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Peatlands and green frogs: A relationship regulated by acidity?[1]

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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 the 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 living *Sphagnum* moss and two media associated with uplands (*i.e.,* water with pH *ca* 6.5 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 viable summering habitat to amphibians, which highlights the value of these threatened environments in terrestrial amphibian ecology.

Keywords: amphibians, anurans, movements, peatlands, pH, reproduction.

Résumé : Les répercussions des précipitations acides sur les populations d'amphibiens ont été intensivement étudiées au cours des 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. J'ai d'abord comparé la fréquentation et la reproduction des grenouilles dans les étangs de tourbières à celles des étangs en milieu terrestre. J'ai ensuite caractérisé les mouvements des grenouilles entre les milieux tourbeux et les milieux forestiers adjacents, afin de déterminer s'ils correspondent à des migrations de reproduction ou d'après reproduction. Finalement, j'ai évalué lors d'une expérience menée sur le terrain la valeur des tourbières comme milieux de réhydratation pour les amphibiens : j'ai mis des grenouilles déshydratées en deça de leur perte vitale en eau en présence de sphaigne vivante et de deux substrats associés aux milieux non tourbeux (eau avec pH d'environ 6,5 et terre saturée en eau). La reproduction des grenouilles vertes dans les étangs de tourbière est un phénomène rare et aucun mouvement net de grenouilles vertes n'a été détecté entre les milieux forestiers et tourbeux. Néanmoins, les grenouilles temporairement déshydratées n'évitent pas la sphaigne. Malgré la faible probabilité de reproduction des grenouilles vertes dans les tourbières et l'absence de mouvements massifs 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.

Mots-clés : amphibiens, anoures, mouvements, pH, reproduction, tourbières.

Nomenclature: Marie-Victorin, 1964; Crother, 2000.

Introduction

Concern about acidic precipitation, especially in the context of amphibian population declines, generated an impressive quantity of papers during the late 1980s and early 1990s (Freda, 1986; Wyman, 1991; Dunson, Wyman & Corbett, 1992). Whether in field or laboratory conditions, most investigations of the effects of low pH have focused on the embryonic or larval stages (Gosner & Black, 1957; Saber & Dunson, 1978), with few studies on juvenile and adult amphibians (but see Wyman, 1988; Sugalski & Claussen, 1997; Simon *et al.,* 2002). Several have shown the adverse effects of pH alone or in combination with other variables (*e.g.,* predation or competition, concentrations of certain toxic metals) on amphibian development (Horne & Dunson, 1995; Pehek, 1995; Pahkala *et al.,* 2001). Although some species successfully breed in naturally acidic environments (*e.g., Rana arvalis*: Andrén, Mårdén & Nilson, 1989; *Hyla andersonii* and *Rana virgatipes*: Pehek, 1995; Bunnell & 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 (Stockwell & Hunter, 1989; Karns, 1992a,b).

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Peatlands are naturally acidic wetlands covering approximately 4 10^6 km^2 of the planet's surface. They occur mostly in boreal countries, mainly Canada and the states of the former Soviet Union (Maltby & Proctor, 1996). The deep peat deposits in some types of peatlands, namely bogs, have faced increasing pressure from the peat mining industry, and few in western Europe have remained unaltered (Wheeler & Shaw, 1995; Poulin & Pellerin, 2001; Joosten & 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, such as wood frogs (*Rana sylvatica*) and green frogs (*Rana clamitans melanota*) are known to occur in bogs (Marshall & Buell, 1955; Bellis, 1965; Stockwell & Hunter, 1989; Karns, 1992a,b), it remains unclear to what extent they use these habitats (*i.e.,* breeding *versus* 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 & Swihart, 1999; Woodford & 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 living *Sphagnum* moss as a substrate for rehydration when offered as a choice against two media from upland sites (*i.e.,* water or water-saturated soil).

