

Landscape resistance to frog movements

M.J. Mazerolle and A. Desrochers

Abstract: An animal's capacity to recolonize a patch depends on at least two components: its ability to detect the patch and its ability to reach it. However, the disruption of such processes by anthropic disturbances could explain low animal abundance patterns observed by many investigators in certain landscapes. Through field experiments, we compared the orientation and homing success of northern green frogs (*Rana clamitans melanota* Rafinesque, 1820) and northern leopard frogs (*Rana pipiens* Schreber, 1782) translocated across disturbed or undisturbed surfaces. We also monitored the path selected by individuals when presented with a choice between a short distance over a disturbed surface and a longer, undisturbed route. Finally, we measured the water loss and behaviour of frogs on substrates resulting from anthropogenic disturbances and a control. When presented with a choice, 72% of the frogs avoided disturbed surfaces. Although able to orient towards the pond of capture when translocated on disturbed surfaces, frogs had a lower probability of homing successfully to the pond than when translocated at a similar distance on an undisturbed surface. Frogs lost the most water on substrates associated with disturbance and in the absence of cover. Our data illustrate that anthropically disturbed areas devoid of cover, such as mined peatlands and agricultural fields, disrupt the ability of frogs to reach habitat patches and are likely explanations to their reduced abundance patterns in such environments.

Résumé : La capacité d'un animal à recoloniser avec succès une parcelle du paysage dépend d'au moins deux composantes, sa capacité à détecter la parcelle et sa capacité à l'atteindre. Les perturbations de ces processus par certaines activités anthropiques pourraient expliquer les patrons de faible abondance observés par plusieurs chercheurs dans certains paysages. Lors d'expériences sur le terrain, nous avons comparé l'orientation et le succès du retour de grenouilles vertes (*Rana clamitans melanota* Rafinesque, 1820) et de grenouilles léopards (*Rana pipiens* Schreber, 1782) déplacées au delà de surfaces naturelles ou perturbées. Nous avons également évalué, chez des individus relocalisés, la préférence entre un parcours court et perturbé et un parcours plus long, mais naturel. Finalement, nous avons quantifié la perte en eau et le comportement chez des grenouilles exposées à différents substrats résultant de perturbations anthropiques et chez des grenouilles témoins. Lorsqu'une surface naturelle est disponible, 72 % des grenouilles évitent les surfaces perturbées lors de leurs déplacements. Bien que capables de s'orienter avec succès vers l'étang d'origine après relocalisation sur des surfaces perturbées, les grenouilles ont une plus faible probabilité de retour qu'après relocalisation à des distances semblables sur une surface naturelle. Les grenouilles perdent le plus d'eau sur les substrats associés aux perturbations anthropiques et dépourvus de couverture végétale. Nous concluons que les surfaces perturbées par les activités anthropiques qui résultent en une perte de couverture végétale, telles que les tourbières exploitées et les terres agricoles, entravent les déplacements des grenouilles vers les parcelles d'habitat et expliquent vraisemblablement leurs patrons de densité réduite dans ces milieux.

Introduction

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

lished that habitat loss and fragmentation, through the establishment of roads or certain forestry and agricultural practices, reduce amphibian abundance, species richness, or genetic diversity (e.g., deMaynadier and Hunter 1995; Hitchings and Beebe 1998; Vos and Chardon 1998; Kolozsvar and Swihart 1999; Joly et al. 2001; Scribner et al. 2001). However, evidence for the processes behind these patterns remains scarce (but see Johnston and Frid 2002; Rothermel and Semlitsch 2002; Chan-McLeod 2003).

Matrix-dependent mobility is one of the key processes behind population responses to habitat fragmentation. Patch colonization is assumed to depend mainly on the distance between patches (Hanski and Gilpin 1991), but there is growing evidence that the quality of the matrix (e.g., cover, temperature, humidity) is important for animal movements (e.g., amphibians: Rothermel and Semlitsch 2002; Chan-McLeod 2003; mammals: Desrochers et al. 2003). The capacity of an animal to successfully recolonize a patch will depend on two major components. First, individuals must be able to detect the patch through their perceptual range (sensu

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M. J. Mazerolle^{1,2} and A. Desrochers. Centre de Recherche en Biologie Forestière, Pavillon Abitibi-Price, Université Laval, Québec, QC G1K 7P4, Canada.

