



Effet à retardement de l'ouverture de la canopée et de l'hydropériode sur le développement, la sélection d'habitat et la survie de la grenouille des bois

Mémoire

Morgane Labadie

Maîtrise en sciences forestières
Maître ès sciences (M. Sc.)

Québec, Canada

© Morgane Labadie, 2017

Effet à retardement de l'ouverture de la canopée et de l'hydropériode sur le développement, la sélection d'habitat et la survie de la grenouille des bois

Mémoire

Morgane Labadie

Sous la direction de :

Marc J. Mazerolle, directeur de recherche
Louis Imbeau, codirecteur de recherche

RÉSUMÉ

La variation des conditions environnementales pendant le développement larvaire peut engendrer des effets à retardement sur des stades ultérieurs d'un individu. L'exploitation forestière (coupes forestières, prélèvement de biomasse) modifie les microhabitats terrestres et aquatiques des amphibiens en perturbant les conditions environnementales et la qualité de l'habitat. Notre projet visait à comprendre l'impact de l'ouverture de la canopée et la variation de l'hydropériode sur le développement larvaire de la grenouille des bois (*Lithobates sylvaticus*) ainsi que l'effet à retardement de ces conditions sur la survie et la sélection d'habitats des juvéniles. Nous avons émis l'hypothèse que le développement des têtards est plus rapide avec une hydropériode réduite en canopée ouverte qu'en canopée fermée, mais que cela occasionne un coût physiologique lors de la métamorphose. Nous avons suivi le développement de 1440 têtards de grenouille des bois dans 24 mésocosmes disposés en 4 blocs complets aléatoires en forêt boréale mixte dans la région de l'Abitibi en faisant varier la canopée (ouverte ou fermée) et l'hydropériode (réduite ou constante). Après leur métamorphose, 275 juvéniles préalablement marqués ont été placés dans 3 enclos expérimentaux contenant chacun une combinaison de deux traits des débris ligneux, à savoir, leur configuration spatiale (agrégée ou homogène) et leur taille (fin ou grossier). À l'aide de modèles de capture-marquage-recapture, nous avons estimé la survie et la sélection d'habitats des juvéniles. Nos résultats montrent un développement plus rapide en canopée ouverte avec une réduction de l'hydropériode, mais que les individus ont une masse et une taille plus petite à la métamorphose que dans les autres traitements. De plus, en milieu terrestre, la sélection d'habitats des juvéniles n'était pas influencée ni par l'hydropériode ni par l'ouverture de la canopée subie pendant le stade larvaire. De plus, la survie des juvéniles de grenouille des bois en milieu terrestre ne semble pas varier à court terme dans notre étude. Globalement, nous n'avons détecté aucun effet de report des conditions pendant le stade larvaire sur la survie et le comportement des juvéniles en milieu terrestre.

Mots-clés : amphibien, développement larvaire, métamorphose, survie, hydropériode, ouverture de canopée, juvénile, sélection d'habitats, enclos terrestre, capture-marquage-recapture.

ABSTRACT

Environmental variation during the development of an individual can have long-term effects at later life stages. Logging (cut and biomass harvesting) modifies the terrestrial and aquatic microhabitats of amphibians by disrupting environmental conditions and habitat quality. Our project aimed at understanding the impact of opening the stand canopy and hydroperiod on the larval development of the wood frog (*Lithobates sylvaticus*) as well as the delayed effect of this impact on the survival and habitat selection of juveniles. We hypothesized that the development of tadpoles is faster with reduced hydroperiod under open canopies than under closed canopies, but that this incurs a physiological cost after metamorphosis. We followed the development of 1440 wood frog tadpoles in 24 mesocosms arranged in four randomized complete block designs varying canopy openness (open or closed) and hydroperiod (reduced or constant). After metamorphosis, we marked 275 metamorphs from the mesocosms and released individuals in terrestrial enclosures varying the spatial configuration (aggregated or homogeneous) and size (fine or coarse) of coarse woody debris. Using capture-mark-recapture models, we estimated the survival and habitat selection of juveniles. Tadpoles developed more quickly under an open canopy and a reduced hydroperiod than in other treatments, but reached a smaller size at metamorphosis. Habitat selection by juveniles was neither influenced by the hydroperiod nor the opening of the forest canopy during the larval stage. In addition, we found no evidence of short-term delayed effects on the survival of juveniles in the terrestrial environment. Overall, our study shows the absence of a delayed effect of larval conditions on the survival and behavior of juveniles in terrestrial environments.

Keywords : amphibian, larval development, metamorphosis, survival, hydroperiod, canopy opening, juvenile, habitat selection, terrestrial enclosure, capture-mark-recapture.

TABLE DES MATIERES

RÉSUMÉ	iii
ABSTRACT	iv
TABLE DES MATIERES	v
LISTE DES TABLEAUX	vi
LISTE DES FIGURES	vii
LISTE DES ANNEXES	viii
REMERCIEMENTS	ix
AVANT PROPOS	x
INTRODUCTION	1
Objectifs de l'étude	4
La grenouille des bois comme espèce à l'étude	4
Hypothèses et prédictions de l'étude	5
1. Stade larvaire en milieu aquatique	5
2. Stade juvénile en milieu terrestre	6
3. Effet de report sur le stade juvénile	6
BIBLIOGRAPHIE	8
CHAPITRE PRINCIPAL	14
RÉSUMÉ	15
ABSTRACT	16
Introduction	17
Methods	20
Study Area	20
Experimental design	20
Experimental design of aquatic experiment	20
Experimental design of terrestrial experiment.....	21
Building terrestrial enclosures	21
Capture-mark-recapture (CMR)	23
Statistical Analyses	24
Results	28
Aquatic experiment.....	28
Terrestrial experiment	29
Habitat selection	29
Survival of wood frog juvenile in terrestrial habitat.....	29
Discussion	35
Aquatic experiment.....	35
Terrestrial experiment	37
Habitat selection of juveniles in experimental enclosures.....	37
Survival of juveniles in experimental enclosures.....	38
Conclusion.....	41
Acknowledgements	41
Appendix	42
References	45
CONCLUSION GÉNÉRALE	52
BIBLIOGRAPHIE	56

LISTE DES TABLEAUX

TABLE 1 : Model selection based on AIC_c for the multinomial logistic regressions to quantify the effect of conditions during larval development and weather on habitat selection of juvenile wood frogs in 2016 in terrestrial enclosures in the Lake Duparquet Teaching and Research Forest, northwestern Quebec. Frogs could select among four habitats varying woody debris size and their spatial configuration (coarse homogeneous, coarse aggregated, fine homogeneous, fine aggregated). Explanatory variables included canopy cover (open or closed), hydroperiod (full or half), amount of rain 24 h before capture (Rain.previous24h), mass at metamorphosis, and air temperature 24 h before capture (Temp.previous24h). 32

TABLE 2: Model selection based on $QAIC_c$ of Cormack-Jolly-Seber models on data from 100 or 124 juveniles wood frogs having developed under a closed or open canopy with either full or half hydroperiod to estimate apparent survival (ϕ) or recapture probability (p). Models are adjusted for overdispersion ($c= 1.20$ or $c= 1$, for closed and open canopy, respectively). 34

LISTE DES FIGURES

Figure 1 : Location of mesocosms and terrestrial enclosures in the Lac Duparquet teaching and research forest (FERLD) in Abitibi-Témiscamingue (Québec, Canada). Each black triangle corresponds to the block of 4 mesocosms, the black square corresponding to an experimental terrestrial enclosure. 26

Figure 2: Diagram of (A) the terrestrial enclosures, (B) the distribution of woody debris in an arm of the experimental enclosure, (C) snapshot inside of an arm (homogeneous coarse woody debris treatment) with the camera trap fixed to the external wall of the central chamber. Note the horizontal line under the camera which delimits the door leading to the central chamber. 27

Figure 3: Effects of canopy and hydroperiod on tadpole probability of reaching metamorphosis (a), snout-vent length (b), mass at metamorphosis (c), and number of days to reach metamorphosis (d) in aquatic mesocosms at Lake Duparquet Teaching and Research Forest, northwestern Quebec, in 2016. Error bars denote 95% confidence intervals. 31

Figure 4 : Model-averaged odds of habitat selection of wood frog juveniles for three habitats compared to the coarse wood homogenous (CWH) reference level: fine wood aggregated (FWA), fine wood homogeneous, (FWH), and coarse wood aggregated (CWA). (a) Odds of selecting a given habitat over CWH for juvenile wood frogs originating from mesocosms under closed canopy. (b) Odds of selecting a given habitat over CWH for juvenile wood frogs originating from mesocosms with full hydroperiod. Error bars denote 95% unconditional confidence intervals. Confidence intervals intersecting the horizontal dashed line indicate that both habitats are as likely to be selected, whereas confidence intervals below 1 denote a preference for the reference habitat (CWH) relative to the other habitat in the comparison. 33

LISTE DES ANNEXES

Appendix 1: Date of introduction of juveniles and their numbers in each enclosure of our study.	42
Appendix 2: Average water temperature in mesocosms during the aquatic experiment with a 95% confidence interval. (a) Maximum temperature (°C) across treatments. (b) Minimum temperature (°C) across treatments.	43
Appendix 3 : Apparent survival (ϕ) or recapture probability (p) with multimodel inference based on QAICc of Cormack-Jolly-Seber models on data from 124 or 100 juveniles wood frogs having developed under a closed or open canopy with either full or half hydroperiod.	44

REMERCIEMENTS

« La reconnaissance est la mémoire du cœur ».

[Hans Christian Andersen]

En premier lieu, je tiens à exprimer mes remerciements à Marc J Mazerolle, mon directeur de recherche, pour m'avoir tant enseigné pendant toute ma maîtrise. Merci de ta patience, malgré mes incessantes questions, nos nombreuses réunions et merci de m'avoir accompagnée sur ce chemin d'apprentissage qu'est la maîtrise. Grâce à ta supervision, j'ai énormément appris. Je te suis ô combien reconnaissante de m'avoir donné l'opportunité de travailler sur ce merveilleux sujet de maîtrise ! Tes commentaires, corrections et avis éclairés m'ont guidée tout au long de ce parcours. Ce mémoire n'aurait pu être finalisé sans ton aide.

Je remercie mon second guide lors de ce voyage tumultueux, Louis Imbeau. Je n'aurais pu rêver de meilleur co-directeur. Tu m'as apporté par tes commentaires et réflexions éclairées une autre vision de mon projet, me permettant ainsi de pousser mon raisonnement toujours plus loin. Vous êtes tous les deux, Louis et Marc, un duo tellement complémentaire que c'était un privilège d'avoir l'occasion de travailler à vos côtés.

Je ne peux oublier dans ces remerciements Pierre Drapeau qui a participé activement à différents aspects du projet. A bien des égards, je te considère comme mon deuxième co-directeur.

À vous trois, Marc, Louis, Pierre, je tiens encore à vous adresser mes sincères remerciements pour votre implication tout au long de ces deux dernières années.

Je tiens aussi à remercier pour leur aide, conseils et amitié Jean Marchal et Mathilde Lapointe St Pierre. À vous aussi, mes chers parents, pour vos encouragements à poursuivre mes rêves.

J'ai été particulièrement bien entourée par mes deux assistants de terrain Antoine LeBlet et Sonia Robert, à qui j'adresse mes plus chaleureux remerciements. Vous m'avez suivie avec le sourire sans jamais me maudire malgré les erreurs et les problèmes dus à notre chantier de construction en plein milieu de la forêt abitibienne. Merci à vous deux, ce fut un été plein de surprises, de découvertes et de bonne humeur malgré les difficultés. Mention spéciale à Sonia, qui m'a accompagnée pendant presque 4 mois de terrain, par vent et marée, ou plutôt pluie et vent, jour et nuit, chaud et froid, sans jamais te plaindre et toujours dans la bonne humeur.

Je voudrais aussi remercier ma chère bande de mineurs : Nicolas, Benjamin, Roberto et Gaspard, d'être venus nous aider lors de vos jours de repos, dans ce projet fou de construire des enclos en pleine cambrousse.

Cette expérience de vie et de travail à la station de recherche avec vous tous (Sonia, Antoine, Laurianne, Marion, Abel, Nicolas, Benjamin, Gaspard, Andréane, Rejean, Robin, Jonathan, Laurence, Rebecca, Raynald, Marie, ...) reste à ce jour l'un de mes plus beaux étés.

Je dédie donc ce mémoire, à vous tous, sans votre contribution, grande ou petite, ce projet et ce mémoire n'auraient jamais vu le jour.

Une petite pensée aussi à mes grenouilles pour leur rôle clef dans ce projet et qui j'espère vivront une longue vie.

AVANT PROPOS

Ma maîtrise est présentée avec l'insertion d'un article scientifique rédigé en anglais dans le but de le soumettre et le publier dans le journal scientifique *Ecological Applications*. Je suis la première auteure de ce mémoire et de l'article présent dans le chapitre principal. Mon directeur de maîtrise, Marc J. Mazerolle professeur au département de foresterie de l'université Laval sera coauteur de l'article. Les troisième et quatrième co-auteurs de cet article seront respectivement, Louis Imbeau (UQAT) et Pierre Drapeau (UQAM).

INTRODUCTION

Depuis de nombreuses décennies, les scientifiques rapportent un déclin global des taxons animaux et plus particulièrement des amphibiens (Beebee et Griffiths, 2005). À la fin des années 1990 et début 2000, une évaluation globale des amphibiens a révélé qu'un tiers des espèces existantes étaient menacées d'extinction (Alford et Richards, 1999; Houlihan et al., 2000; Stuart et al., 2004), soit 32,5% des espèces d'amphibiens contre respectivement 23% des mammifères et 12% des espèces d'oiseaux (Blaustein et Kiesecker, 2002; Stuart et al., 2004). Actuellement, de multiples dangers affectent directement ou indirectement les populations d'amphibiens dans leurs environnements, tels que le réchauffement climatique, les maladies, la contamination de l'environnement, l'augmentation de l'exposition aux rayons ultraviolets B, la récolte des individus sauvages et l'impact des espèces invasives (Blaustein et Kiesecker, 2002; IUCN, 2008). Cependant, les principales menaces qui touchent les amphibiens sont la perte et la fragmentation de leurs habitats (Petranka et al., 1993; Petranka et al., 1994; DeMaynadier et Hunter, 1995; Gibbs, 1998; Semlitsch, 2000; Trottier, 2006; Sodhi et al., 2008). Or, deux habitats essentiels aux amphibiens – les étangs temporaires et les zones humides boisées – font partie des habitats les plus menacés dans le monde (Holland et al., 1995; Dahl, 2000; Brinson et Malvárez, 2002; Range, 2003). De plus, Haddad et al. (2015) ont démontré que la fragmentation de l'habitat entraîne la modification des mécanismes essentiels des écosystèmes et diminue la biodiversité jusqu'à 75%.

Les changements des caractéristiques des habitats affectent fortement les amphibiens en raison de certaines de leurs spécificités physiologiques. Ils dépendent des biotopes humides en raison de la perméabilité de leurs tissus (e.g., peau, branchies) qui les rend vulnérables à la dessiccation. Ainsi, les amphibiens doivent se protéger contre les fortes températures et la sécheresse. En outre, les amphibiens qui se reproduisent dans les étangs ont des cycles de vie complexes avec un cycle biphasique (milieu aquatique et terrestre), un domaine vital souvent restreint, une faible dispersion et un fort comportement philopatric vis-à-vis leur site de reproduction (Wilbur, 1980; Blaustein et Wake, 1990; Sinsch, 1990; Dunson et al., 1992; Blaustein, 1994; Duellman et Trueb, 1994; DeMaynadier et Hunter, 1995; DeMaynadier et Hunter, 1998). Par conséquent, tout bouleversement ou dérèglement dans l'habitat aquatique et terrestre peut influencer négativement les populations d'amphibiens, par exemple en diminuant le recrutement des jeunes ou les déplacements des adultes (Richter et Azous, 1995; Semlitsch, 1998; Semlitsch et Bodie, 1998; Pope et al., 2000; Marsh et Trenham, 2001; Guerry et Hunter, 2002; Gibbons, 2003).

Les pratiques sylvicoles comme la coupe totale dégradent et fragmentent les microhabitats terrestres et aquatiques des amphibiens en perturbant les paramètres abiotiques et biotiques. Les coupes forestières enlèvent la canopée arborescente et modifient à plus ou moins long terme le microclimat en diminuant l'humidité dans le milieu terrestre et en augmentant la température dans le milieu aquatique et terrestre (Dupuis et al., 1995; Chen et al., 1999; Skelly et al., 2002). Elles peuvent aussi impacter sur l'hydropériode qui est la durée de temps pendant laquelle un étang est en eau avant de s'assécher

(Smith, 1983, 1987; Rowe et Dunson, 1995; Wilbur, 1987; Pechmann et al., 1989; Snodgrass et al., 2000; Baldwin et al., 2006). Or, ce paramètre joue un rôle clef dans la reproduction et développement larvaire des amphibiens (Smith, 1983, 1987; Rowe et Dunson, 1995; Wilbur, 1987; Pechmann et al., 1989; Snodgrass et al., 2000; Baldwin et al., 2006). De plus, les activités de déboisement peuvent engendrer un compactage des débris ligneux et de la litière et réduire la quantité de débris ligneux au sol (Petranka et al., 1993; DeMaynadier et Hunter, 1995; Waldick, 1997; DeMaynadier et Hunter, 1999; Waldick et al., 1999). En outre, l'ouverture de la canopée par l'exploitation forestière engendre des modifications en cascade dans les caractéristiques des habitats des amphibiens. La disparition de la canopée arborescente augmente la température et le taux d'évaporation dans les étangs, engendrant une modification de l'hydropériode (DeMaynadier et Hunter, 1995; Waldick, 1997; Waldick et al., 1999). Ces pratiques peuvent aussi modifier la concentration en oxygène, l'abondance et la composition des ressources alimentaires et ainsi affecter le développement et la distribution des amphibiens (Blaustein et al., 2001; Skelly, 2001; Skelly et al., 2002). En Abitibi, l'utilisation de la machinerie pour l'exploitation forestière sur un sol argileux et souvent humide, provoque la formation d'ornières (MFFP, 2012). Celles-ci vont modifier le drainage des habitats et créer des étangs temporaires en milieu ouvert, pouvant être utilisée par les amphibiens (Cromer et al., 2002; DiMauro et Hunter, 2002). Ce type d'habitat pourrait avoir des conséquences à plus ou moins long terme sur le cycle de vie des amphibiens (DiMauro et Hunter, 2002; Barry et al., 2008).

Récemment, la demande de biocarburant dans le monde a augmenté de façon exponentielle (White, 2010; Riffell et al., 2011). Afin de répondre à cette demande, les compagnies forestières ont commencé à récolter la biomasse ligneuse dans les forêts et on peut y récolter jusqu'à 50% de la biomasse forestière au sol (Thiffault et al., 2009). Cependant, la durabilité d'une telle exploitation dans les forêts et l'impact que cela peut entraîner sur les organismes vivants ont été peu étudiés (Homyack et al., 2013). Des études sur l'impact du prélèvement de biomasse ligneuse ont été entreprises principalement aux États-Unis et au Canada. Des études comme celle d'Homyack et al. (2013) semblent montrer l'absence d'impact sur les populations d'amphibiens à court terme. À l'inverse, Owens et al. (2008), Davis et al. (2010) et Otto et al. (2013) ont démontré l'impact négatif du prélèvement de la biomasse sur certaines caractéristiques des amphibiens (masse, survie) et sur leur cycle de vie. Le prélèvement de biomasse réduit fortement les refuges humides indispensables au maintien des conditions favorables aux amphibiens, entrave leurs déplacements et leurs activités occasionnant des changements dans leurs comportements (Walmsley et Godbold, 2010; Fritts et al., 2015).

De nombreuses études ont permis de révéler la relation entre la canopée arborescente et le développement larvaire des amphibiens. La vitesse de développement des stades larvaires peut être affectée positivement par les coupes dans le milieu aquatique à l'inverse des stades juvéniles et adultes dans le milieu terrestre (Chelgren et al., 2006; Semlitsch et al., 2009). En effet, les amphibiens qui exploitent des habitats transitoires ont souvent une forte plasticité phénotypique (Rudolf et Rödel, 2007). Cette plasticité peut favoriser l'accélération de la croissance des stades larvaires et permettre aux individus de survivre dans plusieurs habitats. Mais ce phénomène a un coût énergétique élevé sur les

individus, occasionnant une diminution de la taille des juvéniles après la métamorphose (Semlitsch et al., 2009). La disparition du couvert forestier dans le milieu terrestre expose les juvéniles et les adultes à un ensoleillement direct créant des conditions thermiques et hygrométriques qui leur sont néfastes (Semlitsch et al., 2009). Ainsi, la réduction de la canopée arborescente engendre un microclimat inhospitalier qui peut augmenter la mortalité, réduire le taux de croissance des juvéniles, la survie et les mouvements des amphibiens suite à leur métamorphose (Rothermel, 2004; Rittenhouse et Semlitsch, 2006; Semlitsch et al., 2009).

L'écologie comportementale des animaux a révélé la tendance générale des individus à se distribuer de manière idéale dans un habitat. Ainsi, ils privilégient des habitats qui favorisent leur fitness et leur longévité et cela influe sur leur taux de survie et de reproduction (Fretwell et Lucas, 1970; Coulson et al., 2006). De plus, le fitness des amphibiens varie en fonction de leur capacité à se soustraire au stress physiologique et de leurs interactions comportementales entre les individus, les proies et les prédateurs (Blomquist et Hunter, 2010). Ainsi, les amphibiens exploitent des habitats qui contiennent les ressources essentielles et qui sont compatibles avec leurs contraintes physiologiques. La structure complexe du sol (végétation, litière, la présence et la quantité de débris ligneux au sol), l'humidité du sol, le couvert forestier et la température font partie des paramètres clefs expliquant la sélection d'habitats par les amphibiens (Constible et al., 2001; Blomquist et Hunter, 2010). De plus, leurs déplacements et leurs comportements peuvent varier en fonction des conditions climatiques (pluie, sécheresse), de la température, de la couverture du sol et de l'humidité de l'air (Chan-McLeod, 2003; Baldwin et al., 2006; Rittenhouse et Semlitsch, 2007; Timm et al., 2007; Blomquist et Hunter, 2010).