Methods

STUDY AREA

I conducted this study in eastern New Brunswick, Canada (Figure 1). The study area includes Kouchibouguac National Park, which is protected under federal legislation and remains relatively little disturbed, 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 of ombrotrophic peat bogs, *i.e.,* peatlands of pH *ca* 4.0 with mineral and water inputs depending chiefly on precipitation (Schwintzer, 1981; Gorham, Bayley & Schindler, 1984; Vitt, 1994). Upland habitats mainly consist of 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 *VERSUS* 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 (Figure 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^{-1}) 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 I.

Several metres of decomposing peat at the bottom of the bog ponds rendered wading impossible at these sites. Thus, I 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, the number of which can be counted), 3 (chorus, individuals cannot be distinguished). Each pond was sampled on two occasions during the green frog breeding season, except for two upland ponds which had dried up. The first sweep was conducted

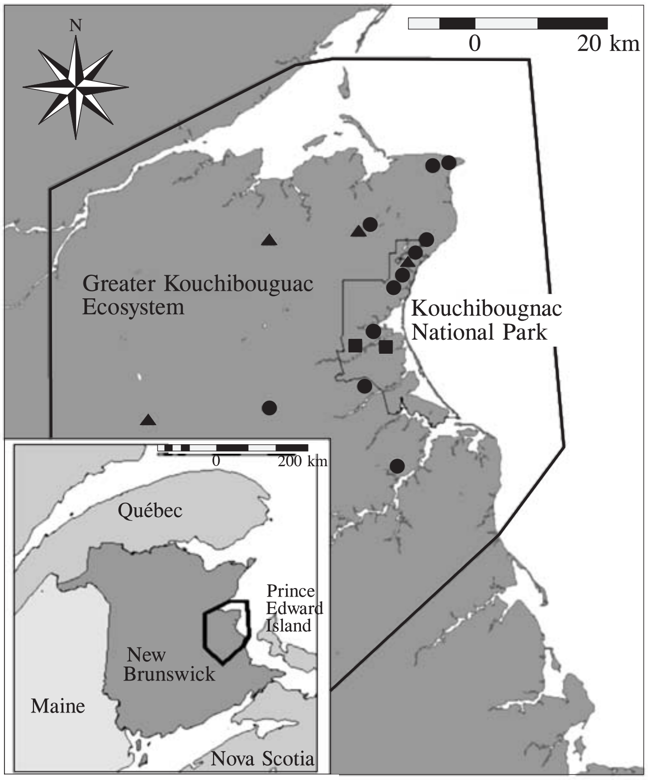

FIGURE 1. Location of green frog sampling sites in the Greater Kouchibouguac Ecosystem in eastern New Brunswick, Canada. Circles indicate upland or bog pond sites for the pond use study, triangles indicate drift-fence sites for the study of movements at the bog–forest interface, and squares represent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

TABLE I. Habitat characteristics (mean ± SD) of bog and upland ponds of eastern New Brunswick, Canada.

Variable	Bog pond (n = 12)	Upland ponds (n = 12)
Perimeter (m)	279.3 ± 192.2	194.2 ± 111.6
Depth 1 m from the shore	0.72 ± 0.23	0.23 ± 0.12
Water chemistry		
pH	3.67 ± 0.27	5.54 ± 0.98
Conductivity (μS)	55.8 ± 17.9	271.3 ± 551.0
Vegetation structure		
Overhanging vegetation (%)	0	0.2 ± 3.2
Floating vegetation (%)	9.0 ± 11.9	11.1 ± 22.5
Emergent vegetation (%)	8.1 ± 14.3	32.2 ± 30.5
Trees (> 3 m) on perimeter (%)	0.2 ± 0.3	60.0 ± 27.7
Shrubs (< 3 m) on perimeter (%)	7.7 ± 9.0	18.4 ± 21.1

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 (± SD) of 19.4 ± 2.6 °C, low wind, and no precipitation. I used minnow traps in each pond to sample tadpoles (see Mazerolle & 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 m^2 and an additional trap each time the area doubled *sensu* Adams, Richter & Leonard, 1997). Between 4 and 10 traps were placed in the ponds. These were checked for three consecutive days between 21-27 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, Liang & Zeger, 1994; Horton & Lipsitz, 1999; Stokes, Davis & Koch, 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 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 its standard error and computed 95% confidence intervals to measure the influence of each variable on frog abundance at the ponds (Pan, 2001; Burnham & Anderson, 2002).