¹Corresponding author (e-mail: mmazerolle@usgs.gov).

²Present address: USGS Patuxent Wildlife Research Center, 12100 Beech Forest Road, Laurel, MD 20708-4017, USA.

Zollner and Lima 1997). Perceptual range can vary across species, distance, and weather conditions (Yeomans 1995; Zollner and Lima 1997, 1999; Gillis and Nams 1998), but its extent of variation across habitat types remains undetermined. Second, individuals must reach the patches that are detected, which relates to the landscape's permeability to movements, also termed landscape resistance (Ricketts 2001). Impediments to an animal's mobility include the matrix quality, the distance between patches, as well as increased predation and metabolic risks (Sjögren-Gulve 1994; Larsen and Boutin 1994; Rothermel and Semlitsch 2002; Turcotte and Desrochers 2003).

Pond-breeding amphibians use several habitats at different times of the year to complete their life cycles (Sinsch 1990; Pope et al. 2000). Amphibians can undertake migrations of a few kilometres, but most move less than 400 m during such movements (Dodd 1996; Semlitsch and Bodie 2003). In human-disturbed landscapes, reaching the breeding, summering, or overwintering habitats often implies crossing hostile environments that are dry or devoid of cover such as open agricultural fields, forest clearcuts, or peatlands mined for peat (Bury 1983; Chen et al. 1993; Wheeler and Shaw 1995; Price 1997). For amphibians, this can become a perilous endeavor. With their permeable skin, amphibians require moist environments, and few venture far from them (Sinsch 1990). Most species do not tolerate water losses exceeding 60% of their body water content (Thorson and Svihla 1943). Thus, amphibian movements over areas devoid of cover can be costly, not only because of increased predation risk but also because of physiological costs.

We addressed issues of patch detection and landscape resistance through a series of field experiments. We predicted that amphibian movements over anthropogenically disturbed surfaces are more difficult than on undisturbed surfaces. We evaluated the ability and costs of moving over hostile areas for northern green frogs (*Rana clamitans melanota* Rafinesque, 1820) and northern leopard frogs (*Rana pipiens* Schreber, 1782), two species commonly found in eastern North America (Wright and Wright 1949; Conant and Collins 1991). Although common in the study area, both species are sensitive to changes in the landscape resulting from urban development, forestry, agriculture, and peat-mining activities (Bonin et al. 1997; Knutson et al. 1999; Koložsvary and Swihart 1999; Mazerolle 2001, 2003; Woodford and Meyer 2003). In addition, these species exhibit strong site fidelity for their breeding and summering areas (Martof 1953; Dole 1968). Using frogs translocated from their summering habitat, we compared the initial orientation and homing success of the individuals moving across undisturbed and anthropogenically disturbed surfaces. We also tested whether individuals avoid moving over a hostile surface, when given a choice against a safer but longer route. Finally, we determined the water loss and behaviour (e.g., burrowing, hiding, propped up above substrate) associated with the exposure to different types of substrates stemming from different anthropogenic disturbances. These data will provide useful parameters in the development of predictive models of the effects of habitat disturbance in the landscape (e.g., spatially explicit models: Dunning et al. 1995; South 1999; Collingham and Huntley 2000).

Materials and methods

Study area

All the experiments herein were conducted in eastern New Brunswick, in the area surrounding Kouchibouguac National Park. Mixed forest (*Picea mariana* (P. Mill.) B.S.P., *Abies balsamea* (L.) P. Mill., *Betula alleghaniensis* Britt., *Betula papyrifera* Marsh., *Acer saccharum* Marsh., and *Acer rubrum* L.) and peatlands form most of the landscape. Intense forestry and peat-mining activities are the main disturbances in the study area. These severely modify the landscape, leaving bare soil or bare peat as potential barriers to amphibian movements. Northern green frogs and northern leopard frogs are common in eastern New Brunswick and occur in various wetland habitats (Gorham 1970; McAlpine 1997). We used individuals of both species in the experiments described below in accordance with the Canadian Council on Animal Care guidelines.