Depuis plus d'une décennie, la littérature scientifique s'intéresse aux « effets de report » ou effets à retardement chez de nombreux taxons dont celui des arthropodes, des oiseaux et des amphibiens (Giménez et Torres, 2004; Norris et al., 2004; Johnsson et Bohlin, 2006; Norris et Marra, 2007; Harrison et al., 2011; Lee et al., 2013). Un stress initial dans l'environnement peut avoir des conséquences à plus ou moins long terme dans le cycle de vie des individus. Ainsi, les effets à retardements dans l'environnement peuvent se dérouler autant lors d'une période saisonnière (hibernation, migration) que lors d'un stade biologique distinct (développement, reproduction, métamorphose) (Benard et McCauley, 2008). Des études ont montré que les facteurs environnementaux rencontrés lors de la croissance larvaire des amphibiens comme la température (Kaplan et Phillips, 2006), l'ouverture de la canopée (Werner et al., 2007; Boes et Benard, 2013), les conditions nutritionnelles (Metcalf et Monaghan, 2001; Scott et al., 2007; Van Allen et al., 2010) et les effets maternels (Räsänen et al., 2003; Kaplan et Phillips, 2006) vont affecter les individus post métamorphique à différents niveaux lors de leur cycle de vie. Ces différentes conditions lors du développement peuvent engendrer des conséquences sur le comportement, le phénotype et la performance des individus. Par exemple, Altwegg et al. (2003) ont démontré que les juvéniles de certaines espèces de ranidés (*Rana lessonae* et *R. esculenta*) ont une plus grande chance de survie en milieu terrestre. Une étude de Boes et Benard (2013), quant à elle, a montré que l'ouverture de la canopée influence négativement la performance locomotrice des juvéniles de grenouille des bois (*Lithobates sylvaticus*) en milieu terrestre. Enfin, des recherches récentes ont

établi qu'en raison de conditions défavorables lors de leur développement, certains individus peuvent utiliser une croissance compensatoire. Cependant, ce type de mécanisme engendre souvent des coûts plus ou moins à long terme dans la vie adulte de ces individus (Metcalf et Monaghan, 2001).

Au Québec, les forêts couvrent une superficie de 761 000 km², soit près de la moitié du territoire (MFFP, 2015). En 2013, la fabrication de produits en bois à l'échelle de la province a rapporté 6,2 milliards de dollars (CIFQ, 2015). L'industrie forestière joue un rôle de premier plan dans l'économie de plusieurs régions au Québec, dont celle de l'Abitibi-Témiscamingue qui est la deuxième région ayant récolté le plus important volume de bois en 2012 (Gouv.Québec, 2014). Dans ce contexte, une meilleure compréhension de l'impact de l'exploitation forestière sur la performance des amphibiens permettra de prendre des mesures afin de protéger les populations de ce taxon et d'atténuer l'impact anthropique dans ce milieu.

Objectifs de l'étude

Les principaux objectifs de ce projet sont de documenter les conséquences de deux pratiques forestières – l'ouverture de la canopée et le prélèvement de débris ligneux au sol - sur deux stades de développement distincts de la grenouille des bois. Dans le milieu aquatique, nous avons évalué le développement des têtards en quantifiant la survie, la vitesse de développement, la taille et la masse à la métamorphose en fonction de la variation de l'ouverture de la canopée et de l'hydropériode. Lors de la phase terrestre, des juvéniles venant de la phase aquatique de notre étude et préalablement marqués ont été suivis dans des enclos expérimentaux. Chacun de ces enclos contenait quatre traitements où nous avons fait varier la taille et la disposition des débris ligneux. Grâce à une technique de capture-recapture, nous avons pu estimer la survie et la sélection d'habitat des individus.

Cette étude permettra d'étayer les connaissances sur: (1) l'effet à retardement des conditions aquatiques lors du développement larvaire (ouverture de la canopée, hydropériode) sur la survie et la sélection d'habitat des juvéniles de grenouille des bois en milieu terrestre, et (2) l'effet de la répartition et de la taille des débris ligneux dans la sélection d'habitats et la survie des juvéniles de la grenouille des bois dans des enclos expérimentaux.

La grenouille des bois comme espèce à l'étude

La grenouille des bois (*Lithobates sylvaticus*) est une espèce d'amphibien répandue en Amérique du Nord et elle est très commune au Québec. Elle appartient à la famille des ranidés et elle a un cycle de vie biphasique. Le milieu aquatique sert lors de la reproduction et du développement larvaire des têtards (Wright et Wright, 1949). Les juvéniles et les adultes utilisent le milieu terrestre pour la protection, l'alimentation, l'hibernation et l'estivation (Baldwin et al., 2006). Les amphibiens sont des bio-indicateurs de la qualité de l'habitat notamment, en raison de leur niveau dans la chaîne trophique et de leur rôle important dans les réseaux trophiques de la forêt en tant que proies et comme prédateurs d'arthropodes (Welsh et Droege, 2001; Trottier, 2006; Semlitsch et al., 2009; Homyack et al., 2013). Dans certains

milieu, la grenouille des bois est très abondante et cette espèce est intimement liée au sol forestier. Chez de nombreux taxons, et plus particulièrement celui des amphibiens, tous les stress physiologiques dans la structure de l'habitat du milieu aquatique et terrestre causés par les perturbations, telles que l'exploitation forestière, peuvent entraîner des effets négatifs sur les stades ultérieurs du cycle de vie (Beckerman et al., 2002; Phillips, 2002; Giménez et Torres, 2004; Chelgren et al., 2006).

Hypothèses et prédictions de l'étude

Ce projet a pour but de comprendre les relations et les effets à court terme de la perte de la canopée et de la disponibilité des débris ligneux sur le développement des stades têtards et juvéniles des grenouilles des bois.

1. Stade larvaire en milieu aquatique

Cette première partie de l'expérimentation vise à mettre en relation la variation de couvert forestier de la canopée et de l'hydropériode sur le développement des têtards des grenouilles des bois. La perte de la canopée peut entraîner des modifications dans le développement des amphibiens tant au niveau temporel (durée du stade larvaire avant métamorphose) que biologique avec des changements de taille et de poids des individus métamorphosés. L'augmentation de la température dans les étangs à canopée ouverte (Skelly et al., 2002) peut favoriser de nombreux processus physiologiques chez les amphibiens (Dodd et Dodd, 1976; Ultsch, 1999) comme le taux de croissance qui va modifier le développement des stades larvaires (Newman, 1998). En outre, la variation de l'hydropériode peut avoir un impact positif (augmentation de la température de l'eau) ou négatif (compétition pour les ressources) (Wilbur, 1987; Howard et al., 2012) sur le développement des stades larvaires. Les conditions environnementales (disponibilité des ressources, température, oxygénation de l'eau, prédation) que subissent les têtards sont susceptibles d'affecter la taille, la physiologie et le rapport de longueur des membres des amphibiens après leur métamorphose (Boes et Benard, 2013). Ainsi, nous prédisons que les individus en fonction de leur plasticité phénotypique sont capables de s'adapter aux changements des conditions environnementales.

Hypothèse 1.1 : L'atteinte à la métamorphose des têtards augmentent avec l'ouverture de la canopée et la réduction de l'hydropériode. Le développement des têtards de la grenouille des bois s'accélère en raison de l'interaction de l'ouverture de la canopée et de l'hydropériode qui favorise un haut niveau de productivité primaire.

Hypothèse 1.2 : Cette vitesse de développement influence par conséquent la masse et la taille corporelle à la métamorphose.

Prédiction 1.1 :

La probabilité d'atteindre la métamorphose des têtards de grenouilles des bois sera plus élevée en milieu ouvert avec une hydropériode réduite (interaction ouverture de canopée x hydropériode) en réponse à la température accrue et à la disponibilité des ressources.

Prédiction 1.2 :

Nous prédisons que le temps pour atteindre la métamorphose des têtards sera plus rapide en canopée ouverte avec hydropériode réduite (interaction ouverture de canopée x hydropériode).

Prédiction 1.3 :

Un développement plus rapide lors du stade larvaire des grenouilles des bois occasionnera une masse et taille après métamorphose plus faible des individus, particulièrement en canopée ouverte avec l'hydropériode réduite.

2. Stade juvénile en milieu terrestre

La deuxième partie du projet vise à étudier l'impact de la disponibilité de débris ligneux (taille et répartition spatiale) récemment coupés sur la survie des juvéniles de grenouille des bois et sur leur sélection d'habitats en relation avec les conditions environnementales lors du stade larvaire. Dans nos traitements, la taille des débris ligneux peut être séparée en deux catégories : les débris ligneux grossiers (= 15 cm de diamètre) et les débris ligneux fins (= 5 cm de diamètre). Selon Sumner (2006), Jacobs et al. (2007) et Christie et al. (2012) les débris ligneux grossiers sont cruciaux comme habitat pour de nombreuses espèces d'invertébrés et de vertébrés.

Hypothèse 2.1: Les individus juvéniles privilégient les amas de débris ligneux grossiers comme habitat, mais ces comportements varient en fonction des conditions climatiques et selon leur expérience pendant le stade larvaire (Fritts et al., 2015).

Hypothèse 2.2 : Lorsque le risque de dessiccation est élevé (forte température et aucun événement de précipitation), les juvéniles vont privilégier les amas de débris ligneux grossiers comme habitat et plus particulièrement comme refuge diurne (Fritts et al., 2015).

Prédiction 2.1 :

La configuration spatiale des débris ligneux (homogène ou agrégée) aura un effet sur le comportement de sélection d'habitats des juvéniles de la grenouille des bois. Les juvéniles choisiront les traitements ayant les débris ligneux grossiers en tas agrégés qui doivent être de meilleurs refuges particulièrement pour la conservation de l'humidité.

3. Effet de report sur le stade juvénile

La variation environnementale d'un habitat lors du développement d'un individu peut avoir des effets à long terme durant le cycle de vie d'un organisme (Pechenik, 2006). Ces variations peuvent modifier ou altérer divers aspects d'un phénotype d'un animal y compris sa taille, sa forme et sa physiologie (Pechenik, 2006). À long terme, l'effet de report peut affecter les mécanismes écologiques et évolutifs, alors qu'à plus court terme, il peut influencer le fitness et la performance des individus (Lindström, 1999; Benard et McCauley, 2008). Des études récentes, réalisées sur des stades larvaires d'invertébrés marins, démontrent un effet de report qui modifie les paramètres démographiques y compris la reproduction et la survie (Dias et Marshall, 2010; Crean et al., 2011). Chelgren et al. (2006) suggèrent que la taille du corps et la date de métamorphose sont des facteurs sensibles au stress aquatique. Ces facteurs peuvent influencer les mouvements et les stratégies de survie post-métamorphique lors de la

phase terrestre d'une grenouille (Chelgren et al., 2006). Ainsi, selon Berven (1990), l'augmentation de la taille à la métamorphose améliorerait la survie des grenouilles des bois. Cependant, Bernardo (1996), Heath et Blouw (1998), et Beck et Congdon (1999) estiment que l'effet de report serait plus important à court terme qu'à long terme. D'ailleurs, Beck et Congdon (1999) rapportent une forte corrélation entre la taille à la métamorphose du crapaud criard (*Anaxyrus terrestris*) et la croissance après dix jours, mais que cet effet disparaît au bout de deux mois.

Hypothèses : Les individus ayant eu un développement larvaire plus rapide, mais qui ont atteint une petite taille à la métamorphose sont moins performants que les individus ayant eu un cycle de développement larvaire sans perturbation anthropique (non perturbé par la réduction d'hydropériode ni par l'ouverture de la canopée). En effet, nous émettons l'hypothèse que les individus de petite taille sont désavantagés dans un milieu perturbé (habitat récemment exploité avec peu d'ombrage).

Prédiction 3.1:

Nous prédisons que la survie sera plus faible pour les individus de petite taille que les individus de plus grande taille.

Prédiction 3.2 :

Nous estimons que la sélection d'habitats dans les enclos expérimentaux pourra différer entre les individus en raison de leur histoire de vie lors de leur phase de développement larvaire (ouverture de la canopée et hydropériode).

BIBLIOGRAPHIE

- Alford, R. A. et Richards, S. J. (1999). Global amphibian declines: a problem in applied ecology. *Annual review of Ecology and Systematics*, 30(1), 133-165.
- Altwegg, R., Reyer, H.-U. et Merilä, J. (2003). Patterns of natural selection on size at metamorphosis in water frogs. *Evolution*, 57(4), 872-882.
- Baldwin, R. F., Calhoun, A. J. K. et DeMaynadier, P. G. (2006). Conservation planning for amphibian species with complex habitat requirements: a case study using movements and habitat selection of the Wood Frog (*Rana sylvatica*). *Journal of Herpetology*, 40(4), 442-453.
- Barry, D. S., Pauley, T. K. et Maerz, J. C. (2008). Amphibian use of man-made pools on clear-cuts in the Allegheny Mountains of West Virginia, USA. *Applied Herpetology*, 5(2), 121-128.
- Beck, C. W. et Congdon, J. D. (1999). Effects of individual variation in age and size at metamorphosis on growth and survivorship of southern toad (*Bufo terrestris*) metamorphs. *Canadian Journal of Zoology*, 77(6), 944-951.
- Beckerman, A., Benton, T. G., Ranta, E., Kaitala, V. et Lundberg, P. (2002). Population dynamic consequences of delayed life-history effects. *Trends in Ecology & Evolution*, 17(6), 263-269.
- Beebee, T. J. et Griffiths, R. A. (2005). The amphibian decline crisis: a watershed for conservation biology? *Biological Conservation*, 125(3), 271-285.
- Benard, M. F. et McCauley, S. J. (2008). Integrating across life-history stages: consequences of natal habitat effects on dispersal. *American Naturalist*, 171(5), 553-567.
- Bernardo, J. (1996). Maternal effects in animal ecology. *American Zoologist*, 36(2), 83-105. doi: 10.1093/icb/36.2.83
- Berven, K. A. (1990). Factors affecting population fluctuations in larval and adult stages of the wood frog (*Rana sylvatica*). *Ecology*, 71(4), 1599-1608.
- Blaustein, A. R. et Wake, D. B. (1990). Declining amphibian populations: a global phenomenon? *Trends in Ecology & Evolution*, 5(7), 203-204.
- Blaustein, A. R. (1994). Chicken little or Nero's fiddle? A perspective on declining amphibian populations. *Herpetologica*, 50(1), 85-97.
- Blaustein, A. R., Belden, L. K., Hatch, A. C., Kats, L. B., Hoffman, P. D., Hays, J. B., Marco, A., Chivers, D. P., Kiesecker, J. M. (2001). Ultraviolet radiation and amphibians. Dans C. S. Cockell et A. R. Blaustein (dir.), *Ecosystems, Evolution, and Ultraviolet Radiation* (p. 63-79). Springer : New York.
- Blaustein, A. R. et Kiesecker, J. M. (2002). Complexity in conservation: lessons from the global decline of amphibian populations. *Ecology Letters*, 5(4), 597-608. doi: 10.1046/j.1461-0248.2002.00352.x
- Blomquist, S. M. et Hunter, M. L. (2010). A multi-scale assessment of amphibian habitat selection: Wood frog response to timber harvesting. *Ecoscience*, 17(3), 251-264. doi: 10.2980/17-3-3316
- Boes, M. W. et Benard, M. F. (2013). Carry-over effects in nature: effects of canopy cover and individual pond on size, shape, and locomotor performance of metamorphosing wood frogs. *Copeia*, 2013(4), 717-722. doi: 10.1643/CE-12-091
- Brinson, M. M. et Malvarez, A. I. (2002). Temperate freshwater wetlands: types, status, and threats. *Environmental Conservation*, 29(2), 115-133.
- Chan-McLeod, A. C. A. (2003). Factors affecting the permeability of clearcuts to red-legged frogs. *Journal of Wildlife Management*, 67(4), 663-671.
- Chelgren, N. D., Rosenberg, D. K., Heppell, S. S. et Gitelman, A. I. (2006). Carryover aquatic effects on survival of metamorphic frogs during pond emigration. *Ecological Applications*, 16(1), 250-261.
- Chen, J., Saunders, S. C., Crow, T. R., Naiman, R. J., Brososke, K. D., Mroz, G. D., Brookshire, B. L., Franklin, J. F. (1999). Microclimate in forest ecosystem and landscape ecology variations in

- local climate can be used to monitor and compare the effects of different management regimes. *Bioscience*, 49(4), 288-297.
- Christie, K., Craig, M. D., Stokes, V. L. et Hobbs, R. J. (2012). Home range size and micro-habitat density requirements of *Egernia napoleonis*: implications for restored Jarrah forest of South Western Australia. *Restoration Ecology*, 20(6), 740-746.
- CIFQ. (2015). Industrie forestière en chiffres. Repéré le 11 octobre 2015 à <http://www.cifq.com/fr/industrie/presentation-generale>
- Constible, J. M., Gregory, P. T. et Anholt, B. R. (2001). Patterns of distribution, relative abundance, and microhabitat use of anurans in a boreal landscape influenced by fire and timber harvest. *Ecoscience*, 8(4), 462-470.
- Coulson, T., Benton, T. G., Lundberg, P., Dall, S. R. X., Kendall, B. E. et Gaillard, J. M. (2006). Estimating individual contributions to population growth: evolutionary fitness in ecological time. *Proceedings of the Royal Society B: Biological Sciences*, 273(1586), 547-555.
- Crean, A. J., Monro, K. et Marshall, D. J. (2011). Fitness consequences of larval traits persist across the metamorphic boundary. *Evolution*, 65(11), 3079-3089.
- Cromer, R. B., Lanham, J. D. et Hanlin, H. H. (2002). Herpetofaunal response to gap and skidder-rut wetland creation in a southern bottomland hardwood forest. *Forest Science*, 48(2), 407-413.
- Dahl, T. E. (2000). Status and trends of wetlands in the conterminous United States 1986 to 1997. U.S. Department of the Interior, Fish and Wildlife Service, Washington, D. C. 82 pp.
- Davis, J. C., Castleberry, S. B. et Kilgo, J. C. (2010). Influence of coarse woody debris on herpetofaunal communities in upland pine stands of the southeastern Coastal Plain. *Forest Ecology and Management*, 259(6), 1111-1117.
- DeMaynadier, P. G. et Hunter, M. L. (1995). The relationship between forest management and amphibian ecology: a review of the North American literature. *Environmental Reviews*, 3(3-4), 230-261.
- DeMaynadier, P. G. et Hunter, M. L. (1998). Effects of silvicultural edges on the distribution and abundance of amphibians in Maine. *Conservation Biology*, 12(2), 340-352.
- DeMaynadier, P. G. et Hunter, M. L. (1999). Forest canopy closure and juvenile emigration by pool-breeding amphibians in Maine. *Journal of Wildlife Management*, 63(2), 441-450.
- Dias, G. M. et Marshall, D. J. (2010). Does the relationship between offspring size and performance change across the life-history? *Oikos*, 119(1), 154-162.
- DiMauro, D. et Hunter, J. (2002). Reproduction of amphibians in natural and anthropogenic temporary pools in managed forests. *Forest Science*, 48(2), 397-406.
- Dodd, M. H. I. et Dodd, J. M. (1976). The Biology of metamorphosis. Dans B. Lofts (dir.), *Physiology of the Amphibia* (vol. 3, p. 467-599). Academic Press.
- Duellman, W. E. et Trueb, L. (1994). *Biology of Amphibians*. The Johns Hopkins University Press. Baltimore and London.
- Dunson, W. A., Wyman, R. L. et Corbett, E. S. (1992). A symposium on amphibian declines and habitat acidification. *Journal of Herpetology*, 26(4), 349-352.
- Dupuis, L. A., Smith, J. N. M. et Bunnell, F. (1995). Relation of terrestrial-breeding amphibian abundance to tree-stand age. *Conservation Biology*, 9(3), 645-653.
- Fretwell, S. D. et Lucas, H. (1970). On territorial behavior and other factors influencing habitat distribution in birds. *Acta Biotheoretica*, 19(1), 16-36.
- Fritts, S. R., Grodsky, S. M., Hazel, D. W., Homyack, J. A., Castleberry, S. B. et Moorman, C. E. (2015). Quantifying multi-scale habitat use of woody biomass by southern toads. *Forest Ecology and Management*, 346, 81-88. doi: 10.1016/j.foreco.2015.03.004
- Gibbons, J. W. (2003). Terrestrial habitat: a vital component for herpetofauna of isolated wetlands. *Wetlands*, 23(3), 630-635.

- Gibbs, J. P. (1998). Distribution of woodland amphibians along a forest fragmentation gradient. *Landscape Ecology*, 13(4), 263-268.
- Giménez, K. A. et Torres, G. (2004). Linking life history traits in successive phases of a complex life cycle: effects of larval biomass on early juvenile development in an estuarine crab, *Chasmagnathus granulata*. *Oikos*, 104(3), 570-580.
- Gouv.-Québec. (2014). Bulletin statistique régional : Abitibi-Témiscamingue. Repéré le 26 juin 2017 à <http://www.stat.gouv.qc.ca/statistiques/profils/bulletins/2014/08-Abitibi-Temiscamingue.pdf>
- Guerry, A. D. et Hunter, M. L. (2002). Amphibian distributions in a landscape of forests and agriculture: an examination of landscape composition and configuration. *Conservation Biology*, 16(3), 745-754.
- Haddad, N. M., Brudvig, L. A., Clobert, J., Davies, K. F., Gonzalez, A., Holt, R. D., Lovejoy, T. E., Sexton, J. O., Austin, M. P., Collins, C. D., Cook, W. M., Damschen, E. L., Ewers, R. M., Foster, B. L., Jenkins, C. N., King, A. J., Laurance, W. F., Levey, D. J., Margules, C. R., Melbourne, B. A., Nicholls, A. O., Orrock, J. L., Song, D. X., Townshend, J. R. (2015). Habitat fragmentation and its lasting impact on Earth's ecosystems. *Science Advances*, 1(2).
- Harrison, X. A., Blount, J. D., Inger, R., Norris, D. R. et Bearhop, S. (2011). Carry-over effects as drivers of fitness differences in animals. *Journal of Animal Ecology*, 80(1), 4-18.
- Heath, D. D. et Blouw, D. M. (1998). Are maternal effects in fish adaptive or merely physiological side effects ? Dans T. A. Mousseau, et B. J. Fox, (dir.), *Maternal effects as adaptations* (p. 178-201). Oxford University Press: New York.
- Holland, C. C., Honea, J., Gwin, S. E. et Kentula, M. E. (1995). Wetland degradation and loss in the rapidly urbanizing area of Portland, Oregon. *Wetlands*, 15(4), 336-345. doi: 10.1007/BF03160888
- Homyack, J. A., Aardweg, Z., Gorman, T. A. et Chalcraft, D. R. (2013). Initial effects of woody biomass removal and intercropping of switchgrass (*Panicum virgatum*) on herpetofauna in eastern North Carolina. *Wildlife Society Bulletin*, 37(2), 327-335.
- Houlahan, J. E., Findlay, C. S., Benedikt, R. S., Andrea, H. M. et Sergius, L. K. (2000). Quantitative evidence for global amphibian population declines. *Nature*, 404(6779), 752. doi: 10.1038/35008052
- Howard, J. H., Baldwin, R. F. et Brown, B. L. (2012). Exploratory analysis for complex-life-cycle amphibians: revealing complex forest-reproductive effort relationships using redundancy analysis. *Forest Ecology and Management*, 270, 175-182. doi: 10.1016/j.foreco.2012.01.021
- IUCN. (2008). Species Survival Commission, Conservation International Center for Applied Biodiversity Science. NatureServe, IUCN Global Amphibian Assessment (<http://www.globalamphibians.org>).
- Jacobs, J. M., Spence, J. R. et Langor, D. W. (2007). Influence of boreal forest succession and dead wood qualities on saproxylic beetles. *Agricultural and Forest Entomology*, 9(1), 3-16.
- Johnsson, J. I. et Bohlin, T. (2006). The cost of catching up: increased winter mortality following structural growth compensation in the wild. *Proceedings of the Royal Society B: Biological Sciences*, 273(1591), 1281-1286.
- Kaplan, R. H. et Phillips, P. C. (2006). Ecological and developmental context of natural selection: maternal effects and thermally induced plasticity in the frog *Bombina orientalis*. *Evolution*, 60(1), 142-156.
- Lee, W. -S., Monaghan, P. et Metcalfe, N. B. (2013). Experimental demonstration of the growth rate-lifespan trade-off. *Proceedings of the Royal Society B: Biological Sciences*, 280(1752). doi: 10.1098/rspb.2012.2370
- Lindström, J. (1999). Early development and fitness in birds and mammals. *Trends in Ecology & Evolution*, 14(9), 343-348.
- Marsh, D. M. et Trenham, P. C. (2001). Metapopulation dynamics and amphibian conservation. *Conservation Biology*, 15(1), 40-49.