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 (Figure 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 identified 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*, *Ledum 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 × 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. Each fence was associated with six pitfall traps: three 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 d. Each captured frog was measured (snout-vent length, SVL) and marked with a toe-clip before being released 5 m on the other side of the fence. Trapping was conducted in 2001 (18 May - 1 September) and 2002 (30 June - 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 into two trapping periods (*i.e.,* before/during breeding and following breeding), based on the dates at which green frogs are known to breed in the study area (Oseen & Wassersug, 2002; M. J. Mazerolle, unpubl. data). At each site and for each trapping period, I summed the captures from the bog side of the two fences (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, Liang & Zeger, 1994; Horton & Lipsitz, 1999; Stokes, Davis & Koch, 2000), because each site had a datum for each trapping period (*i.e.,* repeated measures).

I analyzed the two years of data separately. For each, I considered a set of three plausible models explaining the patterns of green frog captures based on mining disturbance (undisturbed *versus* adjacent peat mining) and period (breeding *versus* 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 $\mathrm{AIC_c}$ and related measures.

SELECTION OF REHYDRATION SUBSTRATE

Unlike upland habitats, bogs 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 the rehydration-habitat hypothesis, I evaluated experimentally whether acutely dehydrated green frogs actively avoid a bog substrate when it is offered as a choice against media associated with uplands. 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 39 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.

In this experiment, I used living *Sphagnum* moss freshly collected from the perimeter of a bog pond to simulate a bog substrate, whereas the upland habitat media consisted of a sifted sandy loam occurring in the uplands of the study area and well water with pH *ca* 6.5 (to simulate upland pond water). These media were chosen because they reflect the potential rehydrating media in the uplands and peatlands of the study area. The selection experiment was conducted in a plastic container (54.5 39 14 cm depth) divided into three compartments of equal dimensions with wooden lathes and silicone, each containing one of the media. All substrates were saturated with well water (pH *ca* 6.5) 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. Given that *Sphagnum* moss quickly acidifies water (Clymo, 1963; 1964), I considered the *Sphagnum* compartment an efficient approximation to a bog substrate. 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 into a container on one of the three rehydration media (determined randomly). I then recorded the position of the frog (*i.e.,* the medium selected) at 15-min intervals for 3 h, for a total of 12 observations for each individual. Twenty-one frogs (mean SVL ± SD: 5.39 ± 1.55 cm) were submitted to the substrate selection experiment. Each was used only once and was 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 & Nelder, 1989) to evaluate whether substrate selection (*i.e., Sphagnum versus* 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 *VERSUS* 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 2, Table II). Large ponds also had a greater number of calling males, regardless of the pond type (Table II). 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.

FOREST-BOG MOVEMENTS

A total of 159 green frogs were captured across all sites and years, with trap rates (mean ± SD) of 0.021 ± 0.041 and 0.014 ± 0.020 green frogs per trap night for 2001 and 2002, respectively (Figure 3). Neither the trapping period (*i.e.,* breeding *versus* 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). 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