Peat mining

We conducted our study in a peatland-dominated landscape (i.e., bogs and fens). These acidic wetlands, mostly occurring in northern countries (predominantly Canada and Russia), cover approximately 4×10^6 km² worldwide (Maltby and Proctor 1996). However, they have undergone intensive draining for agriculture, forestry, and urbanization and few remain unaltered in certain parts of Europe (Poulin and Pellerin 2001). Attention has recently been directed to the rapidly growing peat-mining industry, which extracts large volumes of peat in Europe and eastern North America for use in horticulture or as fuel (Wheeler and Shaw 1995; Lavoie and Rochefort 1996). For instance, global peat-mining production reached 93.7×10^6 m³ in 1997 (Daigle et al. 2001).

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

Orientation and homing success

To test the detection ability of frogs and landscape resistance, we conducted orientation and homing experiments on barren and undisturbed surfaces. We selected a pond (perimeter = 105 m) in an undisturbed portion of Pointe-Sapin Bog in eastern New Brunswick, Canada (46°57'N, 64°52'W). The pond is 70 m from the edge of barren peat, and is used mostly as summering habitat by northern green frogs and northern leopard frogs (M.J. Mazerolle, unpublished data). In late April 2000, we erected a continuous aluminum drift fence (40 cm high above ground, 20 cm below ground) on the pond's perimeter ca. 2 m from the water's edge. We placed 11.4-L pitfall traps at 5-m intervals on both

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

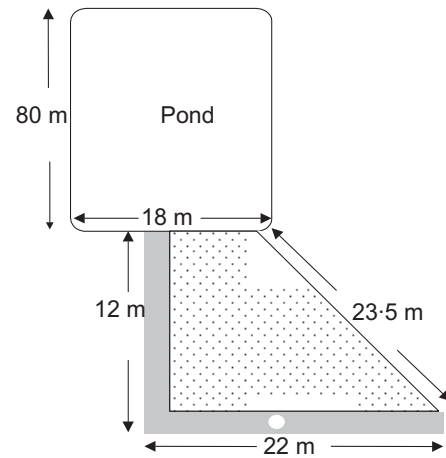
Northern green frogs and northern leopard frogs captured at the pond were measured and marked for individual recognition based on the Donnelly system (Donnelly et al. 1994). Each individual was then placed for 10 min in a release device modified from Yeomans (1995) before starting the experiments. The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

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

We randomly allocated the orientation of the opening of the release device relative to the pond (towards or opposite). At the start of each trial, the investigator opened the trap door and retreated at least 10 m from the frog. The investigator crouched down during the trials and remained behind the frog to minimize disturbance. We recorded the initial orientation of the frog (i.e., first frog movement 1 m from the release area) relative to the pond. That is, we calculated the minimum angular deviation between the orientation of the pond and the frog (i.e., smallest angle between orientation of the frog and that of the pond). Small pieces of flagging tape were placed flush to the ground 1 m around the release device to provide points of reference. The observations were terminated when the frog reached the perimeter delimited by the pieces of tape (i.e., 1 m from the release device), or after 30 min.

We conducted the translocations after 1800 to reduce the disturbance from the peat-mining activities, and to facilitate frog movements, as individuals are usually most active later in the day and evening (Oseen and Wassersug 2002). Air temperature, wind velocity (i.e., low wind or moderate to strong wind), and percent cloud cover were recorded during

Fig. 1. Test arena used to determine the avoidance of barren peat by amphibians (not drawn to scale). The open circle denotes the point of release of the frogs *Rana clamitans melanota* and *Rana pipiens*, the shaded surface corresponds to the vegetated corridor, and the dotted surface represents the barren peat.



each trial. Frogs were used only once in the experiment. Translocated frogs recaptured at the pond, either in pitfall traps or minnow traps, were noted to have successfully homed to the pond.