- Metcalfe, N. B. et Monaghan, P. (2001). Compensation for a bad start: grow now, pay later? *Trends in Ecology & Evolution*, 16(5), 254-260.
- MFFP. (2012). Orniérage dans les coupes de régénération. Repéré le 26 juin 2017 à <https://www.mffp.gouv.qc.ca/publications/enligne/forets/criteres-indicateurs/3/312/312.asp>
- MFFP. (2015). Statistiques forestières. Repéré le 11 octobre 2015 à <https://www.mffp.gouv.qc.ca/forets/connaissances/connaissances-statistiques.jsp>
- Newman, R. A. (1998). Ecological constraints on amphibian metamorphosis: interactions of temperature and larval density with responses to changing food level. *Oecologia*, 115(1), 9-16.
- Norris, D. R. et Marra, P. P. (2007). Seasonal interactions, habitat quality, and population dynamics in migratory birds. *The Condor*, 109(3), 535-547.
- Norris, D. R., Marra, P. P., Kyser, T. K., Sherry, T. W. et Ratcliffe, L. M. (2004). Tropical winter habitat limits reproductive success on the temperate breeding grounds in a migratory bird. *Proceedings of the Royal Society B: Biological Sciences*, 271(1534), 59-64.
- Otto, C. R. V., Kroll, A. J. et McKenny, H. C. (2013). Amphibian response to downed wood retention in managed forests: a prospectus for future biomass harvest in North America. *Forest Ecology and Management*, 304, 275-285. doi: 10.1016/j.foreco.2013.04.023
- Owens, A. K., Moseley, K. R., McCay, T. S., Castleberry, S. B., Kilgo, J. C. et Ford, W. M. (2008). Amphibian and reptile community response to coarse woody debris manipulations in upland loblolly pine (*Pinus taeda*) forests. *Forest Ecology and Management*, 256(12), 2078-2083. doi: 10.1016/j.foreco.2008.07.030
- Pechenik, J. A. (2006). Larval experience and latent effects—metamorphosis is not a new beginning. *Integrative and Comparative Biology*, 46(3), 323-333.
- Pechmann, J. H., Scott, D. E., Gibbons, J. W. et Semlitsch, R. D. (1989). Influence of wetland hydroperiod on diversity and abundance of metamorphosing juvenile amphibians. *Wetlands Ecology and Management*, 1(1), 3-11.
- Petranka, J. W., Eldridge, M. E. et Haley, K. E. (1993). Effects of timber harvesting on Southern *Appalachian salamanders*. *Conservation Biology*, 7(2), 363-370. doi: 10.1046/j.1523-1739.1993.07020363.x
- Petranka, J. W., Brannon, M. P., Hopey, M. E. et Smith, C. K. (1994). Effects of timber harvesting on low elevation populations of southern *Appalachian salamanders*. *Forest Ecology and Management*, 67(1), 135-147. doi: 10.1016/0378-1127(94)90012-4
- Phillips, N. E. (2002). Effects of nutrition-mediated larval condition on juvenile performance in a marine mussel. *Ecology*, 83(9), 2562-2574.
- Pope, S. E., Fahrig, L. et Merriam, H. G. (2000). Landscape complementation and metapopulation effects on leopard frog populations. *Ecology*, 81(9), 2498-2508.
- Range, J. D. (2003). Jurisdiction Under the Clean Water Act: Implications of the SWANCC Decision: A Legal Analysis of the Current Status of Wetlands Protection Commissioned by the Izaak Walton League of America. *Izaak Walton League of America, Gaithersburg, MD*.
- Räsänen, K., Laurila, A., Merilä, J. et Sinervo, B. (2003). Geographic variation in acid stress tolerance of the moor frog, *Rana arvalis*. I. Local adaptation. *Evolution*, 57(2), 352-362.
- Richter, K. O. et Azous, A. L. (1995). Amphibian occurrence and wetland characteristics in the Puget Sound Basin. *Wetlands*, 15(3), 305-312.
- Riffell, S., Verschuyf, J., Miller, D. et Wigley, T. B. (2011). Biofuel harvests, coarse woody debris, and biodiversity—a meta-analysis. *Forest Ecology and Management*, 261(4), 878-887.
- Rittenhouse, T. A. G. et Semlitsch, R. D. (2006). Grasslands as movement barriers for a forest-associated salamander: migration behavior of adult and juvenile salamanders at a distinct habitat edge. *Biological Conservation*, 131(1), 14-22.
- Rittenhouse, T. A. G. et Semlitsch, R. D. (2007). Postbreeding habitat use of wood frogs in a Missouri oak-hickory forest. *Journal of Herpetology*, 41(4), 645-653.

- Rothermel, B. B. (2004). Migratory success of juveniles: a potential constraint on connectivity for pond-breeding amphibians. *Ecological Applications*, 14(5), 1535-1546.
- Rowe, C. L., et Dunson, W. A. (1995). Impacts of hydroperiod on growth and survival of larval amphibians in temporary ponds of central Pennsylvania, USA. *Oecologia*, 102(4), 397-403.
- Rudolf, V. H. W. et Rödel, M.-O. (2007). Phenotypic plasticity and optimal timing of metamorphosis under uncertain time constraints. *Evolutionary Ecology*, 21(1), 121-142.
- Scott, D. E., Casey, E. D., Donovan, M. F. et Lynch, T. K. (2007). Amphibian lipid levels at metamorphosis correlate to post-metamorphic terrestrial survival. *Oecologia*, 153(3), 521-532.
- Semlitsch, R. D. et Bodie, J. R. (1998). Are small, isolated wetlands expendable? *Conservation Biology*, 12(5), 1129-1133.
- Semlitsch, R. D. (1998). Biological delineation of terrestrial buffer zones for pond-breeding salamanders. *Conservation Biology*, 12(5), 1113-1119.
- Semlitsch, R. D. (2000). Principles for management of aquatic-breeding amphibians. *Journal of Wildlife Management*, 64(3), 615-631.
- Semlitsch, R. D., Todd, B. D., Blomquist, S. M., Calhoun, A. J. K., Gibbons, J. W., Gibbs, J. P., Greater, G. J., Harper, E. B., Hocking, D. J., Hunter, M. L., Patrick, D. A., Rittenhouse, T. A. G., Rothermel, B. B. (2009). Effects of timber harvest on amphibian populations: understanding mechanisms from forest experiments. *Bioscience*, 59(10), 853-862. doi: 10.1525/bio.2009.59.10.7
- Sinsch, U. (1990). Migration and orientation in anuran amphibians. *Ethology, Ecology & Evolution*, 2(1), 65-79.
- Skelly, D. K. (2001). Distribution of pond-breeding anurans : an overview of mechanisms. *Israel Journal of Zoology*, 47(4), 313-332.
- Skelly, D. K., Freidenburg, L. K. et Kiesecker, J. M. (2002). Forest canopy and the performance of larval amphibians. *Ecology*, 83(4), 983-992.
- Smith, D. C. (1983). Factors controlling tadpole populations of the chorus frog (*Pseudacris triseriata*) on Isle Royale, Michigan. *Ecology*, 64(3), 501-510.
- Smith, D. C. (1987). Adult recruitment in chorus frogs: effects of size and date at metamorphosis. *Ecology*, 68(2), 344-350.
- Snodgrass, J. W., Komoroski, M. J., Bryan, A. L. et Burger, J. (2000). Relationships among isolated wetland size, hydroperiod, and amphibian species richness: implications for wetland regulations. *Conservation Biology*, 14(2), 414-419.
- Sodhi, N. S., Bickford, D., Diesmos, A. C., Lee, T. M., Koh, L. P., Brook, B. W., Sekercioglu, C. H., Bradshaw, C. J. A. (2008). Measuring the meltdown: drivers of global amphibian extinction and decline. *PloS One*, 3(2), e1636-e1636.
- Stuart, S. N., Chanson, J. S., Cox, N. A., Young, B. E., Rodrigues, A. S. L., Fischman, D. L. et Waller, R. W. (2004). Status and trends of amphibian declines and extinctions worldwide. *Science*, 306(5702), 1783-1786. doi: 10.1126/science.1103538
- Sumner, J. (2006). Higher relatedness within groups due to variable subadult dispersal in a rainforest skink, *Gnypetoscincus queenslandiae*. *Austral Ecology*, 31(4), 441-448.
- Thiffault, E., St-Laurent Samuel, A. et Serra, R. (2009). La récolte de biomasse forestière : saines pratiques et enjeux écologiques dans la forêt boréale canadienne, Ressources naturelles, Canada. Repéré le 11 octobre 2015 à : http://publications.gc.ca/collections/collection_2015/rncan-nrcan/Fo114-16-2015-fra.pdf
- Timm, B. C., McGarigal, K. et Compton, B. W. (2007). Timing of large movement events of pond-breeding amphibians in Western Massachusetts, USA. *Biological Conservation*, 136(3), 442-454.
- Trottier, J. Impact de l'exploitation forestière sur la richesse et l'abondance des amphibiens de la forêt boréale méridionale du Bas-Saint-Laurent. 2006. Thèse de doctorat. Université du Québec à Rimouski (UQAR).

- Ultsch, G. R. (1999). Physiology: coping with the environment dans : *McDiarmid, R.W. and Altig, R., Eds., Tadpoles :The biology of anuran larvae*: The University of Chicago Press, Berkeley.
- Van Allen, B. G., Briggs, V. S., McCoy, M. W. et Vonesh, J. R. (2010). Carry-over effects of the larval environment on post-metamorphic performance in two hylid frogs. *Oecologia*, 164(4), 891-898.
- Waldick, R. (1997). Effects of forestry practices on amphibian populations in eastern North America. *Herpetological Conservation*, 1, 191-205.
- Waldick, R. C., Freedman, B. et Wassersug, R. J. (1999). The consequences for amphibians of the conversion of natural, mixed-species forests to conifer plantations in southern New Brunswick. *Canadian Field-Naturalist*, 113(3), 408-418.
- Walmsley, J. et Godbold, D. (2010). Stump harvesting for bioenergy—a review of the environmental impacts. *Forestry*, 83(1), 17-38.
- Welsh, H. H. et Droege, S. (2001). A case for using plethodontid salamanders for monitoring biodiversity and ecosystem integrity of North American forests. *Conservation Biology*, 15(3), 558-569.
- Werner, E. E., Skelly, D. K., Relyea, R. A. et Yurewicz, K. L. (2007). Amphibian species richness across environmental gradients. *Oikos*, 116(10), 1697-1712.
- White, E. M. (2010). *Woody biomass for bioenergy and biofuels in the United States : a briefing paper*. Portland, Or.: U.S. Dept. of Agriculture, Pacific Northwest Research Station.
- Wilbur, H. M. (1980). Complex life cycles. *Annual review of Ecology and Systematics*, 11, 67-93. doi: 10.1146/annurev.es.11.110180.000435
- Wilbur, H. M. (1987). Regulation of structure in complex systems: experimental temporary pond communities. *Ecology*, 68(5), 1437-1452.
- Wright, A. A. et Wright, A. H. (1949). *Handbook of frogs and toads of the United States and Canada*. Ithaca, N.Y.: Comstock Pub. Co.

CHAPITRE PRINCIPAL

Delayed effects of canopy openness and hydroperiod on development, habitat selection, and survival of a forest amphibian

Labadie, M. ¹, Mazerolle, M. J.², Imbeau, L.³ & Drapeau, P.⁴

^{1&2} Centre d'étude de la forêt, Département des sciences du bois et de la forêt, Université Laval, Québec, QC

³ Centre d'étude de la forêt, Institut de recherche sur les forêts, Université du Québec en Abitibi-Témiscamingue, Rouyn-Noranda, QC

⁴ Centre d'étude de la forêt, Département des sciences biologiques, Université du Québec à Montréal, Montréal, QC.

RÉSUMÉ

La variation des conditions environnementales pendant le développement larvaire peut engendrer des effets à retardement sur des stades ultérieurs d'un individu. L'exploitation forestière (coupes forestières, prélèvement de biomasse) modifie les microhabitats terrestres et aquatiques des amphibiens en perturbant les conditions environnementales et la qualité de l'habitat. Notre projet visait à comprendre l'impact de l'ouverture de la canopée et la variation de l'hydropériode sur le développement larvaire de la grenouille des bois (*Lithobates sylvaticus*) ainsi que l'effet à retardement de ces conditions sur la survie et la sélection d'habitats des juvéniles. Nous avons émis l'hypothèse que le développement des têtards est plus rapide avec une hydropériode réduite en canopée ouverte qu'en canopée fermée, mais que cela occasionne un coût physiologique lors de la métamorphose. Nous avons suivi le développement de 1440 têtards de grenouille des bois dans 24 mésocosmes disposés en 4 blocs complets aléatoires en forêt boréale mixte dans la région de l'Abitibi en faisant varier la canopée (ouverte ou fermée) et l'hydropériode (réduite ou constante). Après leur métamorphose, 275 juvéniles préalablement marqués ont été placés dans 3 enclos expérimentaux contenant chacun une combinaison de deux traits des débris ligneux, à savoir, leur configuration spatiale (agrégée ou homogène) et leur taille (fin ou grossier). À l'aide de modèles de capture-marquage-recapture, nous avons estimé la survie et la sélection d'habitats des juvéniles. Nos résultats montrent un développement plus rapide en canopée ouverte avec une réduction de l'hydropériode, mais que les individus ont une masse et une taille plus petite à la métamorphose que dans les autres traitements. En milieu terrestre, la sélection d'habitats des juvéniles n'était pas influencée ni par l'hydropériode ni par l'ouverture de la canopée subies pendant le stade larvaire. De plus, la survie des juvéniles de grenouille des bois en milieu terrestre ne semble pas varier à court terme dans notre étude. Globalement, notre étude montre l'absence d'un effet de report des conditions pendant le stade larvaire sur la survie et le comportement des juvéniles en milieu terrestre.

Mots-clés : amphibien, développement larvaire, métamorphose, survie, hydropériode, ouverture de canopée, juvénile, sélection d'habitats, enclos terrestre, capture-marquage-recapture.

ABSTRACT

Environmental variation during the development of an individual can have long-term effects at later life stages. Logging (cut and biomass harvesting) modifies the terrestrial and aquatic microhabitats of amphibians by disrupting environmental conditions and habitat quality. Our project aimed at understanding the impact of opening the stand canopy and hydroperiod on the larval development of the wood frog (*Lithobates sylvaticus*) as well as the delayed effect of this impact on the survival and habitat selection of juveniles. We hypothesized that the development of tadpoles is faster with reduced hydroperiod under open canopies than under closed canopies, but that this incurs a physiological cost after metamorphosis. We followed the development of 1440 wood frog tadpoles in 24 mesocosms arranged in four randomized complete block designs varying canopy openness (open or closed) and hydroperiod (reduced or constant). After metamorphosis, we marked 275 metamorphs from the mesocosms and released individuals in terrestrial enclosures varying the spatial configuration (aggregated or homogeneous) and size (fine or coarse) of coarse woody debris. Using capture-mark-recapture models, we estimated the survival and habitat selection of juveniles. Tadpoles developed more quickly under an open canopy and a reduced hydroperiod than in other treatments, but reached a smaller size at metamorphosis. Habitat selection by juveniles was neither influenced by the hydroperiod nor the opening of the forest canopy experienced during the larval stage. In addition, we found no evidence of short-term delayed effects on the survival of juveniles in the terrestrial environment. Overall, our study shows the absence of a delayed effect of larval conditions on the survival and behavior of juveniles in terrestrial environments.

Keywords : amphibian, larval development, metamorphosis, survival, hydroperiod, canopy opening, juvenile, habitat selection, terrestrial enclosure, capture-mark-recapture.

Introduction

Initial stress in the environment during a particular seasonal or biological stage has many delayed consequences on the life cycle of various animal species (Harrison et al., 2011; O'Connor et al., 2014), for taxa ranging from invertebrates (Giménez and Torres, 2004; Dias and Marshall, 2010; Crean et al., 2011) to fish (Johnsson and Bohlin, 2006; O'Connor et al., 2011; Lee et al., 2013), mammals (Perryman et al., 2002; Cook et al., 2004) and birds (Norris et al., 2004; Norris, 2005; Norris and Marra, 2007). These delayed effects may occur during a specific period (hibernation, migration) rather than at distinct stages (development, reproduction, metamorphosis) (Beckerman et al., 2002; Norris, 2005; Benard and McCauley, 2008; Harrison et al., 2011; O'Connor and Cooke, 2015). Environmental factors encountered during amphibian larval development such as temperature (Kaplan and Phillips, 2006) and canopy opening (Werner et al., 2007; Boes and Benard, 2013) affect post-metamorphosis individuals at different levels during their life cycle (Räsänen et al., 2003; Kaplan and Phillips, 2006). These different conditions during development can have consequences on the behaviour, the phenotype, and the performance of individuals (Pahkala et al., 2001; Altwegg, 2002; Altwegg et al., 2003; Van Allen et al., 2010; Boes and Benard, 2013; Earl and Semlitsch, 2013). Some individuals may use compensatory growth when experiencing unfavourable conditions during their development. However, this type of mechanism will often influence the adult life stage in the medium or long term. For example, Altwegg et al. (2003) observed that larger juveniles (*Rana lessonae* and *R. esculenta*) have a greater chance of survival in the terrestrial environment. Similarly, a study by Boes and Benard (2013) showed that canopy opening affects the locomotor performance of wood frog juveniles in a terrestrial environment.

Recently, global demand for biofuels has increased exponentially (White, 2010; Riffell et al., 2011). To meet this demand, forest companies have begun harvesting woody biomass in forests and can harvest up to 50% of the forest biomass on the ground (Thiffault et al., 2009). Moreover, agencies are starting to regulate biomass harvesting (Abbas et al., 2011). The importance of woody debris for many amphibians in terrestrial environments is largely documented (Jaeger, 1980; Hassinger and Payne, 1989; Whiles and Grubaugh, 1996; Butts and McComb, 2000; Fritts et al., 2015). Indeed, Craig et al. (2012) and other studies (Loeb, 1999; Lohr et al., 2002) showed the strong relationship between the diversity of forest wildlife communities and coarse woody debris. The composition of forest fauna appears to be influenced by the type and amount of woody debris (Grove, 2002; Vanderwel et al., 2006; Vanderwel et al., 2009; Vanderwel et al., 2010). However, the impacts of woody biomass removal on amphibians have been little studied. Homyack et al. (2013) did not observe an effect on amphibian populations in the short term. Conversely, Owens et al. (2008), Davis et al. (2010) and Otto et al. (2013) showed negative impacts of biomass removal on some amphibian traits such as mass and survival. Removing biomass greatly reduces moist shelters required to maintain favorable conditions for amphibians, but also hinders movements, and activities entailing changes in amphibian behavior (Walmsley and Godbold, 2010; Fritts et al., 2015).

Amphibians with a biphasic cycle such as the wood frog (*Lithobates sylvaticus*) use aquatic environments for breeding and larval development (Wright and Wright, 1949). Juveniles and adults use

the terrestrial environment for protection, foraging, hibernation, and aestivation (Baldwin et al., 2006; Howard et al., 2012). In addition, amphibians are habitat-dependent at several spatial scales, for example for their migration and dispersal (DeMaynadier and Hunter, 1999; Gamble et al., 2008; Baldwin, 2009; Greenwald et al., 2009; Howard et al., 2012). In some environments, the wood frog is very abundant and this species is intimately related to the forest soil. Thus, all physiological stresses in the structure of the aquatic and terrestrial habitat caused by disturbances, such as logging, can have negative long-term effects on later stages of the life cycle (Beckerman et al., 2002; Phillips, 2002; Giménez and Torres, 2004; Chelgren et al., 2006).

Forest canopy loss modifies amphibian development at both temporal (growth during life stage) and biological levels with a change in size of metamorphosed individuals (Boes and Benard, 2013). The increase in temperature in open-canopy ponds (Skelly et al., 2002), which are often created during harvesting operations, may favor many physiological processes in amphibians such as larval development (Dodd and Dodd, 1976; Newman, 1998; Ultsch, 1999). Hydroperiod, the length of time a pond holds water, is a biotic factor that plays on larval development of amphibians (Smith, 1983, 1987; Rowe and Dunson, 1995; Wilbur, 1987; Pechmann *et al.*, 1989; Snodgrass *et al.*, 2000; Baldwin *et al.*, 2006). In addition, variation in hydroperiod may have a positive (water temperature increase) or negative (resource competition) impact on larval development (Wilbur, 1987; Howard et al., 2012). The environmental conditions such as the availability of resources, the temperature, and water oxygenation experienced by tadpoles likely affect the size, physiology, and size ratio of amphibian limbs after metamorphosis (Boes and Benard, 2013).

