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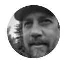
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Article

Effect of variable retention forestry on wood frogs (*Lithobates sylvaticus*) in early successional boreal mixedwood forests

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Abstract

Variable retention forest harvesting aims to reduce negative effects of harvesting on forest biodiversity, but knowledge gaps remain regarding its effects on some taxa over longer post-harvest time frames. To better understand effects of variable retention and environmental features on amphibians, we used pitfall traps to capture wood frogs (*Lithobates sylvaticus* (LeConte, 1825)) across four levels of retention (clearcut (0%), 20%, 50%, and unharvested control (100%)), and two forest types (deciduous and coniferous), in 17-year post-harvest forests in northwest Alberta. We mapped breeding sites and used a LiDAR-based terrain moisture index (depth-to-water) to examine relationships between relative abundance, breeding site proximity, and soil moisture. Retention level alone had no effect on relative abundance of adult wood frogs, but in late summer (July and August), there was a significant interaction between retention level and forest type: capture rates decreased with retention level for deciduous forests, but increased with retention level in conifer forests. During late summer, capture rates were higher in conifer forests than deciduous forests, with soil moisture (lower depth-to-water) positively related to capture rates. Though timber retention may be beneficial to wood frogs in the short term, any impacts of forest harvesting on wood frog abundance were undetectable in stands 17 years post-harvest.

Key words: variable retention, forestry, anuran amphibians, wood frog, *Lithobates sylvaticus*, post-harvest regeneration, LiDAR, depth-to-water

Introduction

The Boreal Forest is one of the largest forest biomes in the world, representing approximately 75% of the productive forest in Canada, as defined by a forest's ability to produce above-ground wood volume (Prepas et al. 2001; Skovsgaard and Vanclay 2008). Public concern over threats to boreal biodiversity and a general shift toward more sustainable resource development have led to forest management techniques that attempt to maintain forest biodiversity while still permitting economically viable resource extraction (Venier et al. 2014). Variable retention harvesting is a technique where live trees and other forest features are retained during harvesting in patterns meant to emulate those found following natural disturbance (Gradowski et al. 2010; Lindenmayer et al. 2012), with the assumption that forest structural heterogeneity, species diversity, and ecosystem function will be maintained within harvested areas at close to natural levels (Gradowski et al. 2010; Lindenmayer et al. 2012).

Amphibians are the most threatened vertebrate group worldwide, with approximately 41% of species threated globally (IUCN 2021); habitat loss and alteration are considered the primary drivers behind most population declines (Houlahan et al. 2000; Collins and Storfer 2003). However, understanding the response of amphibians to disturbance is challenging, due to complex life histories, multiple habitat requirements, and natural fluctuations in population size (Marsh and Trenham 2001; Patrick et al. 2006; Popescu et al. 2012). The effects of timber harvesting and forest management on amphibians have been well examined in North America, but responses vary across studies, with effects depending on the species, life history stage, geographic region, and the temporal and spatial scales of study (DeMaynadier and Hunter 1995; Semlitsch et al. 2009; Popescu et al. 2012).

Timber harvesting and subsequent forest regeneration can affect terrestrial environments by altering conditions important for amphibians, such as forest canopy cover, tree species composition, understory vegetation, and forest microhabitat (DeMaynadier and Hunter 1995, 1999; Patrick et al. 2006). Amphibians are vulnerable to water loss and require cool, moist conditions and adequate refuge sites (DeMaynadier and Hunter 1995; Semlitsch et al. 2009), thus potentially limiting activity and survival in terrestrial environments disturbed by forest harvesting (DeMaynadier and Hunter 1999). For species considered forest specialists (those that prefer closed forest canopy), clearcut harvesting usually results in reductions in abundance relative to intact forest stands (Popescu et al. 2012). Retention-based harvesting techniques have been proposed as an alternative to clearcutting to reduce the negative impacts on forest-associated species (DeMaynadier and Hunter 1995), although the effects of these techniques on amphibian populations have conflicting results, particularly over longer time periods in post-harvest forest ecosystems (Karraker and Welsh 2006; Patrick et al. 2006).