We used linear and logistic regressions to model the log of the angular deviation of frog orientation and the probability of homing successfully to the pond, respectively. For both analyses, the basic model consisted of the intercept and the explanatory variables year, opening orientation of the release device, and species. We fitted a series of plausible models including the variables surface type (i.e., barren vs. undisturbed), the species \times surface-type interaction, distance (i.e., 35 vs. 70 m), snout-vent length (SVL), air temperature, wind (i.e., no/low wind vs. high wind), and percent cloud cover. Model fit was evaluated with the most complex model. We evaluated the strength of evidence for each model based on the second-order Akaike's Information Criterion adjusted for small sample sizes (AIC_c), following Burnham and Anderson (2002). Estimates and standard errors (SEs) for the parameters of interest were obtained with model-averaging techniques (Anderson et al. 2000; Burnham and Anderson 2002).

Avoidance of barren surfaces

As an additional measure of landscape resistance, we tested whether translocated frogs avoid venturing onto barren surfaces when given a choice between a short route on a barren surface and a longer route on an undisturbed surface. In June 2001, we created a testing arena simulating both undisturbed bog vegetation and barren peat surfaces, on an abandoned part of Pointe-Sapin Bog, bordered by a small rectangular pond (Fig. 1). The arena was delimited by a fence 45 cm high made of cloth used in landscaping. Using spades, we collected the surface vegetation (i.e., sphagnum (genus *Sphagnum* L.) moss, ericaceous shrubs, herbs) including the roots and peat from the first 10 cm below the surface of an adjacent undisturbed bog remnant. We then arranged the blocks of vegetation into two perpendicular corri-

dors (2.25 m × 12 m and 2.25 m × 20 m) in the arena. The blocks of vegetation were packed tightly against one another to reduce dehydration and watered every 48 h. The rest of the arena was covered with 10 cm of loose peat found on the barren surface of peat fields.

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

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

Dehydration

We quantified the physiological costs (i.e., dehydration) of frogs moving in matrices within landscapes differing in human disturbance, and used dehydration rates as another measure of landscape resistance. We captured 126 northern green frogs for the experiments described below during mornings at several breeding ponds in the study area. Individuals were temporarily housed in plastic containers with water for no more than 24 h before starting the experiments. Each was used only once. After the experimental trial, the individual was marked by clipping a single digit and released at its point of capture at the end of the day. We conducted the experiments between 20 June and 15 August 2002, under similar meteorological conditions, between 1200 and 1800.

Before the start of each trial, each frog was carefully cleaned to remove any particles on the skin and blotted dry with a paper towel. We gently pressed on the abdomen of the frog to empty the bladder. The frog was then weighed to the nearest 0.1 g using a portable electronic scale (Acculab, Huntingdon, Pennsylvania, USA). Following the initial weighing, the frog was placed in a plastic container (54.5 cm × 22 cm × 39 cm) that had a layer of 5 cm of one of three substrates. We used a bare-soil substrate (sifted sandy soil) to simulate conditions encountered during movements over areas remaining after certain agricultural or forestry practices, whereas a bare-peat substrate (loose peat) was used to simulate movements over bogs undergoing peat mining. A third substrate, consisting of a living carpet of moist sphagnum moss taken from a peat bog in the study area acted as a control treatment. These substrates were likely to be encountered by frogs during migrations in the study area. During the experimental trials, a single frog was introduced in each

container. The allocation of individuals to treatments was completely randomized.

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

Researchers have reported that certain species adopt specialized behaviours, such as burrowing in the soil or retreating to cavities, to reduce water losses under dry conditions (Bentley 1966; Katz 1989; Schwarzkopf and Alford 1996; Prather and Briggler 2001; Rohr and Madison 2003). We recorded the behaviour of the frogs in the containers at the end of the first and second hours of the trials. Frogs were approached slowly to avoid modifying their behaviour and position. We characterized five types of behaviour: (1) hidden in cavity (hidden in a small depression in substrate, but not buried), (2) buried (partially or completely buried in substrate), (3) crouched (head and body against substrate), (4) head up (head is above substrate, but rest of body against substrate), and (5) propped up (head and body above substrate, front legs extended). We considered the first three as behaviours minimizing the surface exposed to evaporative water loss (i.e., an attempt to reduce dehydration).