Environmental variation during the development of an individual can have long-term effects at later life stages (Pechenik, 2006). These variations may alter various aspects of an animal's phenotype including its size, shape, and physiology (Pechenik, 2006). In the long term, the carry-over effect can affect ecological and evolutionary mechanisms, whereas it can influence fitness and performance in the short term (Lindström, 1999; Benard and McCauley, 2008). Chelgren *et al.* (2006) suggest that body size and date of metamorphosis are factors sensitive to aquatic stress. These factors can influence post-metamorphic movements and survival strategies during the terrestrial stage of frogs (Chelgren *et al.*, 2006). Berven (1990) suggests that increasing size to metamorphosis improves the survival of wood frogs. However, there is some uncertainty regarding the extent of carry-over effects in time. Indeed, Bernardo (1996), Heath and Blouw (1998), and Beck and Congdon (1999) argue that carry-over effects are greater in the short term than in the long run. Similarly, Beck and Congdon (1999) report a strong correlation between southern toad metamorphosis (*Anaxyrus terrestris*) and growth after ten days, but this effect disappears after two months.

Earl and Semlitsch (2013) documented (1) the delayed effects of aquatic conditions on larval development (amount of litter in the mesocosm and its position in the habitat) on the survival and habitat selection of three amphibian species (wood frogs, (*Anaxyrus americanus*), southern leopard frogs (*Lithobates sphenoccephalus*)) in the environment (2) the effect of individual density and habitat type

(disturbed or not) on the survival of individuals during the larval phase. Our study differs from Earl and Semlitsch (2013) in measuring the impact of opening canopy and hydroperiod on larval development in aquatic environments. For the terrestrial phase, our project aimed to quantify the delayed effect of these two parameters on the performance of juveniles in a disturbed environment. In this paper, we evaluated tadpole development by quantifying the probability of reaching metamorphosis, developmental rate, as well as size and mass at metamorphosis in relation to the variation in canopy opening and the hydroperiod. Using the individuals that had reached metamorphosis, we monitored juveniles during a capture-mark-recapture study in experimental enclosures where we manipulated the spatial distribution and size of woody debris. We then estimated the carry-over effects on apparent survival and habitat selection of individuals. To our knowledge, this study is the first to measure: (1) the delayed effect of the opening of the canopy and hydroperiod during larval development on the survival and habitat selection of juvenile frogs; (2) the effect of the distribution and size of woody debris in habitat selection and survival of juvenile frogs in experimental enclosures. We hypothesized that 1) the probability of tadpoles to reach metamorphosis is greater in the open canopy and reduced hydroperiod than in the closed canopy with full hydroperiod, 2) the development of wood frog tadpoles accelerates under an open canopy and a reduced hydroperiod, but the faster development (number of days to metamorphose into juvenile) during the larval stage entails a lower size and mass at metamorphosis, 3) this lower size incurs costs in terms of juvenile survival in terrestrial environments, and 4) juveniles favor coarse woody debris arranged in clusters as they represent superior refuges in terms of humidity, but selection among juveniles varies with environmental conditions experienced during the larval stage.

Methods

Study Area

We conducted this study at the Lac Duparquet teaching and research forest, in the Abitibi region, northwestern Québec (Canada) (48°30'N, 79°22'O). The study area is located in mixed boreal forest mainly consisting of balsam fir (*Abies balsamea* Mill.), white birch (*Betula papyrifera* Marsh.), quaking aspen (*Populus tremuloides* Michx.), black spruce (*Picea mariana* Mill.), white spruce (*Picea glauca* (Moench) Voss.), and jack pine (*Pinus banksiana* Lamb.) (Leduc, 2013) (Fig. 1).

Experimental design

Our project consisted of two components, an experiment in aquatic mesocosms followed by another experiment in terrestrial enclosures. We describe each component in turn below and follow the same sequence throughout the paper.

Experimental design of aquatic experiment

We selected six sites (blocks) to establish mesocosms based on forest cover, taking into account accessibility (distance from the road) to fill mesocosms with water (pH = 6.8) while also maintaining a minimal distance (15 – 45 m) from the road to avoid anthropic disturbances. We distributed twenty-four plastic cattle watering tanks measuring 89 x 137 x 51 cm (maximum capacity of 416.4 L) in six randomized complete blocks, with four mesocosms in each block. Each block consisted of a site where mesocosms were between 5 to 10 m apart, and we maintained a minimum of 1 km between blocks (Fig. 1). In a given block, each mesocosm contained one of four treatments based on two fully crossed factors, namely canopy opening and hydroperiod. We considered two levels of canopy opening, either open (forest cover < 25%) or closed (forest cover > 75%) (Skelly et al., 2002; Boes and Benard, 2013). The opening of the canopy on three sites had been caused by former logging and on the other three sites had natural openings. We also considered two levels for hydroperiod at either full (constant water level maintained at 50 cm) or half (50 cm reduced to a constant water level maintained at 25 cm one week into the experiment). Thus, in a given block, each mesocosm received one of the following treatments: (1) open canopy with full hydroperiod, (2) closed canopy with full hydroperiod, (3) open canopy with half hydroperiod, and (4) closed canopy with half hydroperiod.

In each experimental mesocosm, we added 229 g of a mixture of deciduous leaf litter found at our study sites (Popescu and Hunter, 2011). All mesocosms were at first filled to their maximum water level (50 cm) with filtered water collected from Hébécourt Lake between 8 June and 10 June 2016. Each pool was protected with a mosquito screening from colonization of other

organisms (Popescu and Hunter, 2011). We introduced eight small cellulose sponges (8 x 4 cm) in each mesocosm to avoid the drowning of recently metamorphosed individuals.

Between 14 May 2016 and 16 May 2016, we collected twenty-seven wood frog egg masses on nineteen sites of the study area. We transferred the egg masses to three round plastic swimming pools of 1.2 m in diameter and 19 cm high with nine egg masses per pool. Each pool was maintained at the research station at Lac Duparquet. We supplemented the tadpoles that emerged from the egg masses with tadpoles from two additional sites. Tadpoles were fed with organic lettuce ad libitum until they reached Gosner stages 26 to 29 (Gosner, 1960). We randomly selected 60 tadpoles of different stages and transferred them in each of the 24 experimental mesocosms. In total, 1440 wood frog tadpoles were used in the experiment.

On 14 June 2016, tadpoles were introduced inside each mesocosm. A week later (21 June 2016), we reduced the water level to 25 cm in two pools of each block – one in closed canopy and one in open canopy in order to implement the half-hydroperiod treatment. Thus, the density of tadpoles per liter was 0.14 tadpoles for mesocosms with the full hydroperiod and 0.28 tadpoles per liter in the half hydroperiod treatment. These densities are consistent with those observed in natural environments and in other studies (Skelly et al., 2002; Harper and Semlitsch, 2007) (i.e density of 0.02 to 0.38 tadpoles per liter; Skelly et al., 2002). After 21 June 2016, the water level of each mesocosm was maintained constant at its respective level (50 cm or 25 cm) until the metamorphosis of all individuals or the end of the experiment.

Mesocosms were visited initially at 2 to 3 day intervals. As soon as we detected the first metamorphosed individual (presence of a tail stub, Gosner stage 45), we monitored mesocosms daily. Each metamorphosed juvenile (Gosner stage 45) was weighed to nearest 0.01 g using a microbalance (© Ohaus SP202 Scout Pro, New Jersey, USA) and measured to snout-vent length (SVL) to the nearest 0.1 mm using a Vernier caliper. In each mesocosm, we installed maximum and minimum thermometers (© Sper Scientific LTD, Arizona, USA) (Barry et al., 2008). Throughout the experiment, we collected temperature data three times a week (every 2 to 3 days) until the end of the study. The aquatic experiment was terminated four months after its initiation, on 3 September 2016.

Experimental design of terrestrial experiment

Building terrestrial enclosures

We established a terrestrial enclosure at each of three sites characterized by an open canopy large enough to accommodate the enclosures. These enclosures were inspired by experiments of Popescu and Hunter (2011), Cline and Hunter (2014) and Altwegg (2002). Specifically, we constructed an experimental enclosure at each of three sites from silt fences (Fig 2). Silt fences

were supported by wooden stakes to form a 6 m long x 2 m wide x 60 cm high arm (10 cm buried in the soil). Each enclosure consisted of four arms arranged perpendicular to each other in a cross pattern, where each arm of the cross was connected to a central experimental chamber (2 m x 2 m). This central chamber was constructed from 1.90 cm thick plywood panel. Each panel had a rectangular door cut from it. The door measured 80 cm wide x 50 cm high and started at the ground level. The four doors of the central chamber were hinged for easy closing with a deadbolt and opening to allow amphibians to move around the experimental enclosure.

All vegetation on the ground was removed from the enclosures during their construction. In each enclosure arm, we spread a 2 cm layer of deciduous leaf litter collected from the study sites. The ground in the central experimental chamber was barren to create a hostile environment and motivate frogs to move into one of the four arms at the start of experiment. Inside each arm of the enclosures, we installed three pairs of pitfall traps along the walls, two of which were placed near the entrance of the arm, two at the mid-point of the arm (3 m), and two pitfall traps at the end corners of the arm (Fig 2A). These traps were built from sections of ABS pipes measuring 5 cm in diameter and 25 cm in height. We fitted an ABS plug of the same diameter as the pipes to seal the bottom of pitfall traps. Traps were buried flush with the ground. The bottom of a trap was filled with c.a 2 cm of water to avoid desiccation of the captured individuals and we inserted a piece of cellulose sponge as a float. We used ABS plugs to close the top of the pitfall traps between trapping occasions.

Each arm of the cross received one of four treatments based on a combination of two fully crossed factors that varied the size and the spatial configuration of woody debris (Fig 2B). Specifically, building on Riffell et al. (2011), we distinguished two types of woody debris size classes: coarse woody debris (15 cm in diameter) and fine woody debris (5 cm in diameter). All woody debris were recently cut quaking aspen (*Populus tremuloides*). We chose quaking aspen because of its wide distribution in our study area. We considered two levels of spatial configuration of woody debris, namely, homogeneous (woody debris spaced at regular intervals) and aggregated (woody debris arranged in a single pile). Each pile of woody debris (coarse or fine) was made up of two levels to maintain a certain amount of humidity. All piles of coarse and fine woody debris in the experimental enclosures had an identical contact surface and distance to the walls of the enclosure and to each other. Thus, the four treatments were: (1) homogeneous distribution of coarse woody debris over the entire surface, (2) homogeneous distribution of fine woody debris over the entire surface, (3) aggregate distribution of a single large pile of coarse woody debris, and (4) aggregate distribution of fine woody debris into a single large heap. In order to monitor trespassing by potential predators of the juveniles frogs in the enclosures, we installed four motion-detection cameras (Bushnell Trophy Cam Agressor No Glow, © Bushnell Outdoor Products, Kansas, USA) per enclosure on each external wall of the central chamber looking into each arm of the cross (Fig 2C). The cameras were triggered by the movements (day and night)

and they took a series of three pictures. If after a period of ten seconds, the movement was still detected a new series of three pictures was taken.

Capture-mark-recapture (CMR)

Wood frog density in previous terrestrial enclosure studies ranges from 1 to 10 individuals per square meter (Harper and Semlitsch, 2007; Patrick et al., 2008). In the present study, we selected a density of 2.08 individuals/m² (100 individuals/48 m²). As a result, each enclosure was planned to receive 100 wood frog juveniles (25 of each aquatic treatment from the mesocosm experiment above). Immediately after measuring mass and SVL, we marked 275 newly metamorphosed juveniles from the aquatic experiment using VI Alpha tags (1.2 x 2.7 mm tags © Northwest Marine Technology Incorporation, Shaw Island, USA) (Castellano et al., 2009; Courtois et al., 2013; Courtois et al., 2017). Each tag was coded with one black letter and two black numbers on a fluorescent orange background. We inserted these tags in the ventral side of individuals using an injector needle, previously sterilized with 90% ethanol. In order to facilitate marking, individuals were immersed (1- 2 min) in a solution of 0.2 g/L of MS-222, until loss of swimming movement (Castellano et al., 2009). To facilitate tag insertion, we gently lifted the skin of the belly of the frog with forceps. After marking, the individuals were awakened in a bath of fresh water. In total, the handling time was less than 5 minutes with a very fast awakening of amphibians anesthetized after the procedure (\pm 8 min). After tagging, all juveniles were kept under observation in 1.22 m diameter pools containing mixed litter and woody debris between 3 and 10 days to monitor activity and tag retention.

We introduced the marked juveniles in the experimental enclosures in groups of 25 individuals from each aquatic treatment (example: 25 juveniles from the open canopy and half hydroperiod). Thanks to the unique codes of the VI Alpha tags, we knew the life history of all marked juveniles (mesocosm number, canopy and hydroperiod treatments, weight, size, date of metamorphosis) and their date of introduction into the enclosure. At the end of the holding period, we introduced juvenile frogs two hours after sunset (Cline and Hunter, 2016) in the center chamber of the enclosure in groups of 25. During 5 days following release, the chamber doors remained opened and the pitfall traps were closed to allow individuals to move freely in the entire enclosure. On the evening of the fifth day, we closed the four doors of the central chamber to prevent individuals from moving between treatments and we opened the pitfall traps in each arm. We monitored the pitfalls traps at 12 h intervals (at 8:00 am and 8:00 pm) during three consecutive days. Each individual captured in pitfall traps in the arms of each enclosure was identified based on its tag and its mesocosm treatment. Identification of the captured individuals was done using the VI Alpha tags (unique ID) which was fluorescent with the UV lamp (© Northwest Marine Technology Incorporation, Shaw Island, USA). We immediately released the individual at the center of the arm in which it was captured. At the end of the three days of trapping, the traps were closed and the doors of the central chamber were reopened for a five-day interval. We repeated this process

for all terrestrial enclosures up to five capture occasions from the time we had the four groups of 25 individuals of each aquatic treatment ($25 * 4 = 100$ individuals). New individuals could only be introduced into enclosures at the start of the 5-day period when individuals move (5 days or 4 days before opening traps). Due to the differences in dates of metamorphosis relative to canopy opening, we had two distinct subgroups depending on the aquatic treatments (Appendix 1). A group of 124 individuals consisted of tagged individuals from mesocosms under open canopy and another group of 100 individuals originated from mesocosms under closed canopy.

The first group of juveniles was introduced on 14 July 2016 and the last on 17 August 2016. We originally planned to use 300 juveniles in the three experimental enclosure (25 individuals x 4 treatments x 3 enclosures = 300). However, due to the extended larval period of individuals in certain aquatic treatments and the low number of juveniles recaptured in some enclosures, we ultimately introduced only 275 individuals (N = 75 in enclosure 1, and N = 100 in each of enclosures 2 and 3). From the date of introduction of the juveniles in the enclosures, the terrestrial field experiment spanned across 7 weeks, whereas the mesocosm experiment continued for more than 11 weeks. Among the 275 individuals released in the terrestrial enclosures, there were 122 captures in our three enclosures during our study. Thus, we caught 77 juveniles once and 8 juveniles more than once.

Statistical Analyses

Data from the aquatic and terrestrial components were analyzed separately. All analyses were conducted in R 3.3.2 (R Development Core Team, 2016). For the aquatic phase, we compared the fixed effects of canopy, hydroperiod, and their interaction on the probability of reaching metamorphosis for tadpoles using a generalized mixed model (binomial distribution) with a random effect of the mesocosm (Gelman and Hill, 2007; Zuur et al., 2009). We could not include a block (site) random effect and a random effect of the mesocosm nested in the site due to convergence issues for this model. Similarly, we quantified the main effects and interaction of the factors on size and mass of the wood frogs at metamorphosis with linear mixed effects models using a normal distribution with a random effect of the mesocosm (Pinheiro and Bates, 2000). We could not include a block random effect due to a convergence problem. We used a linear mixed effects model to test the effect of treatments on the number of days to reach metamorphosis with random effects of site and mesocosm nested within block. Using a linear mixed effects model with the same fixed and random effect structures as above, we also compared maximum and minimum water temperatures across treatments. Generalized linear mixed models were conducted with the lme4 package (Bates et al., 2015), whereas linear mixed models were implemented in the nlme package (Pinheiro et al., 2016). Residual diagnostics of models did not suggest departures from model assumptions.

For the terrestrial component, we estimated the probability of juvenile wood frogs to select a habitat among the four combinations of woody debris size and spatial configuration with a multinomial logistic regression implemented in the VGAM package (Agresti, 2002; Yee, 2017). Here, we used the treatment where each individual was captured as its choice in the experimental enclosure. Some individuals were caught in different treatments between two capture sessions. In the analyses, we used only the first capture. We examined habitat selection of juvenile wood frogs among the four combinations of woody debris size and spatial configuration (coarse homogeneous, coarse aggregated, fine homogeneous, fine aggregated). We considered nine candidate models (Table 1) to test our hypotheses on carry-over effects of environmental conditions during larval development, mass at metamorphosis, as well as precipitation and air temperature 24 hours before the capture of individuals (Rain.previous24h and Temp.previous24h). Due to model complexity, we did not include random effects in multinomial logistic regressions. We compared the different models using the Akaike information criterion for small sample size (AIC_c) and derived measures (Burnham and Anderson, 2003). We used multimodel inference to quantify the impact of larval conditions on the habitat selection of juvenile wood frogs released in the experimental enclosures implemented in the AICcmodavg package (Mazerolle, 2017).

We estimated the apparent survival of the individuals in all the enclosures combined with a Cormack-Jolly-Seber (CJS) model implemented in Program MARK with the RMark package (Cormack, 1964; Jolly, 1965; Seber, 1965; White and Burnham, 1999; Williams et al., 2002; Laake, 2013). Specifically, we pooled captures during the three consecutive days into a single capture occasion. Among the 275 individuals released in the terrestrial enclosures, we only considered individuals exposed to 3 to 5 capture sessions (i.e., 23 and 40 days) in the analyses. In order to have a minimum of 3 capture session periods in the analysis. Juveniles in mesocosms with the open canopy treatments emerged early in the season, whereas juveniles from the closed canopy treatments emerged later in the season. Thus, we separated capture histories into two distinct groups based on the canopy treatment: 124 individuals from mesocosms under open canopy and 100 individuals from mesocosms under closed canopy. Our goal here was to estimate the impact of larval conditions on the apparent survival of juveniles in the experimental enclosures, relating to canopy closure and hydroperiod. However, we could not test formally the canopy treatment due to the different dates of introduction of individuals into enclosures (see above). In both groups, we compared the following seven models: (1) ϕ (Hydroperiod) p (Hydroperiod); (2) ϕ (.) p (Hydroperiod); (3) ϕ (Hydroperiod) p (.); (4) ϕ (.) p (.); (5) ϕ (Mass) p (.); (6) ϕ (.) p (Mass) and (7) ϕ (Mass) p (Mass), where Hydroperiod corresponds to the hydroperiod treatment in either open canopy (124 individuals) or closed canopy (100 individuals) during larval development and (.) denotes a parameter consisting only of the intercept. Indeed, we standardized the body mass before including it in the analyses. We used the Fletcher c-hat to assess model fit (Fletcher, 2012). We implemented a model selection and multimodel approach similar to the one described in the previous section to quantify the effect of hydroperiod and

canopy closure on the apparent survival and recapture probabilities of juvenile frogs in the experimental enclosures (Burnham and Anderson, 2003; Mazerolle, 2006).

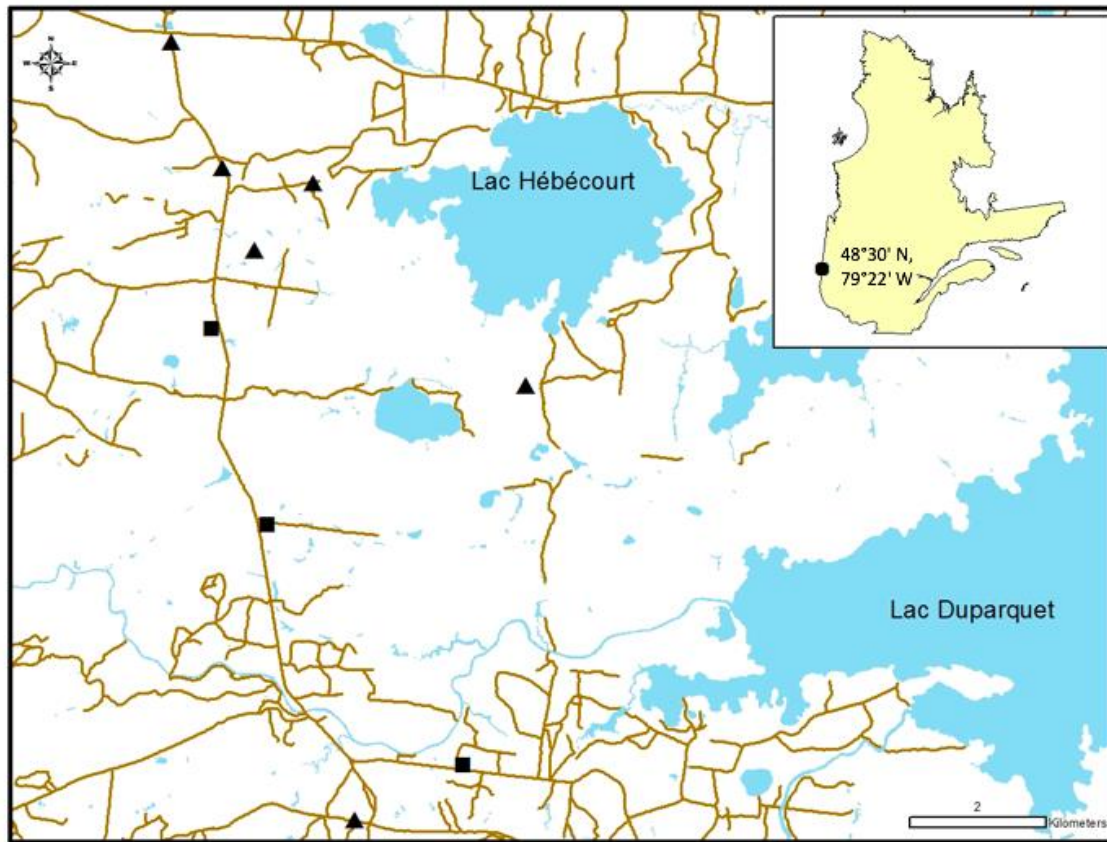


Figure 1 : Location of mesocosms and terrestrial enclosures in the Lac Duparquet teaching and research forest (FERLD) in Abitibi-Témiscamingue (Québec, Canada). Each black triangle corresponds to the block of 4 mesocosms, the black square corresponding to an experimental terrestrial enclosure.