The wood frog (*Lithobates sylvaticus* (LeConte, 1825)) is the most widespread amphibian species in North America (Martof 1970). Although often described as a forest-specialist species in eastern North America (DeMaynadier and Hunter 1995), the wood frog is considered a generalist in many parts in its range (Hannon et al. 2002), and can be found in a variety of habitat types (Rittenhouse and Semlitsch 2007*a*). Outside of the breeding season, adults of this species can be found several hundred metres from aquatic breeding sites (Baldwin et al. 2006*b*; Rittenhouse and Semlitsch 2007*a*, 2009).

Although previous research has been conducted on wood frogs and other amphibians in relation to forest management, studies have typically been performed on populations centered on large wetlands and lakes (Hannon et al. 2002; Macdonald et al. 2006; Browne et al. 2009). In this study, we investigated patterns of relative abundance of wood frogs in uplands under two levels of tree retention (20% and 50%), clearcut harvest (0% retention), and unharvested stands (100% retention) of two forest cover types (deciduous and coniferous) in 17-year post-harvest forests in northwest Alberta. Our objectives were to determine (1) whether terrestrial use by wood frogs differed in relation to tree retention levels or forest types in early seral forest; and (2) which factors (i.e., forest habitat, breeding site proximity, and predicted soil moisture) best explained seasonal variation in abundance of wood frogs in uplands.

Previous studies in Alberta have found that wood frogs tend to be associated with deciduous forest cover rather than conifer forest (Roberts and Lewin 1979; Constible et al. 2001; Browne et al. 2009). Changes in structural elements of forest microhabitats from forest harvesting, such as distribution and abundance of coarse woody debris (DeMaynadier and Hunter 1995; Patrick et al. 2006; Semlitsch et al. 2009), understory vegetation cover (Chen et al. 1999; Dodd 2010), and leaf litter (DeMaynadier and Hunter 1995; Constible et al. 2001; Rittenhouse and Semlitsch 2007*b*), may affect wood frog and other amphibian populations, as these elements provide refuge and foraging habitat in post-harvest forests. We therefore hypothesized that wood frog abundance would be greater in forest stands with more mature deciduous canopy cover, as this type of forest would be expected to provide greater abundance of preferred forest microhabitats (e.g., leaf litter, woody debris).

Among the two forest types, we predicted wood frog capture rates to be higher in deciduous relative to conifer forests, as they would provide more suitable microhabitats resulting from deciduous leaf litter inputs. For deciduous forests, we predicted greater relative abundance (more captures per unit effort) of wood frogs in unharvested controls (100% retention) and 50% retention, relative to 20% retention and clearcut (0% retention) treatments. For conifer forests, we expected the opposite trend—with higher relative abundance in lower retention (20%) and clearcuts, as 17 years of aspen regeneration and understory development would provide more suitable refuge and foraging habitats at these sites compared with mature conifer (controls) and 50% retention stands. We also predicted that the relative abundance of wood frogs would be positively associated with breeding site proximity, as adults are highly philopatric and have maximum migration distances between 300 and 350 m (Baldwin et al. 2006*b*; Freidenfelds et al. 2011). Finally, on a smaller scale, we predicted that relative abundance would be related to local measures of soil moisture, as wood frogs seek out moist microhabitats during post-breeding movements (Baldwin et al. 2006*b*; Rittenhouse and Semlitsch 2007*a*). Thus, we expected abundance to be higher at sites characterized by higher predicted soil moisture, irrespective of retention treatment or forest type. We also predicted a stronger effect of retention and soil moisture later in the active season (e.g., late summer), when lower soil moisture may reduce wood frog activity. Mid-spring movements of adult wood frogs should correspond with post-breeding migrations from breeding sites to upland foraging habitat, whereas the late summer period corresponds to movements related to foraging activity and travel to overwintering sites by adults and recently metamorphosed frogs.