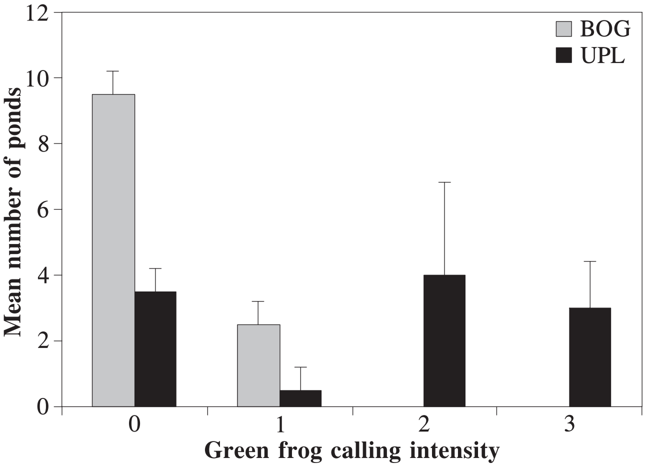

FIGURE 2. Green frog calling rate at bog (BOG) and upland (UPL) ponds sampled in 2002. Mean number + SD is shown for each calling class: 0 (no frogs calling), 1 (1 individual calling), 2 (> 1 individual calling, countable), 3 (chorus, individuals cannot be distinguished).

TABLE II. Highest-ranking Poisson regression models for repeated measures (delta $AIC_c < 5$) assessing green frog abundance at bog and upland ponds. 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

Estimates (unconditional SE in parentheses) obtained from model averaging.

Pond type (bog *versus* upland)	Log of pond perimeter	Pond depth	x	y
-2.304	**0.859**	-0.003	-0.477	-2.387
(0.525)	**(0.260)**	(0.028)	(2.389)	(1.640)

period or mining disturbance (*i.e.,* based on 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 rehydration media associated to upland habitats (Table III). 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.

Discussion

BOGS AS BREEDING SITES

Green frogs rarely bred in bog ponds relative to upland sites, as indicated by calling and minnow trapping surveys. In studies conducted solely in bogs of the same region, Mazerolle and Cormier (2003) and M. J. 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 (LC 50 of pH 3.36: Freda & Taylor, 1992; see also Dale, Freedman & Kerekes, 1985), the average bog pond pH of 3.67 presumably reduced the successful development of embryos and larvae. Similarly, Saber and Dunson (1978), Dale, Freedman, and Kerekes (1985), and Karns (1992a) observed few successful breeding attempts of wide-ranging species of amphibians in peatlands. Thus, compared to surrounding uplands, peat bogs are not productive breeding sites for most amphibians (but see Bunnell & Zampella, 1999).

BOGS AS SUMMERING SITES

Though Bellis (1962), Schroeder (1976), and Karns (1992b) hypothesized that amphibians summer in bogs after leaving upland ponds, I did not detect any net frog movements into bogs from adjacent forest habitats either during or 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. I found as many individuals moving into bogs as 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. During their bog studies, Karns (1992b) and Mazerolle (2001) observed an increase of amphibian captures following the breeding period, which also indicates that some amphibians use bogs as summering sites.