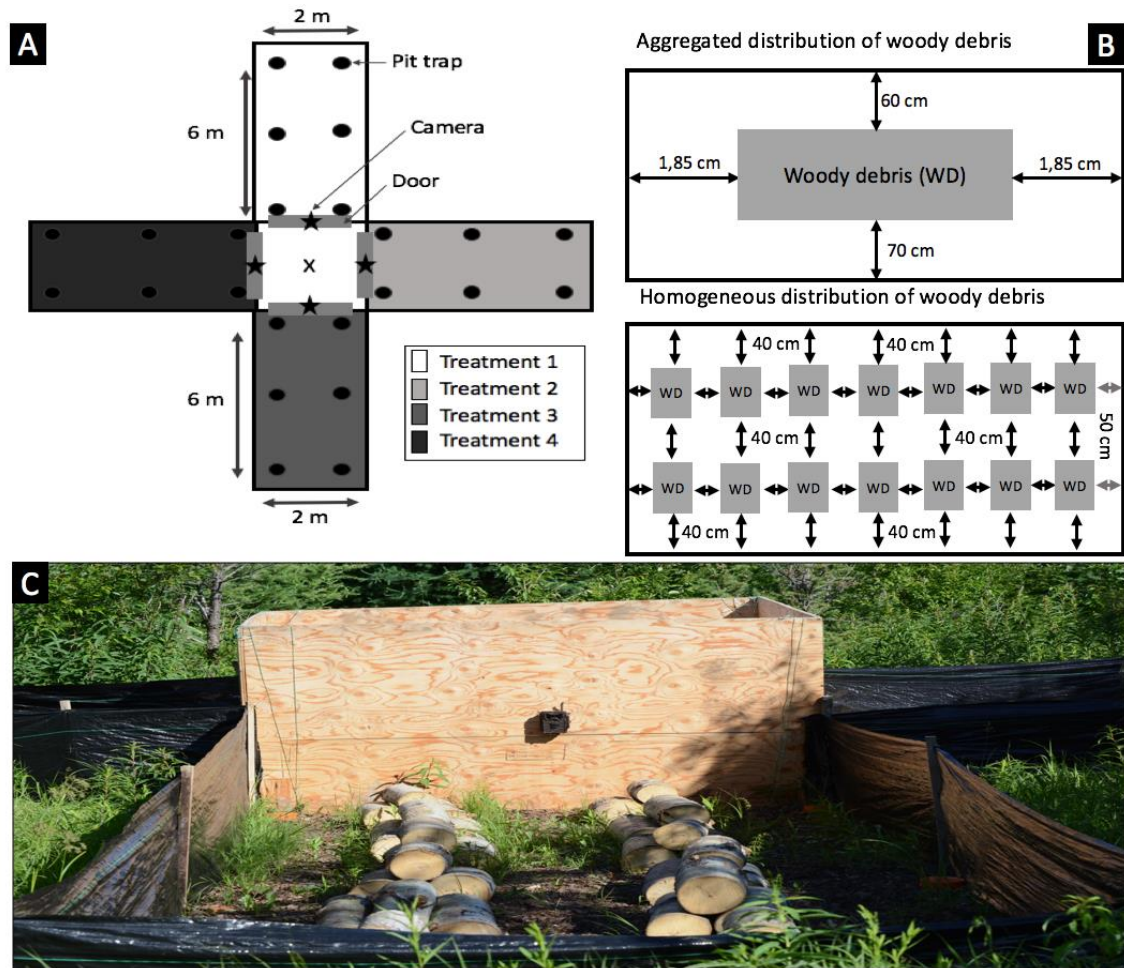


Figure 2: Diagram of (A) the terrestrial enclosures, (B) the distribution of woody debris in an arm of the experimental enclosure, (C) snapshot inside of an arm (homogeneous coarse woody debris treatment) with the camera trap fixed to the external wall of the central chamber. Note the horizontal line under the camera which delimits the door leading to the central chamber.

Results

Aquatic experiment

For the aquatic component of the study, we used the data collected on the 1440 tadpoles introduced in the mesocosms at the beginning of the experiment. At the end of our experiment on 1 September 2016, 587 tadpoles had survived in mesocosms, 525 of which had metamorphosed (Gosner stage 45), and 62 remained at Gosner stages 32-43. The remaining 62 individuals in the mesocosms were released into ponds from which we had collected egg masses.

The effect of canopy opening on the probability of wood frog tadpoles of reaching metamorphosis depended on the hydroperiod (canopy opening x hydroperiod interaction, Fig. 3a). Specifically, the probability of attaining metamorphosis in mesocosms was higher under an open canopy with reduced hydroperiod than with the full hydroperiod ($\beta_{\text{CanopyOpen:HydroHalf}}$: 0.038, 95% CI: [0.018, 2.575]).

Newly metamorphosed juveniles under an open canopy had a smaller snout-vent length in the reduced hydroperiod than in the full hydroperiod (canopy opening x hydroperiod interaction; $\beta_{\text{CanopyOpen:HydroHalf}}$: -0.188, 95% CI: [-0.345, -0.037]). Despite interactive effects of canopy closure and hydroperiod, individuals in mesocosms under closed canopies were larger than those under open canopies (Fig. 3b). The mass of newly metamorphosed wood frog juveniles followed the same pattern as for snout-vent length (canopy opening x hydroperiod interaction, $\beta_{\text{CanopyOpen:HydroHalf}}$: -0.159, 95% CI: [-0.287, -0.035], Fig. 3c). Tadpoles in mesocosms under a closed canopy tended to have greater mass than under an open canopy, although differences were not as marked as for snout-vent length (Fig. 3c). For individuals that eventually metamorphosed in the mesocosms, the number of days to reach metamorphosis varied between open and closed canopies (Fig. 3d). Indeed, there was an average difference of 15.5 days for juveniles to reach metamorphosis between closed and open canopy ($\beta_{\text{CanopyOpen:estimate}}$: -15.49, 95% CI: [-19.48, -11.51]), but no variation occurred between reduced and full hydroperiods (Fig. 3d).

The maximum water temperature in mesocosms under open canopy was warmer in full hydroperiod than in reduced hydroperiod (canopy opening x hydroperiod interaction; $\beta_{\text{CanopyOpen:HydroHalf}}$: -2.85, 95% CI: [-4.47, -1.28], Appendix 2a). Despite this interaction, mesocosms under an open canopy were substantially warmer than those under closed canopy (Appendix 2a). For a given hydroperiod, minimum water temperature in mesocosms was warmer under open canopy than closed canopy ($\beta_{\text{CanopyOpen}}$: 2.47, 95% CI: [0.89, 4.08], Appendix 2a) and warmer in reduced than full hydroperiod ($\beta_{\text{HydroHalf}}$: 2.82, 95% CI: [0.88, 4.69]; Appendix 2b). However, there was no evidence of a canopy opening x hydroperiod interaction on the minimum water temperature ($\beta_{\text{CanopyOpen:HydroHalf}}$: -0.63, 95% CI: [-2.48, 1.16]).

Terrestrial experiment

For the terrestrial experiment, we combined capture-recapture data of 274 tagged juveniles of the three experimental enclosures. In total, we recaptured 47 individuals once and 29 juveniles have been recaptured more than twice.

Habitat selection

Among the 275 individuals released in the terrestrial enclosures, 122 of these were recaptured at least once during the terrestrial component of our study. Juveniles preferred treatment with coarse wood homogeneous (N = 41), followed by fine wood homogeneous (N = 29), coarse wood aggregated (N = 27) and fine wood aggregated (N = 25). The multinomial logistic regressions compared the probability of selecting one of three woody debris treatments (fine wood homogeneous, fine wood aggregated, coarse wood aggregated) relative to the coarse wood homogeneous reference level. Among the models considered, the most parsimonious consisted of the explanatory variables canopy cover, hydroperiod, and amount of rain in the previous 24 hours ($\omega_i = 0.32$). This model was followed closely by the model with the same structure but that excluded precipitation ($\omega_i = 0.25$) (Table 1). Multimodel inference indicated that juveniles exposed to the reduced hydroperiod during larval development had the same probability to select the homogeneous coarse wood as all other woody debris treatments (circle, Fig. 4a). In the same way, juveniles that had developed as tadpoles under a full hydroperiod were indistinctively found in the homogeneously distributed coarse wood (CWH) and in the other three woody debris treatments (triangle, Fig. 4a). Similarly, individuals having developed as tadpoles in mesocosms under either closed or open canopies did not favor the coarse wood homogeneous treatment compared to the other treatments (Fig. 4b).

Survival of wood frog juvenile in terrestrial habitat

For the 124 juveniles that developed as tadpoles in mesocosms under an open canopy, model fit was adequate with no overdispersion (Fletcher : $\hat{C} = 1$). We found no evidence of apparent survival varying with hydroperiod (Effect size: $\phi_{full} - \phi_{half} = -0.03$, 95% CI: [-0.18, 0.13]). Indeed, the null model $\phi(.)p(.)$ was the most parsimonious among the models considered ($\omega_i = 0.26$; Table 2). Similarly, the models for the 100 individuals having developed in mesocosms under a closed canopy did not suggest lack-of-fit (model fit with low overdispersion; Fletcher : $\hat{C} = 1.20$). Again, the top-ranked model was the null model $\phi(.)p(.)$ ($\omega_i = 0.27$; Table 2). Thus, apparent survival of juveniles from the closed canopy mesocosms did not vary with hydroperiod (Effect size: $\phi_{full} - \phi_{half} = -0.05$, 95% CI: [-0.37, 0.28]). The apparent survival and recapture rate for 100 and 124 juveniles by hydroperiod with their 95% confidence interval are presented in Appendix 3.

Camera traps

There were 35 detections of American woodcocks (*Scolopax minor*) and three detections of black bears (*Ursus americanus*) in one terrestrial enclosure. In another enclosure, there were two detections of American woodcocks, three of moose (*Alces alces*), and two of black bears. Cameras in the last enclosure only detected an American woodcock and a moose.

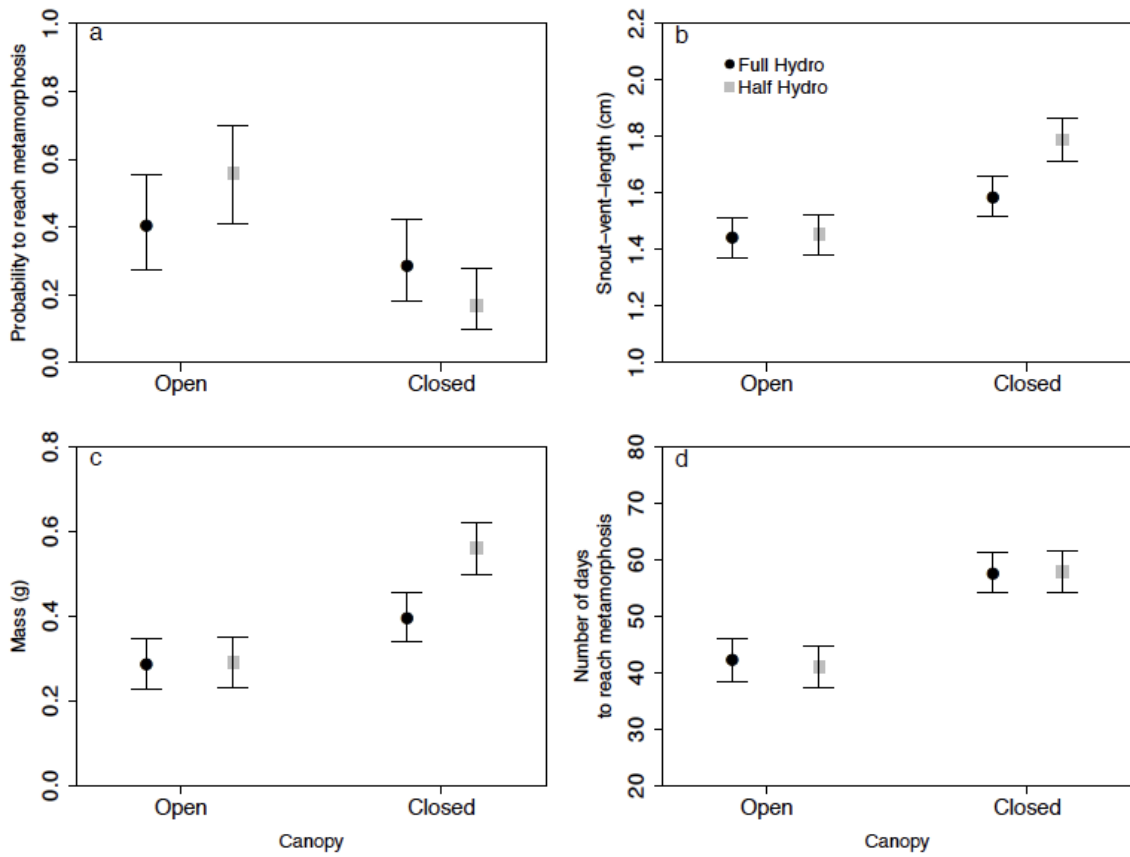


Figure 3: Effects of canopy and hydroperiod on tadpole probability of reaching metamorphosis (a), snout-vent length (b), mass at metamorphosis (c), and number of days to reach metamorphosis (d) in aquatic mesocosms at Lake Duparquet Teaching and Research Forest, northwestern Quebec, in 2016. Error bars denote 95% confidence intervals.

TABLE 1 : Model selection based on AIC_c for the multinomial logistic regressions to quantify the effect of conditions during larval development and weather on habitat selection of juvenile wood frogs in 2016 in terrestrial enclosures in the Lake Duparquet Teaching and Research Forest, northwestern Quebec. Frogs could select among four habitats varying woody debris size and their spatial configuration (coarse homogeneous, coarse aggregated, fine homogeneous, fine aggregated). Explanatory variables included canopy cover (open or closed), hydroperiod (full or half), amount of rain 24 h before capture (Rain.previous24h), mass at metamorphosis, and air temperature 24 h before capture (Temp.previous24h).

Model	K	AIC_c	ΔAIC_c	Akaike weight (ω_i)
Canopy + Hydroperiod + Rain.previous24h	12	236.87	0.00	0.32
Canopy + Hydroperiod	9	237.33	0.47	0.25
Rain.previous24h	6	237.94	1.07	0.19
Null model (intercept only)	3	239.35	2.48	0.09
Canopy + Hydroperiod + Temp.previous24h	12	239.70	2.84	0.08
Temp.previous24h	6	240.69	3.83	0.05
Rain.previous24h + Mass	9	244.33	7.46	0.01
Mass	6	244.80	7.93	0.01
Temp.previous24h + Mass	9	246.16	9.29	0.00

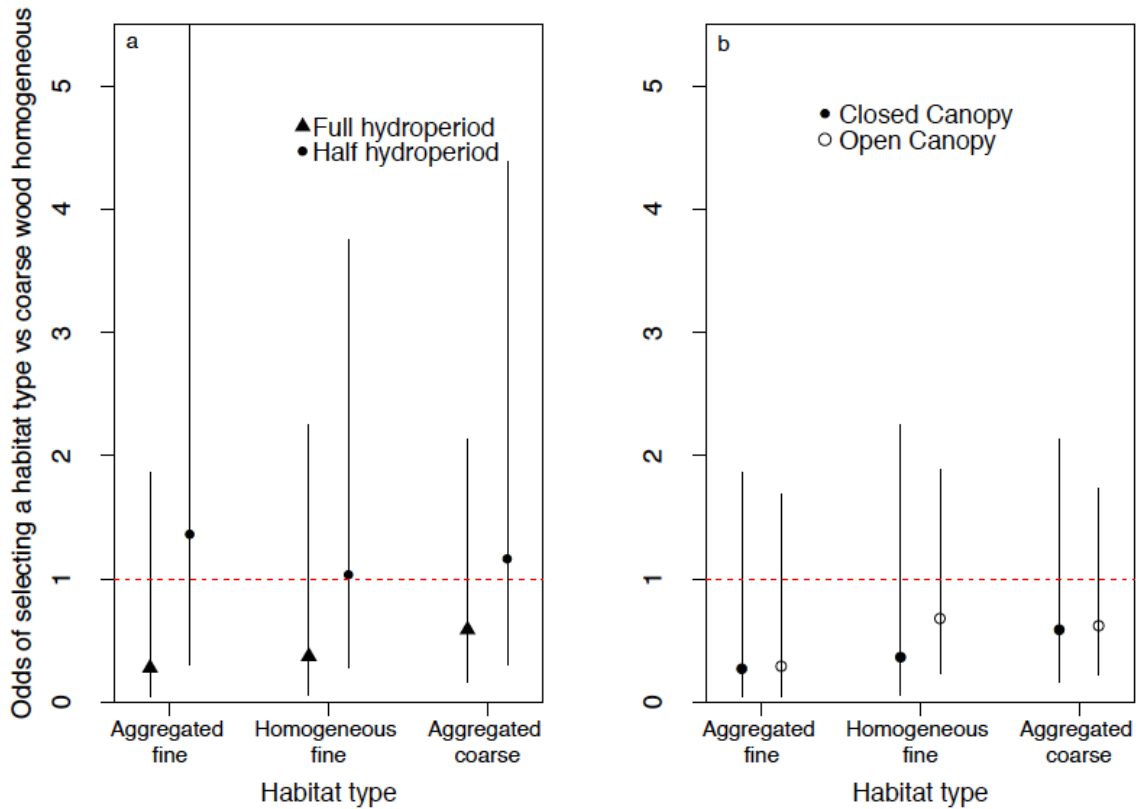


Figure 4 : Model-averaged odds of habitat selection of wood frog juveniles for three habitats compared to the coarse wood homogeneous (CWH) reference level: fine wood aggregated (FWA), fine wood homogeneous, (FWH), and coarse wood aggregated (CWA). (a) Odds of selecting a given habitat over CWH for juvenile wood frogs originating from mesocosms under closed canopy. (b) Odds of selecting a given habitat over CWH for juvenile wood frogs originating from mesocosms with full hydroperiod. Error bars denote 95% unconditional confidence intervals. Confidence intervals intersecting the horizontal dashed line indicate that both habitats are as likely to be selected, whereas confidence intervals below 1 denote a preference for the reference habitat (CWH) relative to the other habitat in the comparison.

TABLE 2: Model selection based on QAIC_c of Cormack-Jolly-Seber models on data from 100 or 124 juveniles wood frogs having developed under a closed or open canopy with either full or half hydroperiod to estimate apparent survival (ϕ) or recapture probability (p). Models are adjusted for overdispersion ($\hat{c}= 1.20$ or $\hat{c}= 1$, for closed and open canopy, respectively).

Canopy cover during larval development	Model	K	QAIC_c	ΔQAIC_c	Akaike weight (ω_i)
Open canopy	ϕ (.) p (.)	3	226.59	0.00	0.26
Open canopy	ϕ (Hydroperiod) p (.)	4	227.10	0.52	0.20
Open canopy	ϕ (.) p (Mass)	4	227.26	0.67	0.19
Open canopy	ϕ (.) p (Hydroperiod)	4	228.15	1.56	0.12
Open canopy	ϕ (Mass) p (.)	4	228.62	2.03	0.09
Open canopy	ϕ (Hydroperiod) p (Hydroperiod)	5	229.20	2.62	0.07
Open canopy	ϕ (Mass) p (Mass)	5	229.23	2.64	0.07
Closed canopy	ϕ (.) p (.)	3	105.31	0.00	0.27
Closed canopy	ϕ (Hydroperiod) p (.)	4	105.80	0.49	0.21
Closed canopy	ϕ (.) p (Mass)	4	106.39	1.08	0.16
Closed canopy	ϕ (.) p (Hydroperiod)	4	106.51	1.20	0.15
Closed canopy	ϕ (Mass) p (.)	4	107.36	2.05	0.10
Closed canopy	ϕ (Hydroperiod) p (Hydroperiod)	5	107.94	2.63	0.07
Closed canopy	ϕ (Mass) p (Mass)	5	108.40	3.09	0.06

Discussion

Our results highlight the importance and the effect of the opening of the canopy and the variation of the hydroperiod on the larval development and the fitness of the wood frog. However, our study did not observe a delayed effect of the aquatic phase on the short-term survival and habitat selection of juveniles in terrestrial environments.

Aquatic experiment

The opening of the canopy and hydroperiod are known to be among the factors that most strongly influence the larval development of amphibians. Indeed, hydroperiod (the period during which a pond holds water) influence the composition of species in wetlands (Calhoun et al., 2014). The increase in temperature in open-canopy ponds (Skelly et al., 2002) may favor many physiological processes in amphibians (Dodd and Dodd, 1976; Ultsch, 1999), such as the rate of growth that will modify larval development (Newman, 1998). In addition, the variation of hydroperiod may have a positive (water temperature increase) or negative impact (competition for resources) (Wilbur, 1987; Rowe and Dunson, 1995; Wellborn et al., 1996; Skelly et al., 2002; Howard et al., 2012) on the development of larval stages. Forest cover influences the quality of resources and their availability (Skelly et al., 2002; Halverson et al., 2003; Skelly and Golon, 2003; Schiesari, 2006; Hocking and Semlitsch, 2008; Williams et al., 2008), while playing an important role on amphibian performance (survival, development, and growth) (Werner and Glennemeier, 1999; Skelly et al., 2002; Schiesari, 2006; Thurgate and Pechmann, 2007). The environmental conditions (availability of resources, temperature, water oxygenation, predation) experienced by tadpoles are likely to affect the size, physiology, and length ratio of amphibian limbs after their metamorphosis (Boes and Benard, 2013). Boes and Bernard (2013) were interested in the impact of canopy variation on the locomotor performance of wood frogs. The authors demonstrated that individuals growing in open canopies tended to jump shorter distances than individuals from a closed canopy (Boes and Benard, 2013).