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

We analyzed the change in mass with regression models using generalized estimating equations (GEEs) (Diggle et al. 1994; Horton and Lipsitz 1999; Stokes et al. 2000) from the GENMOD procedure in SAS/STAT[®] version 8.01 (SAS Institute Inc. 1993). GEEs are an extension of generalized linear models and are specially adapted for repeated measures (e.g., successively measuring mass in the same individual at three different periods), yielding robust estimates of parameters and SEs. We used a normal regression for repeated measures to evaluate the effects of shade, substrate type, wind speed, cloud cover, and air temperature, on the mass (square root transformed) lost each hour to dehydration. We expected a curved response of mass loss with frog size (SVL), because small frogs have a greater surface to volume ratio than large frogs, and thus, lose water faster (Thorson 1955; Schmid 1965). Therefore, we included initial frog mass (i.e.,

Table 1. Highest ranked linear regression models (i.e., change in Akaike's Information Criterion adjusted for small sample sizes ($\Delta AIC_c \leq 2$) and estimates explaining the initial orientation (i.e., angular deviation) of frogs (*Rana clamitans melanota* and *Rana pipiens*) across undisturbed and disturbed surfaces ($n = 76$ frogs).

Model	Number of parameters	ΔAIC_c^*	Akaike weight	Model-averaged parameter \pm unconditional SE
Year, opening, species, air temperature, wind velocity, cloud cover, surface	8	0	0.35	
Year, opening, species, surface	5	0.92	0.22	
Year, opening, species, snout-vent length (SVL), surface	6	1.89	0.14	
Parameter				
Species (northern green vs. northern leopard frogs)				-0.168 \pm 0.357
SVL				-0.153 \pm 0.129
Distance (35 vs. 70 m)				0.209 \pm 0.311
Surface (barren vs. undisturbed)				-2.540\pm0.292
Air temperature				-0.033 \pm 0.021
Wind velocity				0.496 \pm 0.283
Cloud cover				0.003 \pm 0.003

Note: R^2 of the most complex models was 0.66. Estimate in boldface type indicates that 0 is excluded from the 95% confidence interval and that the variable influences frog orientation. Interaction terms did not influence frog orientation and were not shown for brevity.

* AIC_c of highest ranked model was 242.05.

Table 2. Highest ranked logistic regression models (i.e., $\Delta AIC_c \leq 2$) and estimates explaining the probability of homing across undisturbed and disturbed surfaces ($n = 84$ frogs).

Model	Number of parameters	ΔAIC_c^*	Akaike weight	Model-averaged parameter \pm unconditional SE
Year, opening, species, SVL, distance, surface	7	0	0.26	
Year, opening, species, SVL, surface	6	1.04	0.15	
Year, opening, species, distance, surface	6	1.64	0.11	
Year, opening, species, SVL	5	1.95	0.10	
Parameter				
Species (northern green vs. northern leopard frogs)				0.364 \pm 0.746
SVL				0.528\pm0.269
Distance (35 vs. 70 m)				-1.044 \pm 0.663
Surface (barren vs. undisturbed)				-1.386 \pm 0.727
Air temperature				-0.072 \pm 0.056
Wind velocity				-1.144 \pm 0.665
Cloud cover				-0.012 \pm 0.008

Note: R^2 of the most complex models was between 0.12 and 0.13. Estimate in boldface type indicates that 0 is excluded from the 95% confidence interval and that the variable influences frog homing success. Interaction terms did not influence homing and were not shown for brevity.