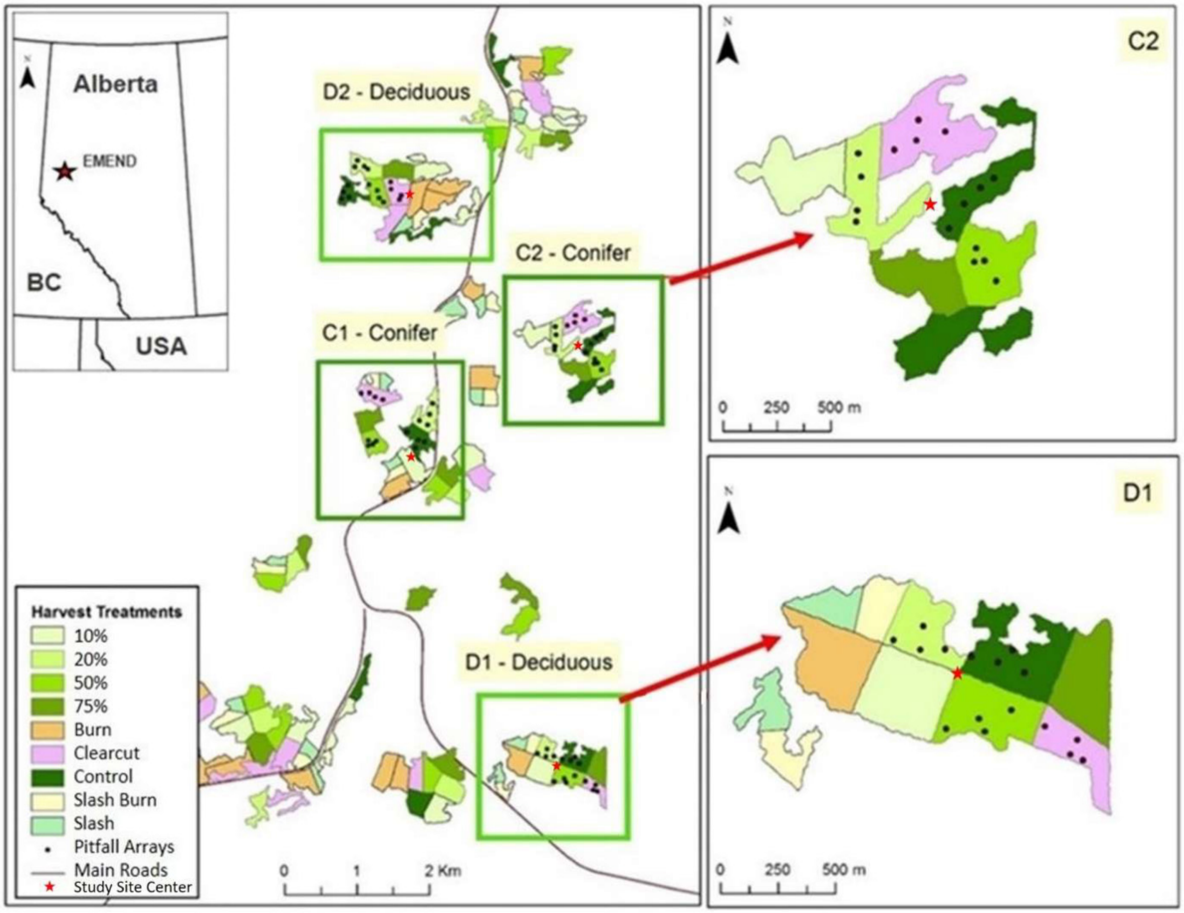
Materials and methods

Study area

Study sites were located at the Ecological Management Emulating Natural Disturbance (EMEND) research forest (56°46′13″N, 118°22′28″W) located in the Clear Hills Uplands, Lower Foothills Ecoregion of Alberta, approximately 90 km northwest of the town of Peace River (56°14′02″N, 117°17′21″W). The area lies within the boreal mixedwood and is characterized by a mosaic of uniform and mixed forest stands. Dominant tree species include trembling aspen (*Populus tremuloides* Michx.), balsam poplar (*Populus balsamifera* Lyall), and white spruce (*Picea glauca* (Moench)) in drier upland sites, and black spruce (*Picea mariana* (Mill.) Britton, Sterns & Poggenb.), tamarack (*Larix laricina* (Du Roi) K. Koch), and paper birch (*Betula papyrifera* (Marsh.)) in wetter lowland sites (Prepas et al. 2001; Natural Regions Committee 2006). Understory vegetation includes woody shrubs, mosses, sedges, and graminoids. Dominant soil types are grey luvisols in uplands and mesisols in wetlands (Natural Regions Committee 2006). The hydrological landscape of the region is highly varied, with stretches of forest interspersed with lakes, rivers, and wetlands. Wetlands are predominantly treed and shrubby fens on organic deposits with about 5% being marshes and other mineral wetlands.

The EMEND research forest is approximately 1000 ha and is divided into 10 timber harvest units (hereafter, blocks), located in the DMI (Daishowa-Marubeni International) P2 forest management area, in the townships 89 and 90 Range 03 W6M (Fig. 1). Each block is categorized as one of four forest cover types: conifer-dominated (>70% conifer canopy cover),

Fig. 1. Location of EMEND research forest (red star on top left inset map) in northwest Alberta, Canada, in the boreal mixedwood forest, as well as location of pitfall arrays ($n = 64$) within retention harvest treatments of four study sites sampled at EMEND in 2015. Sites C2 (top right) and D1 (bottom right) shown at smaller scale for detail. The matrix areas (white) surrounding the EMEND research forest consist of a patchwork of mixedwood forest stands of varying age and harvest histories, interspersed with lakes, rivers, wetlands, and streams. Both the base map and polygons showing EMEND harvest treatments are from the EMEND database and were ultimately provided by Mercer Peace River Pulp Ltd. (1999). Map projection: NAD83, UTM Zone 11U.



