of the spotted tree frog *Litoria spenceri*: an in-stream experiment. *Biol. Conserv.* 106: 141–150.
- Gorham E., Bayley S.E. and Schindler D.W. 1984. Ecological effects of acid deposition upon peatlands: a neglected field of “acid rain” research. *Can. J. Fish. Aqua. Sci.* 41: 1256–1268.
- Haddad N.M. 1999. Corridor and distance effects on interpatch movements: a landscape experiment with butterflies. *Ecol. Appl.* 9: 612–622.
- Haddad N.M. and Baum K.A. 1999. An experimental test of corridor effects on butterfly densities. *Ecol. Appl.* 9: 623–633.
- Henein K. and Merriam G. 1990. The elements of connectivity where corridor quality is variable. *Landscape Ecol.* 4: 157–170.
- Hitchings S.P. and Beebe T.J.C. 1998. Loss of genetic diversity and fitness in common toad (*Bufo bufo*) populations isolated by inimical habitat. *J. Evol. Biol.* 11: 269–283.
- Hosmer D.W. and Lemeshow S. 1989. *Applied Logistic Regression*. John Wiley and Sons, New York, USA.
- Hudgens B.R. and Haddad N.M. 2003. Predicting which species will benefit from corridors in fragmented landscapes from population growth models. *Am. Nat.* 161: 808–820.
- Joensuu S., Ahti E. and Vuollekoski M. 2002. Effects of ditch network maintenance on the chemistry of run-off water from peatland forests. *Scandinavian J. Forest Res.* 17: 238–247.
- Johnston B. and Frid L. 2002. Clearcut logging restricts the movements of terrestrial Pacific giant salamanders (*Dicamptodon tenebrosus* Good). *Can. J. Zool.* 80: 2170–2177.
- Joly P., Miaud C., Lehmann A. and Grolet O. 2001. Habitat matrix effects on pond occupancy in newts. *Conserv. Biol.* 15: 239–248.
- Knutson M.G., Sauer J.R., Olsen D.A., Mossman M.J., Hemesath L.M. and Lannoo M.J. 1999. Effects of landscape composition and wetland fragmentation on frog and toad abundance and species richness in Iowa and Wisconsin USA. *Conserv. Biol.* 13: 1437–1446.
- Kolozsvary M.B. and Swihart R.K. 1999. Habitat fragmentation and the distribution of amphibians: patch and landscape correlates in farmland. *Can. J. Zool.* 77: 1288–1299.
- Lebreton J.-D., Burnham K.P., Clobert J. and Anderson D.R. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case-studies. *Ecol. Monogr.* 62: 67–118.
- Lecomte J., Boudjemadi K., Sarrazin F., Cally K. and Clobert J. 2004. Connectivity and homogenisation of population sizes: an experimental approach in *Lacerta vivipara*. *J. Animal Ecol.* 73: 179–189.
- Mader H.-J. 1984. Animal habitat isolation by roads and agricultural fields. *Biol. Conserv.* 29: 81–96.
- Masters J.E.G., Welton J.S., Beaumont W.R.C., Hodder K.H., Pinder A.C., Gozlan R.E. and Ladle M. 2002. Habitat utilisation by pike *Esox lucius* L. during winter floods in a southern English chalk river. *Hydrobiologia* 483: 185–191.
- Mauritzen M., Bergers P.J.M., Andreassen H.P., Bussink H. and Barendse R. 1999. Root vole movement patterns: do ditches function as habitat corridors? *J. Appl. Ecol.* 36: 409–421.
- Mazerolle M.J. 2001. Amphibian activity, movement patterns, and body size in fragmented peat bogs. *J. Herpetol.* 35: 13–20.
- Mazerolle M.J. 2003. Detrimental effects of peat mining on amphibian abundance and species richness in bogs. *Biol. Conserv.* 113: 215–223.
- Mazerolle M.J. and Cormier M. 2003. Effects of peat mining intensity on green frog (*Rana clamitans*) occurrence in bog ponds. *Wetlands* 23: 708–716.
- McCullagh P. and Nelder J.A. 1989. *Generalized Linear Models*. Chapman and Hall, New York, USA.
- Merriam G. 1991. Corridors and connectivity: animal populations in heterogeneous environments. In: Saunders D.A. and Hobbs R.J. (eds), *Nature Conservation 2: The Role of Corridors*. Surrey Beatty and Sons, New South Wales, Australia, pp. 133–142.
- Newcomb Homan R., Regosin J.V., Rodrigues D.M., Reed J.M., Windmiller B.S. and Romero L.M. 2003. Impacts of varying habitat quality on the physiological stress of spotted salamanders (*Ambystoma maculatum*). *Animal Conserv.* 6: 11–18.
- Oseen K.L. and Wassersug R.J. 2002. Environmental factors influencing calling in sympatric anurans. *Oecologia* 133: 616–625.
- Painter D. 1999. Macroinvertebrate distributions and the conservation value of aquatic Coleoptera, Mollusca and Odonata in the ditches of traditionally managed and grazing fen at Wicken Fen, UK. *J. Appl. Ecol.* 36: 33–48.
- Pilliod D.S., Peterson C.R. and Ritson P.I. 2002. Seasonal migration of Columbia spotted frogs (*Rana luteiventris*) among complementary resources in a high mountain basin. *Can. J. Zool.* 80: 1849–1862.