* AIC_c of highest ranked model was 98.39.

before dehydration) and initial frog mass squared in the model. We also added the "shade \times substrate type" interaction, because these factors were crossed in our experiment. Similarly, we evaluated the effect of the same variables mentioned above (except initial frog mass squared) on the frogs' probability of minimizing their body surface exposed during dehydration with a logistic regression for repeated measures. We built a set of plausible candidate models and assessed the strength of evidence for each with the AIC_c to calculate model-averaged parameters and unconditional SEs.

Results

Orientation and homing success

Regardless of the species, frogs translocated on barren

peat tended to orient accurately towards the pond, as opposed to the individuals relocated on undisturbed surfaces (Table 1). The mean (\pm SD) angular deviation of frogs translocated on the undisturbed surface at 35 and 70 m was $86.2^\circ \pm 52.9^\circ$ and $86.9^\circ \pm 54.7^\circ$, respectively, whereas that of frogs 70 m on the barren surface was $20.1^\circ \pm 41.3^\circ$. Frog orientation did not vary across distance, species, frog size (SVL), air temperature, wind velocity, or percent cloud cover. Large frogs were more likely to home successfully than smaller frogs. The effect of surface type on frog homing success was less marked, but it suggested that individuals translocated on the barren surface were less likely to successfully home to the pond than those translocated on the undisturbed surface (Table 2). Indeed, the 95% confidence interval for the variable barely included 0, as indicated by the lower confidence

Table 3. Highest ranked logistic regression models (i.e., $\Delta AIC_c \leq 2$) and estimates explaining the probability of frogs jumping on the barren peat surface when given a choice between short route on barren peat surface and longer route on the undisturbed surface ($n = 25$ frogs).

Model	Number of parameters	ΔAIC_c^*	Akaike weight	Model-average parameter \pm unconditional SE
Opening, species	3	0	0.27	
Opening, SVL, species	4	0.89	0.17	
Opening, SVL	3	1.03	0.16	
Parameter				
Species (northern green vs. northern leopard frogs)				-1.460 \pm 1.083
SVL				0.671 \pm 0.655
Air temperature				-0.087 \pm 0.128
Wind velocity				-0.628 \pm 1.042
Cloud cover				0.011 \pm 0.015

Note: R^2 of the most complex models was between 0.04 and 0.17. The 95% confidence intervals for all the estimates included 0, indicating that the probability of frogs jumping on peat was independent of the variables in the model.

* AIC_c of highest ranked model was 32.89.

limit (i.e., 0.0383). The probability of homing was independent of distance, species, air temperature, wind velocity, and cloud cover.

Avoidance of barren surfaces

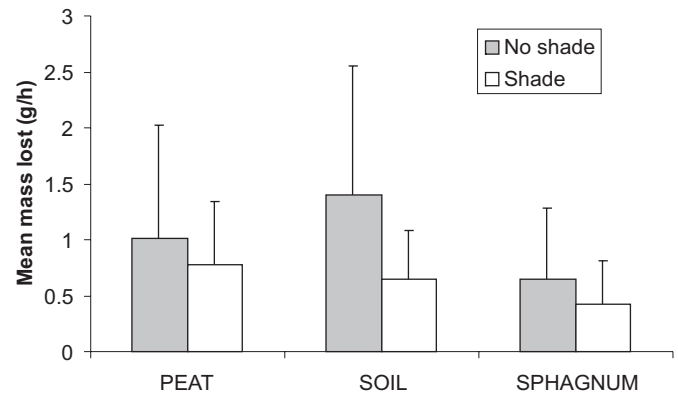
During the selection experiment, the probability of frogs moving across the peat did not vary across frog size (SVL), species, or weather conditions (Table 3). Based on a saturated log-linear model of the frequency of frogs of each species venturing on each substrate, more frogs tended to avoid the barren substrate than venture on it (18 vs. 7 frogs, respectively; type 3 likelihood-ratio statistic = 6.77, $df = 1$, $P = 0.0093$), regardless of species (type 3 likelihood-ratio statistic = 0.02, $df = 1$, $P = 0.8755$). Those that proceeded across peat moved a mean (\pm SD) of 8.6 ± 7.6 m over this surface.