In the first part of our study, we hypothesized that the rate of development of wood frog tadpoles is highest under an open canopy and a reduced hydroperiod, but that this faster development leads to a lower size at metamorphosis. To test this hypothesis, we quantified the effects of canopy cover and hydroperiod on the probability of tadpoles to reach metamorphosis, the time to reach metamorphosis, and the body size at metamorphosis. Our results revealed interactive effects of canopy opening and hydroperiod on the probability of wood frog tadpoles to reach metamorphosis. Tadpoles were more likely to reach metamorphosis in open canopies with a reduced hydroperiod in mesocosms, than in other treatments. Conversely, tadpoles in mesocosms under a closed canopy and a reduced hydroperiod had the lowest probability of reaching metamorphosis. This variation in the probability of reaching metamorphosis between mesocosms can be explained by environmental conditions. Aquatic environments under closed

canopies have lower luminosity, colder water temperature, and lower dissolved oxygen environment (Werner and Glennemeier, 1999; Schiesari, 2006). Noland and Ultsch (1981) showed that a hypoxic environment could lead to a high mortality of the tadpoles and modify their behaviour.

Among the parameters that may have affected the metamorphosis directly or indirectly, the temperature must also be mentioned. Indeed, numerous studies have emphasized the effect of temperature on a multitude of amphibian physiological traits such as growth rate and development (Dodd and Dodd, 1976; Harkey and Semlitsch, 1988; Gatten et al., 1992; Rome et al., 1992; Newman, 1998; Ultsch, 1999; Skelly et al., 2002). In our study, the average minimum temperature was colder in the closed canopy with a full hydroperiod than in the open canopy with a reduced hydroperiod. This result is due to the difference in sunlight in the aquatic environment and the amount of water in the mesocosms. Moreover, in an open environment, water temperature will be more affected by the climatic conditions (wind, sun) than in a closed environment where the trees offer some protection. For the average maximum temperature in mesocosms, we expected the same trend with a higher temperature in mesocosms under an open canopy and reduced hydroperiod. However, we observed the opposite pattern with a higher temperature inside mesocosms with a full hydroperiod. We can not explain this surprising result observed in our study. Indeed, we expected the difference in temperature between the mesocosms to be due to the variation in luminosity (canopy cover) and in the volume of water.

Another factor affecting the probability of tadpoles to reach metamorphosis is intraspecific competition. Indeed, in mesocosms with a reduced hydroperiod, the density of tadpoles per cubic meter was higher than in the full hydroperiod. Thus, despite the absence of predation, competition for resources and space was high between tadpoles. This phenomenon, amplified in some of our mesocosms due to the interaction of canopy opening and hydroperiod, may explain the decrease in survival and mass at metamorphosis of individuals (Brockelman, 1969; Scott, 1990; Goater, 1994; Parris and Ross, 2000). Indeed, wood frogs tend to exploit transient habitats (temporary water pools) for reproduction and larval development (Wilbur, 1980). These types of habitats have their advantages (absence of fish predators), but also certain constraints (reduced hydroperiod). Thus, conditions related to canopy, hydroperiod, food, and temperature may result in a halving of the growth rate of an amphibian species or a delay in development (Skelly et al., 2002).

We expected that opening the canopy and reducing the hydroperiod would decrease the time required for tadpoles to reach metamorphosis. Only part of this hypothesis has been confirmed. Our results show a significant effect of the canopy but not of the hydroperiod on the number of days to reach the metamorphosis. Indeed, the number of days spent in the aquatic environment before reaching metamorphosis was shorter in the open canopy (± 40 days) than under a closed canopy (± 60 days). However, a mesocosm with an open canopy and a reduced hydroperiod will stimulate the development and abundance of primary producers including periphyton and green algae (Hill et al., 1995; Rowe and Dunson, 1995; Werner and Glennemeier, 1999; Skelly et al.,

2002; Werner et al., 2007; Van Buskirk, 2011; Howard et al., 2012). This high availability of resources and the absence of predation will favour herbivorous tadpoles, including wood frog tadpoles (Wilbur, 1980), increasing their growth rate and shortening their time to metamorphosis into juveniles (Rowland et al., 2017). This rapid development can allow the wood frog to breed in ponds that dry quickly like the vernal pools (Baldwin et al., 2006). Conversely, individuals in mesocosms under closed canopy were able to compensate for adverse growth conditions in aquatic environments by extending the larval period which enabled them to reach a larger size at metamorphosis (Capellan and Nicieza, 2007; Dahl et al., 2012; Orizaola et al., 2013; Murillo-Rincón et al., 2017). Such a strategy can be dangerous in vernal pools if the tadpole stage is not complete before pool drying (Snodgrass et al., 2000; Baldwin et al., 2006).

Finally, we also predicted that a faster development in the larval stage of wood frogs would result in lower mass and size at metamorphosis of juveniles. Our results support this prediction because metamorphosed juveniles from an open environment and a reduced hydroperiod have smaller size and mass than individuals from a closed canopy with reduced hydroperiod. The scientific literature has already largely documented the fact that living conditions during larval development lead to changes at different levels of the physiology of tadpoles (Pandian and Marian, 1985; Werner, 1986; Pahkala et al., 2001; Kaplan and Phillips, 2006). Rapid development of wood frog tadpoles results in a physiological cost of reduced size and mass of metamorphosed juveniles (Wilbur, 1977; Pandian and Marian, 1985; Murray, 1990; Skelly et al., 2002).

Terrestrial experiment

Habitat selection of juveniles in experimental enclosures

In the second part of our study, we evaluated the impact of woody debris size and spatial distribution in experimental enclosures on the habitat selection and survival of wood frog juveniles according to their environmental conditions during larval development (canopy opening and hydroperiod). The importance of woody debris in terrestrial environments, particularly coarse woody debris for many invertebrate and vertebrate taxa is broadly documented (Jaeger, 1980; Harmon et al., 1986; Hassinger and Payne, 1989; Whiles and Grubaugh, 1996; Butts and McComb, 2000; Jonsson et al., 2001; Sumner, 2006; Jacobs et al., 2007; Christie et al., 2012; Fauteux et al., 2012; Christie et al., 2013; Fritts et al., 2015). We hypothesised that individuals favor coarse aggregated woody debris relative to other combinations of size and arrangement (homogeneous coarse debris, aggregated or homogeneous fine debris). However, we observed that juveniles did not favor any of the four woody debris treatments (aggregated or homogeneous coarse debris, aggregated or homogeneous fine debris). Yet, many studies have shown that amphibians tend to select habitats with coarse woody debris (Constible et al., 2001; Harper et al., 2015), particularly when they are aggregated (Craig et al., 2012). These habitats provide an adequate environment for them by maintaining a certain moisture to protect themselves from

desiccation and assisting in their thermal regulation (Whiles and Grubaugh, 1996; Jørgensen, 1997; Blomquist and Hunter, 2010). Craig et al. (2014) suggest that the density of coarse woody debris can have a significant effect on the presence of reptiles, frogs and mammals if combined with other factors such as canopy cover. Hence, juveniles were much more vulnerable to high soil temperatures and low humidity than in areas under closed canopy (Chan-McLeod, 2003; Timm et al., 2007), despite the presence of woody debris and leaf litter.

Competition for higher quality habitats might also have occurred between juveniles, resulting in weak individuals selecting lower quality habitats. Habitat quality for amphibians can vary with weather conditions, namely precipitation. Environmental conditions also alter the behavior, physiological stress, and activity of individuals (Chan-McLeod, 2003; Vasconcelos and Calhoun, 2004; Timm et al., 2007; Patrick et al., 2008). But, our results show that juvenile mass at metamorphosis and precipitation in the habitat do not play a role in habitat selection of juveniles in the terrestrial environment. Harper et al. (2015) showed that wood frogs seem to select habitats at several scales (from the coarse to the finest) depending on different resource associations. However, we must modulate our results in the enclosures because of a large number of our juveniles who escaped. Given the number of individuals introduced into each enclosure and the number of traps, we had fewer recapture than expected. This low number of captures (76 juveniles captures only once out of 275 individuals introduced over a minimum period of 24 days) could be due to escapes from the enclosures, despite their height (± 65 cm). We assume that during periods of rain wood frog juveniles adhered to the walls of the silt fences and could climb over the fences. This hypothesis seems most probable since at the end of our study we searched all the pens in search of introduced individuals. We found only 5 individuals and no luminescent tag that could remain at the death of other individuals. However, we considered this emigration permanent.

Survival of juveniles in experimental enclosures

The survival of juveniles in terrestrial environments depends on many factors such as larval development, conditions in the terrestrial environment, or the physiological condition of the metamorphosed juvenile (Berven, 1990; Rittenhouse et al., 2009; Semlitsch et al., 2009; Harper et al., 2015). For example, juvenile growth and survival will be negatively impacted in a disturbed (open canopy) terrestrial environment (Rittenhouse et al., 2008; Semlitsch et al., 2009). In addition, wood frog juveniles have a high probability of mortality in the first six weeks following metamorphosis (Harper et al., 2015). Earl and Semlitsch (2013) tested the impact of forest practices with varying canopy cover and downed wood (control, partial harvest forest, clearcut with downed wood removed or clearcut with downed wood retained) and litter (no litter, grass or leaf litter) in aquatic mesocosms. They tested delayed effect of these treatments on the survival of juvenile of three anuran species (wood frogs, American toads, southern leopard frogs) in terrestrial environments (density of juvenile and disturbed habitat). The terrestrial environment

(forest treatment) was important to predict survival in American toads and southern leopard frogs but not on the wood frog (Earl and Semlitsch, 2013). Green and Bailey (2015) have studied the influences of natal-pond on the survival of wood frog juveniles and their breeding probabilities according to dispersal and age. Their results showed that conductivity in ponds negatively affect the survival of juveniles (Green and Bailey, 2015). Our study differs from that of Boes and Bernard (2013), Earls and Semlitsch (2013) and Green and Bailey (2015), as we tested the delayed effect of environmental conditions under larval development (canopy opening, hydroperiod) on survival and habitat selection (variation size and pattern of woody debris) of wood frog juveniles in terrestrial enclosures. We hypothesized juvenile survival depends on the life history of the larval stage. However, our results did not show any difference in survival between juveniles in terrestrial enclosures during the experiment. We found no evidence that variations in canopy opening and hydroperiod during the larval period influence the survival of wood frog juveniles. We can not rule out the hypothesis of the influence of the canopy on the survival of juveniles in the terrestrial environment since we separated individuals from these two environments (open or closed canopy). However, according to Appendix 4, we might think that opening of the canopy during the larval phase (closed or open) does not impact the survival of the juveniles (survival and 95% CI do not overlap). Moreover, the escape of many individuals from the pens implies that emigration cannot be distinguished from mortality in the survival analyses. Similarly, Earl and Semlitsch (2013) did not find evidence of a carryover effect (control vs forest harvesting) on the survival of juveniles of wood frog in the terrestrial environment. This result could be explained by the strong phenotypic plasticity of wood frog juveniles (Denver, 1997; Buskirk, 2009; Van Buskirk, 2011; Schmidt et al., 2012). Green and Bailey (2015) established a variation in the post metamorphic survival of wood frog juveniles depending on abiotic conditions during larval development. However, post metamorphic survival did not appear to be related to larval density in aquatic environments or to individuals' size at metamorphosis (Green and Bailey, 2015).

Our results evaluate the short-term survival of wood frog juveniles up to $\approx 3 - 7$ weeks after metamorphosis. At the end of the growing season, wood frogs will have to prepare for hibernation. To survive through winter, individuals must have a good physiological condition. Thus, one might expect individuals with larger mass and size to survive better in the long term in the terrestrial environment (Boes and Benard, 2013). Several studies report that the survival of juveniles ranids (wood frog, water frogs (*Rana lessonae* and *R. esculenta*)) is optimal when two conditions are met, namely, a large size at metamorphosis and a short time to reach metamorphosis (Berven, 1990; Altwegg, 2002; Altwegg and Reyer, 2003; Indermaur et al., 2010). Our results did not reveal any effect of the mass at metamorphosis on the survival of juveniles in terrestrial environments. Our study terminated in early September. We can only speculate that the smallest individuals would potentially be able to catch up in size before hibernation. Altwegg and Reyer (2003) suggest that an earlier metamorphosis of water frogs due to rapid larval development leads to higher growth and survival of juveniles in the terrestrial environment. In addition, Altwegg's (2003) study suggested that over a longer period of time larval conditions

would not affect survival of juveniles, but could reduce their growth. Compensatory growth behaviour can have long-term implications for individuals of many taxa (Morgan and Metcalfe, 2001; Yearsley et al., 2004; Johnsson and Bohlin, 2006; Dmitriew, 2011; Lee et al., 2013; O'Connor and Cooke, 2015). Clearly, additional investigation is required to assess the persistence of carryover effects into later life stages.

Carry-over effects

We expected that the habitat selection by wood frog juveniles would differ depending on the environmental conditions experienced during the larval development. Our results do not support this idea. Juveniles that developed as tadpoles under reduced or full hydroperiods select similar types of woody debris. Juveniles having developed as tadpoles under either closed or open canopies did not favor the coarse wood homogeneous treatment or the other treatments (aggregate fine wood, aggregate coarse wood, and homogeneous fine wood).

These absence of differences in behaviour could not be explained by a difference in size and mass at metamorphosis of individuals from reduced and full hydroperiods. Our results refute the study by Chelgren et al. (2006) who suggested that size at metamorphosis and date of metamorphosis may influence the behaviour and movements of individuals during the terrestrial phase. Previously, we showed the effect of the interaction of canopy opening and hydroperiod on the size and mass of the metamorphosed juveniles. However, our results do not show any delayed effects of mass on habitat selection or survival of juveniles in terrestrial environments. Nonetheless, the survival analysis revealed that the null model had the most support, suggesting that the smallest individuals did not have the lowest survival, contrary to our prediction. However, Altwegg and Reyer (2003) showed that individuals with a larger size at metamorphosis were more likely to survive in the terrestrial environment and that late-metamorphosed individuals had a lower survival rate and grew more slowly.

Predation and camera traps

The cameras that we placed in the three experimental enclosures allowed us to quantify the presence of possible predators of wood frog juveniles. In a particular enclosure, we observed a large number of woodcocks, which are not known in the literature for feeding on the juvenile wood frog (Society Ruffed Grouse, 2017). However, we can not rule out the possibility that some individuals have been predated by woodcock. It is difficult for us to quantify predation by snakes (*Thamnophis sirtalis*) in our pens during the duration of our experiment. This species is known to feed on many amphibian species (Arnold and Wassersug, 1978; Desroches and Rodrigue, 2004). However, the infrared cameras could not detect poikilothermic organisms.

Conclusion

Global amphibian populations are threatened by multiple direct or indirect agents such as habitat loss, fragmentation, and disease (Petranka et al., 1993; Petranka et al., 1994; DeMaynadier and Hunter, 1995; Gibbs, 1998; Semlitsch, 2000; Trottier, 2006; Vié et al., 2009). In this context, it is essential to acquire knowledge about the long-term consequences of the delayed effects of a disturbance on the life cycle of amphibians. Unlike protected habitat, a habitat disturbed by logging can modify larval development by generating a more rapid metamorphosis of juveniles. Our study does not show delayed effects of hydroperiod or canopy effect on the habitat selection and survival of wood frog juveniles in terrestrial environments. However, further research on the longer term is needed to investigate this pattern. The next step would involve evaluating carry-over effects of the larval stage on longer-term juvenile condition, such as survival during the first winter and on the possibility of long-term effects on the age at first breeding as well as the breeding success. In Abitibi, as in other parts of North America, where the forest industry is a stakeholder, it is essential for amphibian conservation to consider forest management by taking into account delayed effects.

Acknowledgements

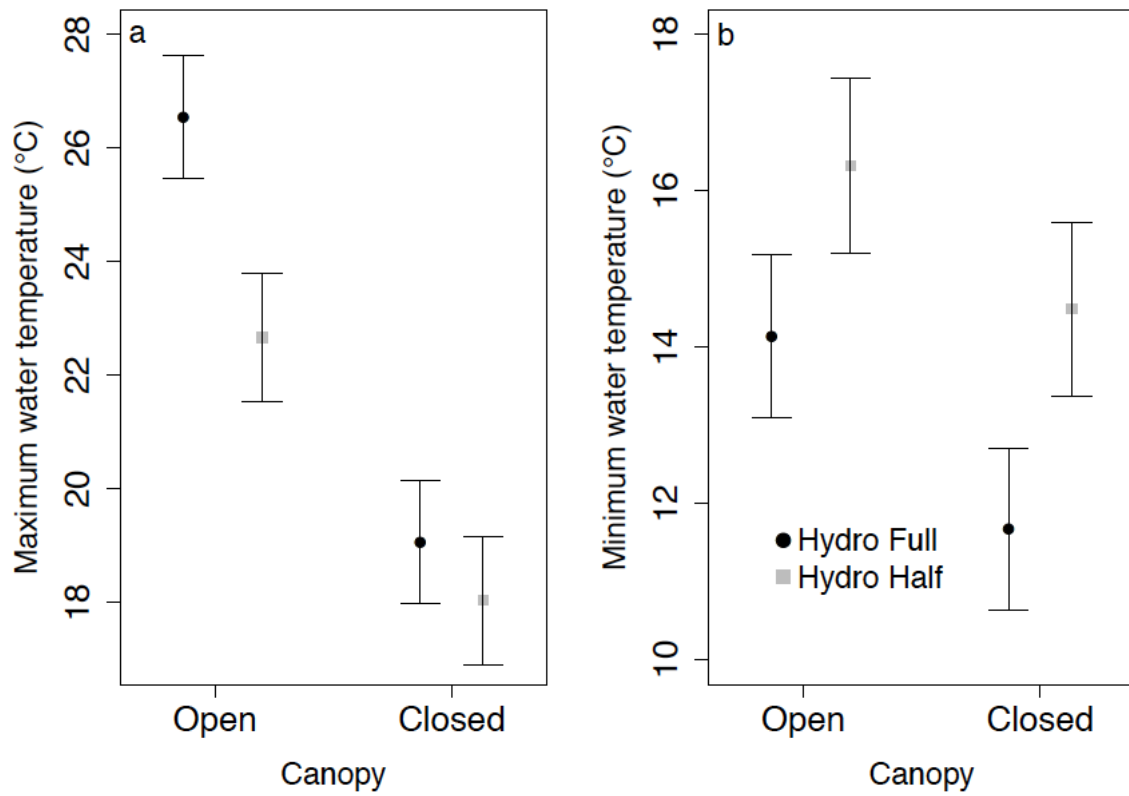
This project was funded by a Collaborative Research and Development grant from the Natural Sciences and Engineering Research Council of Canada (NSERC). S. Robert, A. Leblet, and thanks also to all the people that provided logistic support in the field and at UQAT (Université du Québec en Abitibi-Témiscamingue). This study was approved by the Laval University animal care committee 2016-026.

Appendix

Appendix 1: Date of introduction of juveniles and their numbers in each enclosure of our study.

Date of introduction of juveniles into enclosures	Number of juveniles introduced			Number of days after introduction and the first capture
	Enclosure	Enclosure	Enclosure	
	N°1	N°2	N°3	
14 July 2016	25	0	0	5 days
	25			
19 July 2016	0	25	0	5 days
		25		
22 July 2016	0	0	25	5 days
27 July 2016	0	0	25	1 days
5 August 2016	0	25	0	4 days
08 August 2016	0	25	0	2 days
09 August 2016	0	0	25	4 days
17 August 2016	25	0	25	4 days

Appendix 2: Average water temperature in mesocosms during the aquatic experiment with a 95% confidence interval. (a) Maximum temperature (°C) across treatments. (b) Minimum temperature (°C) across treatments.



Appendix 3 : Apparent survival (ϕ) or recapture probability (p) with multimodel inference based on QAICc of Cormack-Jolly-Seber models on data from 124 or 100 juveniles wood frogs having developed under a closed or open canopy with either full or half hydroperiod.

Canopy cover and hydroperiod	Phi (ϕ)	p
Open canopy – Full hydroperiod	0.35 [0.25, 0.44]	0.77 [0.58, 0.97]
Open canopy – Half hydroperiod	0.32 [0.21, 0.43]	0.76 [0.5, 1.01]
Closed canopy – Full hydroperiod	0.33 [0.08, 0.58]	0.59 [0.13, 1.05]
Closed canopy – Half hydroperiod	0.28 [0.09, 0.47]	0.55 [0.11, 1]

References

- Abbas, D., D. Current, M. Phillips, R. Rossman, H. Hoganson, and K. N. Brooks. 2011. Guidelines for harvesting forest biomass for energy: a synthesis of environmental considerations. *Biomass and Bioenergy* **35**:4538-4546.
- Agresti, A. 2002. Categorical data analysis. 2nd edition. Wiley-Interscience, New York.
- Altwegg, R. 2002. Trait-mediated indirect effects and complex life-cycles in two European frogs. *Evolutionary Ecology Research* **4**:519-536.
- Altwegg, R. 2003. Multistage density dependence in an amphibian. *Oecologia* **136**: 46-50.
- Altwegg, R., and H.-U. Reyer. 2003. Patterns of natural selection on size at metamorphosis in water frogs. *Evolution* **57**:872-882.
- Arnold, S. J., and R. J. Wassersug. 1978. Differential predation on metamorphic anurans by garter snakes (*Thamnophis*): social behavior as a possible defense. *Ecology* **59**: 1014-1022.
- Baldwin, R. F., A. J. K. Calhoun, and P. G. DeMaynadier. 2006. Conservation planning for amphibian species with complex habitat requirements: a case study using movements and habitat selection of the Wood Frog (*Rana sylvatica*). *Journal of Herpetology* **40**:442-453.
- Barry, D. S., T. K. Pauley, and J. C. Maerz. 2008. Amphibian use of man-made pools on clearcuts in the Allegheny Mountains of West Virginia, USA. *Applied Herpetology* **5**:121-128.
- Bates, D., M. Maechler, B. Bolker, and S. Walker. 2015. lme4: Linear mixed-effects models using Eigen and S4. R package version 1.1-7, [En ligne] : <http://cran.r-project.org/package=lme4>>.
- Beck, C. W., and J. D. Congdon. 1999. Effects of individual variation in age and size at metamorphosis on growth and survivorship of southern toad (*Bufo terrestris*) metamorphs. *Canadian Journal of Zoology* **77**:944-951.
- Beckerman, A., T. G. Benton, E. Ranta, V. Kaitala, and P. Lundberg. 2002. Population dynamic consequences of delayed life-history effects. *Trends in Ecology & Evolution* **17**:263-269.
- Benard, M. F., and S. J. McCauley. 2008. Integrating across life-history stages: consequences of natal habitat effects on dispersal. *American Naturalist* **171**:553-567.
- Bernardo, J. 1996. Maternal effects in animal ecology. *American Zoologist* **36**:83-105.
- Berven, K. A. 1990. Factors affecting population fluctuations in larval and adult stages of the wood frog (*Rana sylvatica*). *Ecology* **71**:1599-1608.
- Blomquist, S. M., and M. L. Hunter. 2010. A multi-scale assessment of amphibian habitat selection: wood frog response to timber harvesting. *Ecoscience* **17**:251-264.
- Boes, M. W., and M. F. Benard. 2013. Carry-over effects in nature: effects of canopy cover and individual pond on size, shape, and locomotor performance of metamorphosing wood frogs. *Copeia* **2013**:717-722.
- Brockelman, W. Y. 1969. An analysis of density effects and predation in *Bufo americanus* tadpoles. *Ecology* **50**:632-644.
- Burnham, K. P., and D. R. Anderson. 2003. Model selection and multimodel inference: a practical information-theoretic approach. Springer Science & Business Media: New York.
- Buskirk, J. V. 2009. Natural variation in morphology of larval amphibians: Phenotypic plasticity in nature? *Ecological Monographs* **79**:681-705.
- Butts, S. R., and W. C. McComb. 2000. Associations of forest-floor vertebrates with coarse woody debris in managed forests of Western Oregon. *Journal of Wildlife Management* **64**:95-104.
- Calhoun, A. J. K., J. Arrigoni, R. P. Brooks, M. L. Hunter, and S. C. Richter. 2014. Creating successful vernal pools: a literature review and advice for practitioners. *Wetlands* **34**:1027-1038.
- Capellan, E., and A. G. Nicieza. 2007. Non-equivalence of growth arrest induced by predation risk or food limitation: context-dependent compensatory growth in anuran tadpoles. *Journal of Animal Ecology* **76**:1026-1035.
- Castellano, S., V. Zanollo, V. Marconi, and G. Berto. 2009. The mechanisms of sexual selection in a lek-breeding anuran, *Hyla intermedia*. *Animal Behaviour* **77**:213-224.
- Chan-McLeod, A. C. A. 2003. Factors affecting the permeability of clearcuts to red-legged frogs. *Journal of Wildlife Management* **67**:663-671.