- Pollock K.H., Nichols J.D., Brownie C. and Hines J.E. 1990. *Statistical inference for capture–recapture experiments*. *Wildlife Monogr.* 107: 1–98.
- Pope S.E., Fahrig L. and Merriam H.G. 2000. Landscape complementation and metapopulation effects on leopard frog populations. *Ecology* 81: 2498–2508.
- Poulin M., Rochefort L. and Desrochers A. 1999. Conservation of bog plant species assemblages: assessing the role of natural remnants in mined sites. *Appl. Veg. Sci.* 2: 169–180.
- Poulin M. and Pellerin S. 2001. La conservation des tourbières: le contexte international, canadien et québécois. In: Payette S. and Rochefort L. (eds), *Écologie des tourbières du Québec-Labrador: une perspective nord-américaine*. Presses de l'Université Laval, Québec, Canada, pp. 503–518.

- Power M.E. 1990. Resource enhancement by indirect effects of grazers: armored catfish, algae, and sediment. *Ecology* 71: 897–904.
- Reh W. and Seitz A. 1990. The influence of land use on the genetic structure of populations of the common frog *Rana temporaria*. *Biol. Conserv.* 54: 239–249.
- Reijnen R., Foppen R., ter Braak C.J.F. and Thissen J. 1995. The effects of car traffic on breeding bird populations in woodland. III. Reduction of density in relation to the proximity of main roads. *J. Appl. Ecol.* 32: 187–202.
- Richter S.C., Young J.E., Seigel R.A. and Johnson G.N. 2001. Postbreeding movements of the dark gopher frog, *Rana sevosa goin* and netting: implications for conservation and management. *J. Herpetol.* 35: 316–321.
- Roland J., Keyghobadi N. and Fownes S. 2000. Alpine *Parnassius* butterfly dispersal: effects of landscape and population size. *Ecology* 81: 1642–1653.
- Rosenberg D.K., Noon B.R., Megahan J.W. and Meslow E.C. 1998. Compensatory behavior of *Ensatina eschscholtzii* in biological corridors: a field experiment. *Can. J. Zool.* 76: 117–133.
- Rothermel B.B. and Semlitsch R.D. 2002. An experimental investigation of landscape resistance of forest versus old-field habitats to emigrating juvenile amphibians. *Conserv. Biol.* 16: 1324–1332.
- Ruefenacht B. and Knight R.L. 1995. Influences of corridor continuity and width on survival and movement of deer mice *Peromyscus maniculatus*. *Biol. Conserv.* 71: 269–274.
- Sakai H.F. and Noon B.R. 1997. Between-habitat movement of dusky-footed woodrats and vulnerability to predation. *J. Wildlife Manage.* 61: 343–350.
- Schmidt B.R. and Anholt B.R. 1999. Analysis of survival probabilities of female common toads, *Bufo bufo*. *Amphibia-Reptilia* 20: 97–108.
- Semlitsch R.D. 2000. Principles for management of aquatic-breeding amphibians. *J. Wildlife Manage.* 64: 615–631.
- Semlitsch R.D. and Bodie J.R. 2003. Biological criteria for buffer zones around wetlands and riparian habitats for amphibians and reptiles. *Conserv. Biol.* 17: 1219–1228.
- Simberloff D., Farr J.A., Cox J. and Mehlman D.W. 1992. Movement corridors: conservation bargains or poor investments? *Conserv. Biol.* 6: 493–504.
- Sinsch U. 1990. Migration and orientation in anuran amphibians. *Ethol. Ecol. Evol.* 2: 65–79.
- Tiebout H.M. III and Anderson R.A. 1997. A comparison of corridors and intrinsic connectivity to promote dispersal in transient successional landscapes. *Conserv. Biol.* 11: 620–627.
- Tischendorf L. and Wissel C. 1997. Corridors as conduits for small animals: attainable distances depending on movement pattern, boundary reaction and corridor width. *Oikos* 79: 603–611.
- Vitt D.H. 1994. An overview of factors that influence the development of Canadian peatlands. *Mem. Entomol. Soc. Canada* 169: 7–20.
- Welsh H.H. Jr. and Ollivier L.M. 1998. Stream amphibians as indicators of ecosystem stress: a case study from California's redwoods. *Ecol. Appl.* 8: 1118–1132.
- Wheeler B.D. and Shaw S.C. 1995. Restoration of Damaged Peatlands. HMSO, London, UK.
- White G.C. and Burnham K.P. 1999. Program MARK: Survival estimation from populations of marked animals. *Bird Study* 46(Suppl.): 120–138.
- Williams P., Whitfield M., Biggs J., Bray S., Fox G., Nicolet P. and Sear D. 2004. Comparative biodiversity of rivers, streams, ditches and ponds in an agricultural landscape in Southern England. *Biol. Conserv.* 115: 329–341.
- Woodford J.E. and Meyer M.W. 2003. Impact of lakeshore development on green frog abundance. *Biol. Conserv.* 110: 277–284.
- Wright A.H. and Wright A.A. 1949. Handbook of Frogs and Toads of the United States and Canada. Comstock Publishing Company, Ithaca, New York, USA.