Dehydration

At the end of the 2-h dehydration period, the amount of water lost by northern green frogs on the sphagnum moss substrate was almost half of that lost on either the soil or the peat substrates (Fig. 2). The sphagnum moss, soil, and peat substrates had a water content of $91.3\% \pm 1.1\%$ (mean \pm SE), $10.1\% \pm 0.5\%$, and $63.1\% \pm 1.1\%$, respectively. The mass lost by northern green frogs was greatest on the soil out of the shade (shade \times substrate interaction in Fig. 2 and Table 4). We detected a curvilinear response of water loss with the frog mass before dehydration. Weather conditions also influenced frog dehydration. Although water loss decreased with cloud cover and was greatest under windy conditions, it was independent of air temperature.

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

Fig. 2. Mean (\pm 1 SD) mass of water lost (g) per hour for northern green frogs exposed to three different substrates and two shade treatments.



Discussion

The results of the homing, barren-surface avoidance, and dehydration experiments consistently indicate that barren surfaces devoid of cover, following anthropogenic disturbances such as peat mining, are resistant to amphibian movements. Northern green frogs and northern leopard frogs avoided barren surfaces when offered a choice between moving on the undisturbed and barren surfaces. For the first time, we provide evidence that patterns of abundance in hostile environments are the result of amphibian behaviour and physiology. Indeed, in previous studies exclusively based on trap rates in different environments, researchers concluded that amphibians avoided open habitats without substantial evidence. For instance, deMaynadier and Hunter (1999) and Rothermel and Semlitsch (2002) reported that juvenile wood frogs (*Rana sylvatica* LeConte, 1825), American toads (*Bufo americanus* Holbrook, 1836), and spotted salamanders (*Ambystoma maculatum* (Shaw, 1802)) avoided open-canopy habitats, as fewer individuals were captured in traps in these habitats. Similarly, Gibbs (1998) reported that certain adult amphibians also seem to avoid other environments devoid of

Table 4. Highest ranked normal regression models for repeated measures (i.e., $\Delta AIC_c \leq 2$) and estimates explaining the mass of water lost (square root transformed) during dehydration of northern green frogs on different substrates ($n = 121$ frogs).

Model	Number of parameters	ΔAIC_c^*	Akaike weight	Model-averaged parameter \pm unconditional SE
Shade, substrate, mass, mass squared, air temperature, wind velocity, cloud cover, shade \times substrate	11	0	0.96	
Parameter				
Interaction				
Shade \times peat				0.134 \pm 0.114
Shade \times soil				0.395\pm0.129
Mass				0.064\pm0.007
Mass squared				-0.001\pm0.0002
Air temperature				0.008 \pm 0.006
Wind velocity				0.211\pm0.052
Cloud cover				-0.003\pm0.001

Note: R^2 of the global model was 0.69. Mass was the body mass before dehydration; mass squared was the squared body mass before dehydration. Shade and sphagnum moss were the reference levels for shade and substrate treatments, respectively. Estimates in boldface type indicate that 0 is excluded from the 95% confidence interval and that the variable influences the loss of frog mass. * AIC_c of highest ranked model was 249.88.

Table 5. Highest ranked logistic regression models for repeated measures (i.e., $\Delta AIC_c \leq 2$) and estimates explaining the probability of northern green frogs minimizing the surface exposed to evaporative water loss on different substrates ($n = 118$ frogs).

Model	Number of parameters	ΔAIC_c^*	Akaike weight	Model-averaged parameter \pm unconditional SE
Shade, mass	3	0	0.27	
Shade, substrate, mass, air temperature, shade \times substrate	8	1.38	0.14	
Shade, substrate, mass, air temperature	6	1.5	0.13	
Shade, substrate, mass, shade \times substrate	7	1.84	0.11	
Shade, substrate, mass	5	1.85	0.11	
Parameter				
Shade				1.0662\pm0.475
Substrate				
Peat				0.432 \pm 0.469
Soil				0.300 \pm 0.513
Mass				-0.054\pm0.012
Air temperature				0.056 \pm 0.042
Wind velocity				0.027 \pm 0.431
Cloud cover				0.172 \pm 0.272

Note: R^2 of the global model was 0.18. Mass was the body mass before dehydration. Shade and sphagnum moss were the reference levels for shade and substrate treatments, respectively. Estimates in boldface type indicate that 0 was excluded from the 95% confidence interval and that the variable influences frog behaviour. Interaction terms did not influence frog behaviour and were not shown for brevity.