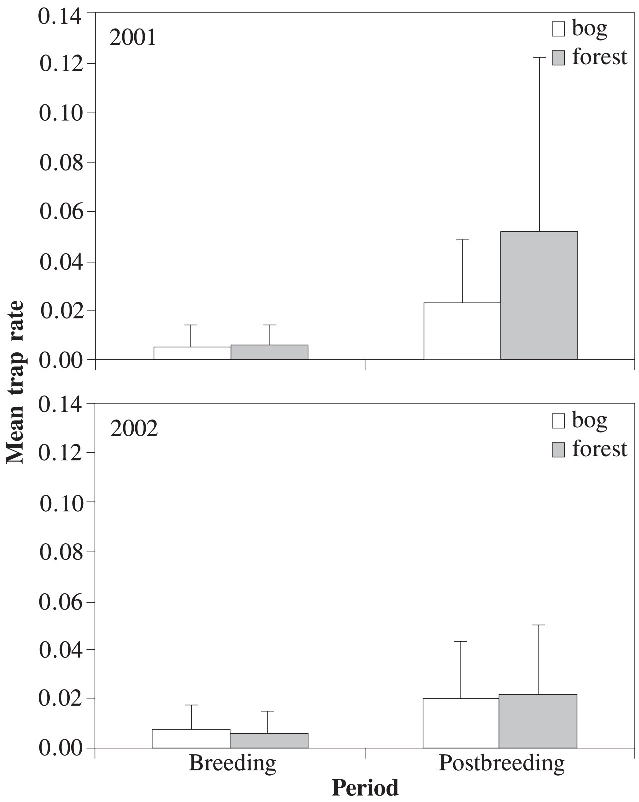

FIGURE 3. Mean green frog trap rates (number of frogs per trap night) at the forest–bog habitat interface, representing the movements of individuals from each habitat during 2001 and 2002. Total trapping effort is 11,880 trap nights. The bars represent 1 SD around each mean.

Most investigations conducted on adult amphibians and their response to pH suggest that individuals of certain species avoid acidic conditions (Karns, 1992b; Vatnick *et al.,* 1999) and that low pH can disrupt sodium balance (Wyman & Hawksley-Lescault, 1987; Frisbie & Wyman, 1992) and result in lower abundances (Wyman, 1988). These results would seem to contradict the notion of amphibians using bogs. Nonetheless, amphibian pH tolerance increases with developmental stage (Pierce, 1985), and also varies among as well as within populations (Pierce, 1985; Glos *et al.,* 2003; Räsänen, Laurila & Merilä, 2003). Furthermore, differences between populations may evolve after exposure to acidic conditions for several generations (Andrén, Mårdén & Nilson, 1989; Pierce & Wooten, 1992). I hypothesize that 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 y ago (Glaser & Janssens, 1986; Warner, Tolonen & Tolonen, 1991). This

TABLE III. Highest-ranked logistic regression models (delta AIC_c < 5) explaining the probability of green frogs choosing *Sphagnum* over 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 (0 included in 95% confidence intervals).

Model	Number of parameters	Delta AIC_c	Akaike weight
Mass	2	0	0.41
Mass massloss	3	0.84	0.27
Intercept-only	1	2.79	0.10
Massloss	2	3.07	0.09
Mass firstsubstrate	4	3.52	0.07

Estimates (unconditional SE in parentheses) obtained from model averaging.

Intercept	Mass	Massloss	First substrate	
			Sphagnum moss	Soil
0.377 (1.843)	-0.362 (0.405)	2.659 (3.662)	1.857 (1.434)	1.191 (1.785)

idea, which needs to be tested formally with populations from regions with and without naturally acidic environments, may be especially pertinent to examination of the anthropic acidification of natural systems.

Based on a review of studies in naturally acidic habitats, Mazerolle (2004) noted that amphibian species richness in such environments is generally lower than that reported in uplands. Nonetheless, acidic habitats can encompass 62-75% of the regional species richness of amphibians in certain geographic regions; this is especially true for New Brunswick and Nova Scotia, where peatlands are common (Mazerolle, 2004). Data from the present study indicate that juvenile and adult green frogs exploit acidic environments close to their physiological limits, particularly in summer. In fact, the results of the selection experiment indicate that frogs do not avoid the *Sphagnum* substrate (which is predominant in bogs) when it is offered against substrates associated with uplands. Though simple, this experiment shows that green frogs can rehydrate on *Sphagnum* substrates and thus that bogs can provide adequate areas in which to rehydrate. Despite their acidity, bogs also harbour an abundance of arthropods (Danks & Rosenberg, 1987; Larson & House, 1990) and moist refugia potentially useful for amphibians.

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 may 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 (2004) observed that the occurrence of amphibians at bog ponds increased with the proximity and number of adjacent ponds, but was independent of the proximity of mined edges.

In conclusion, green frogs rarely breed in bogs, but use these habitats during the summer. As the movement study and substrate-choice experiment indicate, frogs neither prefer nor avoid bogs compared to 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. It will be increasingly important to assay the natural processes involving amphibian adaptations and strategies of coping with harsh acidic conditions in naturally acidic habitats as anthropic acidification reduces the quality of existing breeding sites.

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