deciduous-dominated (>70% deciduous canopy cover), mixedwood (conifer and deciduous canopy cover, each composing 35%–65%), and deciduous-dominated with conifer understory (conifer understory composing at least 50% of canopy height). Blocks are further partitioned into smaller harvest treatment stands (hereafter, compartments), ranging from 3 to 13.5 ha. Each compartment is subject to one of eight different timber harvest treatments, including six levels of dispersed timber retention and two prescribed burn treatments. Timber retention treatments include 10%, 20%, 50%, and 75% dispersed retention, as well as unharvested controls and clearcuts (100% and 0% retention, respectively). Most harvesting treatments were applied in 1998, so amphibian sampling occurred over a 2-year period (2014 and 2015) in treatments representing 16–17 years of post-harvest regeneration.

Selection of study sites

For this study, four study sites (EMEND blocks) were selected based on the following criteria: (1) blocks had conifer or deciduous forest cover; (2) the four desired retention treatments (0%, 20%, 50%, and 100% retention) were adjacent to one another within blocks; and (3) blocks contained active wood frog breeding sites (seasonal, semi-permanent, or permanent wetlands) either within the block or within 500 m of one of the block boundaries. Deciduous and conifer study sites will be henceforth referred as D1/D2 and C1/C2, respectively. One study site in the deciduous category (D2) was originally classified as deciduous-dominated with conifer understory but was mostly deciduous (>70%); other candidate deciduous-dominated sites lacked active breeding sites.

Wood frog sampling

To estimate relative abundance of wood frogs, four pitfall trap and drift fence arrays (hereafter, pitfall arrays) were installed in each treatment compartment, for a total of 64 pitfall arrays across all study sites (4 arrays × 4 treatment compartments × 4 study sites = 64 arrays). Arrays were placed randomly within compartments but were at least 50 m from other arrays, adjacent treatment boundaries, roads, and obvious water features to control for edge effects and