* AIC_c of highest ranked model was 288.83.

cover, such as forest–road edges. These results likely stem from the effects of dehydration observed in dry environments such as clearcuts, mined bogs, or open fields (Bury 1983; Chen et al. 1993; Wheeler and Shaw 1995; Price 1997).

For the first time in a field experiment, we contrasted amphibian dehydration rates and behaviour between substrates associated with different degrees of human disturbance. We found that northern green frogs lost the most water on the

soil substrate without shade. Consequently, cover such as that provided by vegetation can greatly reduce amphibian dehydration rates on dry substrates. Vegetative cover probably reduces evaporative water loss by providing shade and shelter from the wind. Unshaded frogs had a greater tendency to minimize their exposed body surface, whereas the substrate type did not influence their behaviour. Such behaviours to minimize water loss are consistent with other reports of a more fundamental nature than our study (Thorson

and Svihla 1943; Packer 1963; Dole 1967; Parris 1998), and may be an efficient adaptation to reduce water losses in undisturbed environments. However, in regularly disturbed environments, such as mined peat fields (i.e., harrowed several times a day), these behaviours inevitably lead to death or serious injury for animals seeking refuge in the substrate. In other cases, amphibians may refrain altogether from burrowing in substrates associated with human disturbances, even under dry conditions (Jansen et al. 2001). These results suggest that surfaces devoid of cover jeopardize the survival of individuals attempting to cross them, and constitute barriers to frog movements.

Frogs translocated on the barren surface were less likely to home to the pond than those translocated on the undisturbed surface. This suggests that barren surfaces impede frog movements. Habitat loss and fragmentation are known to disrupt the movements of certain taxa, either directly, by lack of cover (amphibians: Rothermel and Semlitsch 2002; Johnston and Frid 2002; birds: St. Clair et al. 1998; Bélisle et al. 2001; Bélisle and Desrochers 2002; mammals: Diffendorfer et al. 1995; reptiles: Stanley 1998), or, less intuitively, by restricting movement activity to optimal weather conditions (Mazerolle 2001; Johnston and Frid 2002; Chan-McLeod 2003). Furthermore, individuals are susceptible to predation during movements (Larsen and Boutin 1994; Bonnet et al. 1999) and are presumably obvious to predators in areas without cover. This might also have decreased the homing probability of frogs translocated on barren surfaces, although predators were rarely seen on mined surfaces. Nonetheless, based on our homing experiment, for routes of equal distances, we should expect individuals moving under cover to have the best chances of reaching a distant habitat patch.

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

Frogs translocated on barren peat oriented and moved towards the pond on the undisturbed surface, whereas those translocated on the undisturbed surface did not have a specific orientation. This may stem from an urgency to flee the hostile conditions on the peat, whereas moisture and cover are high on the undisturbed bog surface and render it suitable for foraging. At the distances we tested, substrate type did not influence the frogs' perceptual range. Small mammals are generally capable of orienting relative to forest habitat, when relocated in fields <30 m from the forest edge (Zollner and Lima 1997; Gillis and Nams 1998). Schooley

and Wiens (2003) also recently reported directional movements of an arthropod in an unsuitable matrix. In our experiments, frogs were 70 m from the pond when translocated on the barren surface, but the undisturbed surface was ca. 3 m from the point of release. We are conscious that this may have helped frog orientation, but maintain that comparison with individuals translocated on the undisturbed surface is warranted. Indeed, additional translocations at greater distances into mined surfaces yielded similar results (M.J. Mazerolle, unpublished data).

Amphibians and landscape resistance

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

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

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