- Chelgren, N. D., D. K. Rosenberg, S. S. Heppell, and A. I. Gitelman. 2006. Carryover aquatic effects on survival of metamorphic frogs during pond emigration. *Ecological Applications* **16**:250-261.
- Christie, K., M. D. Craig, V. L. Stokes, and R. J. Hobbs. 2012. Home range size and microhabitat density requirements of *Egernia napoleonis*: implications for restored Jarrah forest of South Western Australia. *Restoration Ecology* **20**:740-746.
- Christie, K., V. L. Stokes, M. D. Craig, and R. J. Hobbs. 2013. Microhabitat preference of *Egernia napoleonis* in undisturbed Jarrah forest, and availability and introduction of microhabitats to encourage colonization of restored forest. *Restoration Ecology* **21**:722-728.
- Cline, B. B., and M. L. Hunter. 2014. Different open-canopy vegetation types affect matrix permeability for a dispersing forest amphibian. *Journal of Applied Ecology* **51**:319-329.
- Cline, B. B., and M. L. Hunter. 2016. Initial movements of a dispersing amphibian in response to partial harvesting in the Acadian forest of Maine, USA. *Forest Science* **62**:333-342.
- Constible, J. M., P. T. Gregory, and B. R. Anholt. 2001. Patterns of distribution, relative abundance, and microhabitat use of anurans in a boreal landscape influenced by fire and timber harvest. *Ecoscience* **8**:462-470.
- Cook, R. C., J. G. Cook, and L. D. Mech. 2004. Nutritional condition of northern Yellowstone elk. *Journal of Mammalogy* **85**:714-722.
- Cormack, R. M. 1964. Estimates of survival from the sighting of marked animals. *Biometrika* **51**:429-438.
- Courtois, E. A., C. Lelong, O. Calvez, A. Loyau, and D. S. Schmeller. 2013. The use of visible implant alpha tags for anuran tadpoles. *Herpetological Review* **44**:230-233.
- Courtois, E. A., A. Loyau, M. Bourgoïn, and D. S. Schmeller. 2017. Initiation of *Batrachochytrium dendrobatidis* infection in the absence of physical contact with infected hosts—a field study in a high altitude lake. *Oikos* **126**:843-851.
- Craig, M. D., G. E. S. J. Hardy, J. B. Fontaine, M. J. Garkakalis, A. H. Grigg, C. D. Grant, P. A. Fleming, and R. J. Hobbs. 2012. Identifying unidirectional and dynamic habitat filters to faunal recolonisation in restored mine-pits. *Journal of Applied Ecology* **49**:919-928.
- Craig, M. D., A. H. Grigg, R. J. Hobbs, and G. E. S. J. Hardy. 2014. Does coarse woody debris density and volume influence the terrestrial vertebrate community in restored bauxite mines? *Forest Ecology and Management* **318**:142-150.
- Crean, A. J., K. Monro, and D. J. Marshall. 2011. Fitness consequences of larval traits persist across the metamorphic boundary. *Evolution* **65**:3079-3089.
- Dahl, E., G. Orizaola, A. G. Nicieza, and A. Laurila. 2012. Time constraints and flexibility of growth strategies: geographic variation in catch-up growth responses in amphibian larvae. *Journal of Animal Ecology* **81**:1233-1243.
- Davis, J. C., S. B. Castleberry, and J. C. Kilgo. 2010. Influence of coarse woody debris on herpetofaunal communities in upland pine stands of the southeastern Coastal Plain. *Forest Ecology and Management*, **259**: 1111-1117.
- DeMaynadier, P. G., and M. L. Hunter. 1995. The relationship between forest management and amphibian ecology: a review of the North American literature. *Environmental Reviews* **3**:230-261.
- DeMaynadier, P. G., and M. L. Hunter. 1999. Forest canopy closure and juvenile emigration by pool-breeding amphibians in Maine. *Journal of Wildlife Management* **63**:441-450.
- Denver, R. J. 1997. Proximate mechanisms of phenotypic plasticity in amphibian metamorphosis. *American Zoologist* **37**:172-184.
- Desroches, J.-F., and D. Rodrigue. 2004. Amphibiens et reptiles du Québec et des Maritimes. Éditions M. Quintin, Québec: Waterloo.
- Dias, G. M., and D. J. Marshall. 2010. Does the relationship between offspring size and performance change across the life-history? *Oikos* **119**:154-162.
- Dmitriew, C. M. 2011. The evolution of growth trajectories: what limits growth rate? *Biological Reviews* **86**:97-116.
- Dodd, M. H. I., and J. M. Dodd. 1976. The Biology of metamorphosis. Pages 467-599 in B. Loft, editors. *Physiology of the Amphibia*. Academic Press.
- Earl, J. E., and R. D. Semlitsch. 2013. Carryover effects in amphibians: are characteristics of the larval habitat needed to predict juvenile survival? *Ecological Applications* **23**:1429-1442.

- Fauteux, D., L. Imbeau, P. Drapeau, and M. J. Mazerolle. 2012. Small mammal responses to coarse woody debris distribution at different spatial scales in managed and unmanaged boreal forests. *Forest Ecology and Management* **266**:194-205.
- Fletcher, D. 2012. Estimating overdispersion when fitting a generalized linear model to sparse data. *Biometrika* **99**:230-237.
- Fritts, S. R., S. M. Grodsky, D. W. Hazel, J. A. Homyack, S. B. Castleberry, and C. E. Moorman. 2015. Quantifying multi-scale habitat use of woody biomass by southern toads. *Forest Ecology and Management* **346**:81-88.
- Gamble, T., P. B. Berendzen, H. Bradley Shaffer, D. E. Starkey, and A. M. Simons. 2008. Species limits and phylogeography of North American cricket frogs (Acris: Hylidae). *Molecular Phylogenetics and Evolution* **48**:112-125.
- Gatten, R. E., K. Miller, and R. J. Full. 1992. Energetics at rest and during locomotion. Pages 314-377 in *Environmental physiology of the amphibians*. University of Chicago Press, Chicago, IL, USA.
- Gelman, A., and J. Hill. 2007. Data analysis using regression and multilevel hierarchical models. Cambridge University Press New York, NY, USA.
- Gibbs, J. P. 1998. Distribution of woodland amphibians along a forest fragmentation gradient. *Landscape Ecology* **13**:263-268.
- Giménez, K. A., and G. Torres. 2004. Linking life history traits in successive phases of a complex life cycle: effects of larval biomass on early juvenile development in an estuarine crab, *Chasmagnathus granulata*. *Oikos* **104**:570-580.
- Goater, C. P. 1994. Growth and survival of postmetamorphic toads: interactions among larval history, density, and parasitism. *Ecology* **75**:2264-2274.
- Gosner, K. L. 1960. A simplified table for staging anuran embryos and larvae with notes on identification. *Herpetologica* **16**:183-190.
- Green, A. W., and L. L. Bailey. 2015. Reproductive strategy and carry-over effects for species with complex life histories. *Population Ecology* **57**:175-184.
- Greenwald, K. R., J. L. Purrenhage, and W. K. Savage. 2009. Landcover predicts isolation in *Ambystoma salamanders* across region and species. *Biological Conservation* **142**:2493-2500.
- Grove, S. J. 2002. Tree basal area and dead wood as surrogate indicators of saproxylic insect faunal integrity: a case study from the Australian lowland tropics. *Ecological Indicators* **1**:171-188.
- Halverson, M. A., D. K. Skelly, J. M. Kiesecker, and L. K. Freidenburg. 2003. Forest mediated light regime linked to amphibian distribution and performance. *Oecologia* **134**:360-364.
- Harkey, G. A., and R. D. Semlitsch. 1988. Effects of temperature on growth, development, and color polymorphism in the ornate chorus frog *Pseudacris ornata*. *Copeia*:1001-1007.
- Harmon, M. E., J. F. Franklin, F. J. Swanson, P. Sollins, S. V. Gregory, J. D. Lattin, N. H. Anderson, S. P. Cline, N. G. Aumen, J. R. Sedell, G. W. Lienkaemper, K. Cromack, and K. W. Cummins. 1986. Ecology of coarse woody debris in temperate ecosystems. *Advances in Ecological Research* **15**:133-302.
- Harper, E. B., D. A. Patrick, and J. P. Gibbs. 2015. Impact of forestry practices at a landscape scale on the dynamics of amphibian populations. *Ecological Applications* **25**:2271-2284.
- Harper, E. B., and R. D. Semlitsch. 2007. Density dependence in the terrestrial life history stage of two anurans. *Oecologia* **153**:879-889.
- Harrison, X. A., J. D. Blount, R. Inger, D. R. Norris, and S. Bearhop. 2011. Carry-over effects as drivers of fitness differences in animals. *Journal of Animal Ecology* **80**:4-18.
- Hassinger, J. D., and J. Payne. 1989. Dead wood for wildlife. Page Timber management and its effects on wildlife: proceedings of the 1989 Penn State Forest resources issues conference. University Park, PA: Pennsylvania State University.
- Heath, D. D., and D. M. Blouw. 1998. Are maternal effects in fish adaptive or merely physiological side effects? Pages 178-201 in T. A. Mousseau and B. J. Fox, editors. *Maternal effects as adaptations*. Oxford University Press, New York.
- Hill, W. R., M. G. Ryon, and E. M. Schilling. 1995. Light limitation in a stream ecosystem: responses by primary producers and consumers. *Ecology* **76**:1297-1309.
- Hocking, D., and R. Semlitsch. 2008. Effects of experimental clearcut logging on gray treefrog (*Hyla versicolor*) tadpole performance. *Journal of Herpetology* **42**:689-698.
- Homyack, J. A., Z. Aardweg, T. A. Gorman, and D. R. Chalcraft, 2013. Initial effects of woody biomass removal and intercropping of switchgrass (*Panicum virgatum*) on herpetofauna in eastern North Carolina. *Wildlife Society Bulletin* **37**: 327-335.

- Howard, J. H., R. F. Baldwin, and B. L. Brown. 2012. Exploratory analysis for complex-life-cycle amphibians: Revealing complex forest-reproductive effort relationships using redundancy analysis. *Forest Ecology and Management* **270**:175-182.
- Indermaur, L., B. R. Schmidt, K. Tockner, and M. Schaub. 2010. Spatial variation in abiotic and biotic factors in a floodplain determine anuran body size and growth rate at metamorphosis. *Oecologia* **163**:637-649.
- Jacobs, J. M., J. R. Spence, and D. W. Langor. 2007. Influence of boreal forest succession and dead wood qualities on saproxylic beetles. *Agricultural and Forest Entomology* **9**:3-16.
- Jaeger, R. G. 1980. Microhabitats of a terrestrial forest salamander. *Copeia* **1980**:265-268.
- Johnsson, J. I., and T. Bohlin. 2006. The cost of catching up: increased winter mortality following structural growth compensation in the wild. *Proceedings of the Royal Society B: Biological Sciences* **273**:1281-1286.
- Jolly, G. M. 1965. Explicit estimates from capture-recapture data with both death and immigration-stochastic model. *Biometrika* **52**:225-247.
- Jonsson, B. G., and N. Kruys. 2001. Ecology of coarse woody debris in Boreal forest: future research directions. *Ecological Bulletins* **49**:279-281.
- Jørgensen, C. B. 1997. 200 years of amphibian water economy: from Robert Townson to the present. *Biological Reviews* **72**:153-237.
- Kaplan, R. H., and P. C. Phillips. 2006. Ecological and developmental context of natural selection: maternal effects and thermally induced plasticity in the frog *Bombina orientalis*. *Evolution* **60**:142-156.
- Laake, J. L. 2013. RMark: an R interface for analysis of capture-recapture data with MARK. US Department of Commerce, National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Alaska Fisheries Science Center.
- Leduc, A. 2013. Dix-huit ans de changements in situ du couvert forestier dans une chonoséquence de 249 ans de la forêt boréale mixte en Abitibi (Mémoire de maîtrise). Université de Montréal.
- Lee, W. -S., P. Monaghan, and N. B. Metcalfe. 2013. Experimental demonstration of the growth rate-lifespan trade-off. *Proceedings of the Royal Society B: Biological Sciences* **280**.
- Lindström, J. 1999. Early development and fitness in birds and mammals. *Trends in Ecology & Evolution* **14**:343-348.
- Loeb, S. C. 1999. Responses of small mammals to coarse woody debris in a southeastern pine forest. *Journal of Mammalogy* **80**:460-471.
- Lohr, S. M., S. A. Gauthreaux, and J. C. Kilgo. 2002. Importance of coarse woody debris to avian communities in loblolly pine forests. *Conservation Biology* **16**:767-777.
- Mazerolle, M. J. 2006. Improving data analysis in herpetology: using Akaike's Information Criterion (AIC) to assess the strength of biological hypotheses. *Amphibia-Reptilia* **27**:169-180.
- Mazerolle, M. J. 2017. AICcmodavg: Model selection and multimodel inference based on (Q)AIC(c). R package version 2.1-1. <https://cran.r-project.org/package=AICcmodavg>.
- Morgan, I. J., and N. B. Metcalfe. 2001. Deferred costs of compensatory growth after autumnal food shortage in juvenile salmon. *Proceedings of the Royal Society B: Biological Sciences* **268**:295-301.
- Murillo-Rincón, A. P., N. A. Kolter, A. Laurila, and G. Orizaola. 2017. Intraspecific priority effects modify compensatory responses to changes in hatching phenology in an amphibian. *Journal of Animal Ecology* **86**:128-135.
- Murray, D. L. 1990. The effects of food and density on growth and metamorphosis in larval wood frogs (*Rana sylvatica*) from central Labrador. *Canadian Journal of Zoology* **68**:1221-1226.
- Newman, R. A. 1998. Ecological constraints on amphibian metamorphosis: interactions of temperature and larval density with responses to changing food level. *Oecologia* **115**:9-16.
- Noland, R., and G. R. Ultsch. 1981. The roles of temperature and dissolved oxygen in microhabitat selection by the tadpoles of a frog (*Rana pipiens*) and a toad (*Bufo terrestris*). *Copeia* **1981**:645-652.
- Norris, D. R., P. P. Marra, T. K. Kyser, T. W. Sherry, and L. M. Ratcliffe. 2004. Tropical winter habitat limits reproductive success on the temperate breeding grounds in a migratory bird. *Proceedings of the Royal Society B: Biological Sciences* **271**:59-64

- Norris, D. R. 2005. Carry-over effects and habitat quality in migratory populations. *Oikos* **109**:178-186.
- Norris, D. R., and P. P. Marra. 2007. Seasonal interactions, habitat quality, and population dynamics in migratory birds. *The Condor* **109**:535-547.
- O'Connor, C. M., K. M. Gilmour, R. Arlinghaus, S. Matsumura, C. D. Suski, D. P. Philipp, and S. J. Cooke. 2011. The consequences of short-term cortisol elevation on individual physiology and growth rate in wild. *Canadian Journal Fisheries and Aquatic Sciences* **68**:693-705.
- O'Connor, C. M., D. R. Norris, G. T. Crossin, and S. J. Cooke. 2014. Biological carryover effects: linking common concepts and mechanisms in ecology and evolution. *Ecosphere* **5**:1-11.
- O'Connor, C. M., and S. J. Cooke. 2015. Ecological carryover effects complicate conservation. *Ambio* **44**:582-591.
- Orizaola, G., E. Dahl, A. G. Nicieza, and A. Laurila. 2013. Larval life history and anti-predator strategies are affected by breeding phenology in an amphibian. *Oecologia* **171**:873-881.
- Otto, C. R. V., A. J. Kroll, and H. C. McKenny. 2013. Amphibian response to downed wood retention in managed forests: A prospectus for future biomass harvest in North America. *Forest Ecology and Management* **304**: 275-285.
- Owens, A. K., K. R. Moseley, T. S. McCay, S. B. Castleberry, J. C. Kilgo, and W. M. Ford, 2008. Amphibian and reptile community response to coarse woody debris manipulations in upland loblolly pine (*Pinus taeda*) forests. *Forest Ecology and Management* **256**: 2078-2083.
- Pahkala, M., A. Laurila, and J. Merilä. 2001. Carry-over effects of ultraviolet-B radiation on larval fitness in *Rana temporaria*. *Proceedings of the Royal Society B: Biological Sciences* **268**:1699-1706.
- Pandian, T. J., and M. P. Marian. 1985. Predicting anuran metamorphosis and energetics. *Physiological Zoology* **58**:538-552.
- Parris, M. J., and S. Ross. 2000. Experimental analysis of hybridization in leopard frogs (Anura: Ranidae): larval performance in desiccating environments. *Copeia* **2000**:11-19.
- Patrick, D. A., E. B. Harper, M. L. Hunter, and A. J. K. Calhoun. 2008. Terrestrial habitat selection and strong density-dependent mortality metamorphosed amphibians. *Ecology* **89**:2563-2574.
- Pechmann, J. H., D. E. Scott, J. W. Gibbons, and R. D. Semlitsch. 1989. Influence of wetland hydroperiod on diversity and abundance of metamorphosing juvenile amphibians. *Wetlands Ecology and Management* **1**: 3-11.
- Pechenik, J. A. 2006. Larval experience and latent effects—metamorphosis is not a new beginning. *Integrative and Comparative Biology* **46**:323-333.
- Perryman, W. L., M. A. Donahue, P. C. Perkins, and S. B. Reilly. 2002. Gray whale calf production 1994–2000: are observed fluctuations related to changes in seasonal ice cover? *Marine Mammal Science* **18**:121-144.
- Petranka, J. W., M. E. Eldridge, and K. E. Haley. 1993. Effects of timber harvesting on Southern Appalachian Salamanders. *Conservation Biology* **7**:363-370.
- Petranka, J. W., M. P. Brannon, M. E. Hopey, and C. K. Smith. 1994. Effects of timber harvesting on low elevation populations of southern Appalachian salamanders. *Forest Ecology and Management* **67**:135-147.
- Phillips, N. E. 2002. Effects of nutrition-mediated larval condition on juvenile performance in a marine mussel. *Ecology* **83**:2562-2574.
- Pinheiro, J. C., and D. M. Bates. 2000. Linear mixed-effects models: basic concepts and examples. Pages 3-56 in *Mixed-effects models in S and S-Plus*. Springer New York, New York, NY.
- Pinheiro, J., D. Bates, S. DebRoy, and D. Sarkar. 2016. R-Core-Team: nlme: Linear and nonlinear mixed effects models. 2014. R package version:1-3.
- Popescu, V. D., and M. L. Hunter. 2011. Clear-cutting affects habitat connectivity for a forest amphibian by decreasing permeability to juvenile movements. *Ecological Applications* **21**:1283-1295.
- R Development Core Team. 2016. R: A Language and Environment for statistical computing. Vienna, Austria: R Foundation for statistical Computing.
- Räsänen, K., A. Laurila, J. Merilä, and B. Sinervo. 2003. Geographic variation in acid stress tolerance of the moor frog, *Rana arvalis*. I. Local adaptation. *Evolution* **57**:352-362.

- Riffell, S., J. Verschuyl, D. Miller, and T. B. Wigley. 2011. Biofuel harvests, coarse woody debris, and biodiversity—a meta-analysis. *Forest Ecology and Management* **261**:878-887.
- Rittenhouse, T. A. G., E. B. Harper, L. R. Rehard, and R. D. Semlitsch. 2008. The role of microhabitats in the desiccation and survival of Anurans in recently harvested Oak-Hickory forest. *Copeia* **2008**:807-814.
- Rittenhouse, T. A. G., R. D. Semlitsch, and F. R. Thompson. 2009. Survival costs associated with wood frog breeding migrations: effects of timber harvest and drought. *Ecology* **90**:1620-1630.
- Rome, L. C., A. Sosnicki, and I. H. Choi. 1992. The influence of temperature on muscle function in the fast swimming scup. II. The mechanics of red muscle. *Journal of Experimental Biology* **163**:281-295.
- Rowe, C. L., and W. A. Dunson. 1995. Impacts of hydroperiod on growth and survival of larval amphibians in temporary ponds of central Pennsylvania, USA. *Oecologia* **102**:397-403.
- Rowland, F. E., M. B. Rawlings, and R. D. Semlitsch. 2017. Joint effects of resources and amphibians on pond ecosystems. *Oecologia* **183**:237-247.
- Schiesari, L. 2006. Pond canopy cover: a resource gradient for anuran larvae. *Freshwater Biology* **51**:412-423.
- Schmidt, B. R., W. Hödl, and M. Schaub. 2012. From metamorphosis to maturity in complex life cycles: equal performance of different juvenile life history pathways. *Ecology* **93**:657-667.
- Scott, D. E. 1990. Effects of larval density in *Ambystoma opacum*: an experiment large-scale field enclosures. *Ecology* **71**:296-306.
- Seber, G. A. F. 1965. A note on the multiple-recapture census. *Biometrika* **52**:249-259.
- Semlitsch, R. D. 2000. Principles for management of aquatic-breeding amphibians. *Journal of Wildlife Management* **64**:615-631.
- Semlitsch, R. D., B. D. Todd, S. M. Blomquist, A. J. K. Calhoun, J. W. Gibbons, J. P. Gibbs, G. J. Graeter, E. B. Harper, D. J. Hocking, M. L. Hunter, D. A. Patrick, T. A. G. Rittenhouse, and B. B. Rothermel. 2009. Effects of timber harvest on amphibian populations: understanding mechanisms from forest experiments. *Bioscience* **59**:853-862.
- Smith, D. C. 1983. Factors controlling tadpole populations of the chorus frog (*Pseudacris triseriata*) on Isle Royale, Michigan. *Ecology* **64**:501-510
- Smith, D. C. 1987. Adult recruitment in chorus frogs: effects of size and date at metamorphosis. *Ecology* **68** :344-350.
- Skelly, D. K., L. K. Freidenburg, and J. M. Kiesecker. 2002. Forest canopy and the performance of larval amphibians. *Ecology* **83**:983-992.
- Skelly, D. K., and J. Golon. 2003. Assimilation of natural benthic substrates by two species of tadpoles. *Herpetologica* **59**:37-42.
- Snodgrass, J. W., M. J. Komoroski, A. L. Bryan, and J. Burger. 2000. Relationships among isolated wetland size, hydroperiod, and amphibian species richness: implications for wetland regulations. *Conservation Biology* **14**:414-419.
- Society Ruffed Grouse. (2017). Ruffed Grouse Society. Retrieved from <http://www.ruffedgrousesociety.org/Woodcock-Facts#.WTq5UIKmveQ>
- Sumner, J. 2006. Higher relatedness within groups due to variable subadult dispersal in a rainforest skink, *Gnypetoscincus queenslandiae*. *Austral Ecology* **31**:441-448.
- Thiffault, E., A. St-Laurent Samuel, and R. Serra. 2009. La récolte de biomasse forestière: saines pratiques et enjeux écologiques dans la forêt boréale canadienne, Ressources naturelles, Canada. Ressources naturelles, Canada.
- Thurgate, N. Y., and J. H. Pechmann. 2007. Canopy closure, competition, and the endangered dusky gopher frog. *Journal of Wildlife Management* **71**:1845-1852.
- Timm, B. C., K. McGarigal, and B. W. Compton. 2007. Timing of large movement events of pond-breeding amphibians in Western Massachusetts, USA. *Biological Conservation* **136**:442-454.
- Trottier, J. 2006. Impact de l'exploitation forestière sur la richesse et l'abondance des amphibiens de la forêt boréale méridionale du Bas-Saint-Laurent (Doctoral dissertation), Université du Québec à Rimouski.

- Ultsch, G. R. 1999. Physiology: coping with the environment in McDiarmid, R.W. and Altig, R., Editors, *Tadpoles :The biology of anuran larvae*. The University of Chicago Press, Berkeley.
- Van Allen, B. G., V. S. Briggs, M. W. McCoy, and J. R. Vonesh. 2010. Carry-over effects of the larval environment on post-metamorphic performance in two hylid frogs. *Oecologia* **164**:891-898.
- Van Buskirk, J. 2011. Amphibian phenotypic variation along a gradient in canopy cover: species differences and plasticity. *Oikos* **120**:906-914.
- Vanderwel, M. C., J. R. Malcolm, S. M. Smith, and N. Islam. 2006. Insect community composition and trophic guild structure in decaying logs from eastern Canadian pine-dominated forests. *Forest Ecology and Management* **225**:190-199.
- Vanderwel, M. C., S. C. Mills, and J. R. Malcolm. 2009. Effects of partial harvesting on vertebrate species associated with late-successional forests in Ontario's boreal region. *The Forestry Chronicle* **85**:91-104.
- Vanderwel, M. C., J. R. Malcolm, J. P. Caspersen, and M. A. Newman. 2010. Fine-scale habitat associations of red-backed voles in boreal mixedwood stands. *Journal of Wildlife Management* **74**:1492-1501.
- Vasconcelos, D., and A. J. Calhoun. 2004. Movement patterns of adult and juvenile *Rana sylvatica* (LeConte) and *Ambystoma maculatum* (Shaw) in three restored seasonal pools in Maine. *Journal of Herpetology* **38**:551-561.
- Vié, J.-C., C. Hilton-Taylor, and S. N. Stuart. 2009. Wildlife in a changing world: an analysis of the 2008 IUCN Red List of threatened species. IUCN.
- Walmsley, J., and D. Godbold. 2010. Stump harvesting for bioenergy—a review of the environmental impacts. *Forestry* **83**:17-38.
- Wellborn, G. A., D. K. Skelly, and E. E. Werner. 1996. Mechanisms creating community structure across a freshwater habitat gradient. *Annual review of Ecology and Systematics* **27**:337-363.
- Werner, E. E. 1986. Amphibian metamorphosis: growth rate, predation risk, and the optimal size at transformation. *American Naturalist* **128**:319-341.
- Werner, E. E., and K. S. Glennemeier. 1999. Influence of forest canopy cover on the breeding pond distributions of several amphibian species. *Copeia* **1**:1-12.
- Werner, E. E., D. K. Skelly, R. A. Relyea, and K. L. Yurewicz. 2007. Amphibian species richness across environmental gradients. *Oikos* **116**:1697-1712.
- Whiles, M. R., and J. W. Grubaugh. 1996. Importance of coarse woody debris to southern forest herpetofauna. *Biodiversity and coarse woody debris in southern forests: effects on biodiversity*. US Forest Service. GTR-SE-94, 94-100.
- White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study* **46**:S120-S139.
- White, E. M. 2010. Woody biomass for bioenergy and biofuels in the United States: a briefing paper. U.S. Dept. of Agriculture, Pacific Northwest Research Station, Portland, Or.
- Wilbur, H. M. 1977. Interactions of food level and population density in *Rana sylvatica*. *Ecology* **58**:206-209.
- Wilbur, H. M. 1980. Complex Life Cycles. *Annual review of Ecology and Systematics* **11**:67-93.
- Wilbur, H. M. 1987. Regulation of structure in complex systems: experimental temporary pond communities. *Ecology* **68**:1437-1452.
- Williams, B. K., J. D. Nichols, and M. J. Conroy. 2002. Analysis and management of animal populations. Academic Press, New York, USA.
- Williams, B. K., T. A. Rittenhouse, and R. D. Semlitsch. 2008. Leaf litter input mediates tadpole performance across forest canopy treatments. *Oecologia* **155**:377-384.
- Wright, A. A., and A. H. Wright. 1949. Handbook of frogs and toads of the United States and Canada. Comstock Pub. Co., Ithaca, N.Y.
- Yearsley, J. M., I. Kyriazakis, and I. J. Gordon. 2004. Delayed costs of growth and compensatory growth rates. *Functional Ecology* **18**:563-570.
- Yee, T. W. 2017. VGAM: Vector Generalized Linear and Additive Models. R package version 1.0-3. URL <https://cran.r-project.org/package=VGAM>.
- Zuur, A. F., E. N. Ieno, N. J. Walker, A. A. Saveliev, and G. M. Smith. 2009. Mixed effects models and extensions in ecology with R. Springer, New York, NY, USA.

CONCLUSION GÉNÉRALE

Cette étude avait pour objectif global de déterminer les effets de l'ouverture de la canopée et de l'hydropériode lors du développement larvaire de la grenouille des bois et leurs conséquences sur la survie et la sélection d'habitats des juvéniles récemment métamorphosés en milieu terrestre. Pour le volet aquatique, nous avons voulu tester l'hypothèse que la survie et l'atteinte à la métamorphose allaient augmenter avec l'ouverture de la canopée et la réduction de l'hydropériode. Afin de répondre à ces objectifs, nous avons suivi 1440 têtards de grenouille des bois dans des mésocosmes en faisant varier l'ouverture de la canopée et l'hydropériode. Ainsi, nous avons validé l'hypothèse que la probabilité d'atteindre la métamorphose des têtards, le nombre de jours passés dans le milieu aquatique avant de se métamorphoser ainsi que la taille et la masse des juvéniles métamorphosés dépend de l'ouverture de la canopée et de l'hydropériode. Nos résultats montrent qu'une forte ouverture de la canopée et une hydropériode réduite augmentent la probabilité d'atteindre la métamorphose et favorisent le développement plus rapide des têtards.

À l'opposé, les têtards de grenouille des bois en canopée fermée avec une hydropériode réduite ont une plus faible probabilité d'atteindre la métamorphose et se développent plus lentement dans le milieu aquatique. Ainsi, un habitat aquatique avec une forte ouverture de canopée recevra plus de luminosité qu'en milieu fermé, ce qui stimulera le bloom d'algues (Skelly et *al.*, 2002), augmentant la disponibilité de ressources pour les têtards de grenouille des bois qui sont herbivores. Cette augmentation de ressource favorisera le développement et la métamorphose rapide en juvéniles de nos individus surtout en absence de prédation. Cependant, cette accélération dans le développement semble entraîner un coût physiologique. En effet, en canopée ouverte avec une hydropériode réduite, nous observons une plus petite taille et masse des juvéniles à la métamorphose que chez les individus venant d'une canopée fermée avec une hydropériode réduite. À l'inverse, les individus en canopée fermée avec une hydropériode réduite doivent faire face à de nombreux défis avec un milieu pauvre en ressources alimentaires et une forte compétition interspécifique. Cependant, les individus qui survivent et se métamorphosent ont une plus grande taille et masse à la métamorphose. Cela pourrait s'expliquer par leur développement plus lent et par la faible compétition dans le milieu en raison de la forte mortalité des autres individus.

Le second volet de notre étude se concentrait sur les effets de l'ouverture de la canopée et de l'hydropériode lors du développement larvaire sur la survie et la sélection des juvéniles de grenouilles des bois dans des enclos expérimentaux en milieu terrestre. Ces enclos expérimentaux comprenaient quatre traitements faisant varier la disposition et la taille des débris ligneux. Ainsi, nous avons un traitement avec (1) des débris ligneux grossiers (15 cm de diamètre) agrégés, (2) des débris ligneux fins (5 cm de diamètre) agrégés, (3) des débris ligneux grossiers homogènes et (4) des débris ligneux fins homogènes. Nos résultats ne montrent aucune

variation de la survie des juvéniles dans les enclos terrestres en fonction de leur histoire de vie. De la même façon, nous n'observons aucune différence de sélection d'habitats des juvéniles en fonction des conditions lors de leur développement larvaire. Ainsi, les juvéniles ayant subi lors de leur développement larvaire une hypohypémie réduite ou complète, et une canopée ouverte ou fermée, ne semblent favoriser aucun traitement (débris ligneux fins agrégés, bois grossier agrégé, bois grossier homogènes et bois fin homogènes). Dans un milieu ouvert, malgré les différents débris ligneux, nous pouvons émettre l'hypothèse que les conditions environnementales (humidité et la température) étaient équivalentes. De ce fait, les individus ne voyaient aucun bénéfice à privilégier un habitat par rapport à un autre. Enfin, une étude de Patrick et al. (2008) démontre que les juvéniles de grenouille des bois ont un comportement de sélection d'habitat qui varie avec le temps et l'échelle spatiale. Ainsi, après leur métamorphose, les juvéniles semblent privilégier un large habitat forestier de grande qualité (2.2 ha) (Patrick et al., 2008). Après une phase post émigration, les juvéniles vont sélectionner un milieu à une plus fine échelle avec des parcelles d'habitats de haute qualité (1 x 4m ou 10 x 10m) (Patrick et al., 2008).

Cette étude a permis de confirmer l'effet de l'interaction de l'ouverture de la canopée et de l'hypohypémie sur le développement des têtards de grenouille des bois. Ainsi, nos résultats soulignent l'importance de ces deux paramètres et leurs conséquences sur la performance de la grenouille des bois en milieu aquatique et terrestre. De ce fait, comme d'autres études, nous confirmons ainsi l'effet et l'importance des conditions environnementales sur le développement larvaire des têtards (Riha et Berven, 1991; Pechenik et al., 1998; Relyea, 2004; Van Allen et al., 2010; Van Buskirk, 2011). Afin de tester l'effet à retardement de conditions au stade larvaire, il serait pertinent de poursuivre les recherches en ajoutant de nouveaux paramètres telle que l'acidité, la quantité de nourriture et la prédation (Skelly et al., 2002; Räsänen et al., 2003; Relyea et Hoverman, 2003; Vonesh et Bolker, 2005). Ces paramètres peuvent causer une accélération ou un ralentissement du développement pendant la phase larvaire et nous pourrions ainsi observer leur effet à retardement en milieu terrestre sur les amphibiens. Par exemple, Altwegg (2003) a étudié l'effet à retardement de la densité (larvaire et des juvéniles) sur la croissance et la survie en milieu terrestre sur une grenouille d'Europe de la famille des Ranidae (*Rana lessonae*).

Pour le second volet de notre projet qui s'intéresse à la sélection d'habitats des juvéniles et à leur survie en milieu ouvert dans des enclos expérimentaux, nos résultats semblent montrer une absence d'un effet de report à court terme de l'histoire de vie lors du développement larvaire sur la sélection d'habitats et la survie des juvéniles en milieu terrestre. Nos résultats vont à l'encontre des résultats d'autres études (Altwegg et al., 2003; Baldwin et al., 2006). Ce résultat confirme l'étude d'Earl et Semlitsch (2013) qui n'avait pas non plus trouvé d'effet de report sur les juvéniles de grenouille des bois. Altwegg (2003), a quant à lui, démontré l'absence d'un effet à retardement de la densité en milieu aquatique et terrestre sur la survie un an après la métamorphose des individus. A l'inverse, Green et Bailey (2015) ont montré qu'un paramètre

physico-chimique (la conductivité négative) lors du développement larvaire pouvait affecter la survie des juvéniles de grenouille des bois en milieu terrestre. Dans les futurs axes de recherches que nous pourrions explorer nous avons : (1) l'évaluation de la survie des juvéniles pendant l'hibernation ou après le premier hiver et (2) l'étude d'un possible mécanisme de croissance compensatoire des juvéniles avant l'hibernation. Ainsi, les divers résultats de notre étude soulignent la possible importance des étangs situés dans des sites perturbés par la coupe et leur rôle clef comme pouponnières favorisant la reproduction larvaire des grenouilles des bois.

Outre les résultats présentés dans ce mémoire, nous avons aussi mis en place un protocole de marquage de juvénile de grenouille des bois avec des VI Alpha. Malgré la taille des individus, nous n'avons pas observé de mortalité ou d'effet limitant sur le déplacement des juvéniles lors de la période d'observation de 3 à 7 jours après marquage avant la relâche dans les enclos. Cependant, il serait pertinent de procéder à des recherches complémentaires à plus long terme pour évaluer la rétention des marques et les effets à plus long terme sur la survie. A posteriori, il est aussi nécessaire de souligner certaines limites dans notre étude. Dans les enclos terrestres, nous avons constaté par la suite que de nombreux individus s'étaient échappés malgré la hauteur des barrières anti-érosion. Ainsi, certains individus n'ont jamais été capturés ou recapturés lors des 3-7 semaines de l'étude. Afin de pallier à ces problèmes, nous pourrions clôturer les enclos avec des palissades en bois pour éviter la fuite des juvéniles et les peser à la fin des séances de capture. Dans nos analyses de survie, ces émigrations ont été confondues avec la mortalité.

En outre, les caméras placées dans les trois enclos expérimentaux avaient pour but de nous permettre de quantifier la présence de possibles prédateurs pour les juvéniles de grenouille des bois. Dans un enclos en particulier, nous avons observé un grand nombre de bécasses, celles-ci ne sont pas connues dans la littérature pour se nourrir de juvéniles de grenouille des bois (Society Ruffed Grouse, 2017). Cependant, nous ne pouvons écarter l'éventualité que certains individus aient été prédatés par les bécasses. Il nous est difficile de quantifier la prédation réalisée par les couleuvres rayées (*Thamnophis sirtalis*) dans nos enclos pendant la durée de notre expérience. Or, cette espèce est connue pour se nourrir de nombreuses espèces d'amphibiens (Arnold et Wassersug, 1978; Desroches et Rodrigue, 2004). En effet, les caméras à rayons infrarouges n'ont pu détecter les couleuvres en raison de leur petite taille.

Cette étude permettra de compléter les connaissances sur les effets de reports sur les amphibiens (Morgan et Metcalfe, 2001; Yearsley et al., 2004; Johnsson et Bohlin, 2006; Dmitriew, 2011; Earl et Semlitsch, 2013; Lee et al., 2013; Boes et Benard, 2013; O'Connor et Cooke, 2015; Green et Bailey, 2015). Cette étude se distingue par sa particularité de suivre les têtards lors de leur développement larvaire en faisant varier l'ouverture de la canopée et l'hydropériode jusqu'au stade de juvénile en milieu terrestre afin d'estimer l'effet à retardement sur la survie et la sélection d'habitat. Nous apportons ainsi des éléments de réponse sur les effets de report sur la

performance de la juvénile de grenouille des bois en milieu terrestre dû à des perturbations lors de son développement larvaire. De plus, l'absence d'effet de report observé sur la sélection d'habitats de juvéniles de grenouille des bois souligne l'importance de poursuivre les recherches afin de permettre une meilleure compréhension des mécanismes sous-jacents et de mettre en place des plans de gestions et protections adaptés. Enfin, si aucun effet de report n'a été mesuré sur la grenouille des bois qui est une espèce très commune en Amérique du Nord, on pourrait cependant s'attendre potentiellement à observer un effet différent sur d'autres espèces d'amphibiens plus fragiles.

BIBLIOGRAPHIE

- Altwegg, R., Reyer, H.-U. et Merilä, J. (2003). Patterns of natural selection on size at metamorphosis in water frogs. *Evolution*, 57(4), 872-882.
- Altwegg, R., Reyer, H.-U. et Merilä, J. (2003). Patterns of natural selection on size at metamorphosis in water frogs. *Evolution*, 57(4), 872-882.
- Arnold, S. J. et Wassersug, R. J. (1978). Differential predation on metamorphic anurans by garter snakes (Thamnophis): social behavior as a possible defense. *Ecology*, 59(5), 1014-1022.
- Boes, M. W. et Benard, M. F. (2013). Carry-over effects in nature: effects of canopy cover and individual pond on size, shape, and locomotor performance of metamorphosing wood frogs. *Copeia*, 2013(4), 717-722.
- Desroches, J.-F. et Rodrigue, D. (2004). *Amphibiens et reptiles du Québec et des Maritimes*. Éditions M. Quintin, Québec: Waterloo.
- Dmitriew, C. M. (2011). The evolution of growth trajectories: what limits growth rate? *Biological Reviews*, 86(1), 97-116.
- Earl, J. E. et Semlitsch, R. D. (2013). Carryover effects in amphibians: are characteristics of the larval habitat needed to predict juvenile survival? *Ecological Applications*, 23(6), 1429-1442.
- Green, A. W. et Bailey, L. L. (2015). Reproductive strategy and carry-over effects for species with complex life histories. *Population Ecology*, 57(1), 175-184.
- Johnsson, J. I. et Bohlin, T. (2006). The cost of catching up: increased winter mortality following structural growth compensation in the wild. *Proceedings of the Royal Society B: Biological Sciences*, 273(1591), 1281-1286.
- Lee, W. S., Monaghan, P. et Metcalfe, N. B. (2013). Experimental demonstration of the growth rate - lifespan trade-off. *Proceedings of the Royal Society B: Biological Sciences*, 280(1752).
- Morgan, I. J. et Metcalfe, N. B. (2001). Deferred costs of compensatory growth after autumnal food shortage in juvenile salmon. *Proceedings of the Royal Society B: Biological Sciences*, 268(1464), 295-301.
- O'Connor, C. M. et Cooke, S. J. (2015). Ecological carryover effects complicate conservation. *Ambio*, 44(6), 582-591.
- Patrick, D. A., E. B. Harper, M. L. Hunter, and A. J. K. Calhoun. 2008. Terrestrial habitat selection and strong density-dependent mortality metamorphosed amphibians. *Ecology*, 89(9):2563-2574.
- Pechenik, J. A., Wendt, D. E. et Jarrett, J. N. (1998). Metamorphosis is not a new beginning. *Bioscience*, 48(11), 901-910.
- Räsänen, K., Laurila, A., Merilä, J. et Sinervo, B. (2003). Geographic variation in acid stress tolerance of the moor frog, *Rana arvalis*. I. Local adaptation. *Evolution*, 57(2), 352-362.
- Relyea, R. A. (2004). Fine-tuned phenotypes: tadpole plasticity under 16 combinations of predators and competitors. *Ecology*, 85(1), 172-179.
- Relyea, R. A. et Hoverman, J. T. (2003). The impact of larval predators and competitors on the morphology and fitness of juvenile treefrogs. *Oecologia*, 134(4), 596-604.
- Riha, V. F. et Berven, K. A. (1991). An analysis of latitudinal variation in the larval development of the wood frog (*Rana sylvatica*). *Copeia*, 1, 209-221.
- Skelly, D. K., Freidenburg, L. K. et Kiesecker, J. M. (2002). Forest canopy and the performance of larval amphibians. *Ecology*, 83(4), 983-992.
- Society Ruffed Grouse. (2017). Ruffed Grouse Society. Repéré à <http://www.ruffedgrousesociety.org/Woodcock-Facts-.WTq5UIKmveQ>
- Van Allen, B. G., Briggs, V. S., McCoy, M. W. et Vonesh, J. R. (2010). Carry-over effects of the larval environment on post-metamorphic performance in two hylid frogs. *Oecologia*, 164(4), 891-898.
- Van Buskirk, J. (2011). Amphibian phenotypic variation along a gradient in canopy cover: species differences and plasticity. *Oikos*, 120(6), 906-914.
- Vonesh, J. R. et Bolker, B. M. (2005). Compensatory larval responses shift trade-offs associated with predator-induced hatching plasticity. *Ecology*, 86(6), 1580-1591.
- Yearsley, J. M., Kyriazakis, I. et Gordon, I. J. (2004). Delayed costs of growth and compensatory growth rates. *Functional Ecology*, 18(4), 563-570.