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confounding variables (Figs. 1 and A1). Each pitfall array consisted of four pitfall traps (7.5 L buckets, Pro Western Plastics©, St. Albert, Alberta) connected by woven silt fencing (Everbilt©—Model# 883132 EB). Buckets were approximately 25 cm in diameter and 30 cm deep. Arrays had one trap located centrally and connected to three terminal traps by 5 m sections of silt fencing radiating from the center trap and separated by ~120° (Fig. A2). Fencing was embedded in a 10 cm deep trench and buried to prevent frogs from burrowing underneath. Once buried, fencing was approximately 50 cm high. Buckets were buried so tops were flush with the soil. Bucket lids were suspended 20 cm above traps by three small sticks to provide shade and prevent flooding and entry of excess debris. A moist sponge and 1–2 cm of water were placed in each trap to maintain a cool, moist environment for captured frogs. To prevent captured frogs from escaping, a piece of black polyethylene sheeting (4 mm thick; HDX©—Model# CF0404-50B) was secured over the top of each trap, and two bisecting openings were cut that extended just short of the bucket edge (forming a cross-pattern). This allowed frogs to fall freely into buckets but created a small barrier at the edge that discouraged escape. A small stick was placed in each trap to allow small mammals to escape.

Pitfall trapping sessions

Sampling was conducted at two study sites in 2014 (D1 and C1) over two trapping sessions: (1) July 14–August 1 and (2) August 7–25. In May 2015, arrays were installed at two additional study sites (D2 and C2) and trapping was conducted in all four study sites over four trapping sessions (with one exception; see below): (1) May 10–June 3, (2) June 8–July 2, (3) July 7–31, and (4) August 5–24, effectively encompassing the main active season of the study species. In C2, installation of pitfall arrays was not complete until the start of June. As such, trapping was conducted over trapping sessions 2–4 at C2 in 2015. Captures for trapping sessions were separated into (1) early (sessions 1 + 2) and (2) late (sessions 3 + 4) season categories, to assess seasonal differences in wood frog abundance (see the section "Statistical analysis").

During trapping sessions, all traps were open and arrays were checked every 2–4 days. Captured frogs were weighed to the nearest 0.1 g, measured snout-to-urostyle length (SUL; mm), marked using toe clipping, and released 10–15 m away from the site of capture. Frogs were given a mark specific to each pitfall array and year of capture, but not specific to individuals. Each animal was marked by the removal of the distal two phalanges of 2–3 toes using sterilized scissors. One toe was clipped to specify the year of capture, and 1–2 additional toes were clipped to specify the trapping array; this allowed identification of individuals from other pitfall arrays and prevented recounting individuals in abundance estimates. Between trapping sessions, lids were secured on top of traps to prevent unintentional capture and mortality of amphibians or small mammals. All capture, marking, and handling procedures received ethics approval from the University of Alberta Animal Care and Use Committee (Protocol 00001162) and Alberta Fish and Wildlife (Research Permit and Collection Licenses: 56484 and 56485). All handling and marking procedures followed guidelines provided by the Canadian Council on Animal Care. All field data collection followed the Government of Alberta's Capture and Handling Protocol for Amphibians (ESRD 2005) and the Government of British Columbia's Interim Hygiene Protocols for Amphibian Field Researchers and Staff (Ministry of Environment British Columbia 2008) to minimize transmission of pathogens between individual amphibians and locations.

Wood frog age and body size classes

Wood frogs were separated into two age classes based on body size and date of capture. Individuals were classed as adults if they were >27 mm SUL or if they were ≤27 mm SUL and caught in May or June (sessions 1 and 2). These latter individuals were assumed to be frogs that had metamorphosed the previous year and survived the winter. Individuals ≤27 mm SUL and captured in July and August (sessions 3 and 4) were assumed to be recently emerged froglets, based on known dates of metamorphosis from nearby breeding sites, and classed as young-of-the-year (YOY). The earliest date a frog was captured that was clearly a newly metamorphosed YOY (Gosner stages 45–46; Gosner 1960) on breeding sites that we were monitoring within and up to 13 km from the EMEND research forest in 2014 and 2015 was July 11 (M. Robinson, unpublished data). Adults do not necessarily represent sexually mature individuals, but rather individuals that have survived at least one winter.

Locating breeding sites and egg mass surveys

The geometric center for each study site polygon was determined using the "Find Centroid" tool in ArcMap. The polygon used for each study site incorporated all harvest treatment compartments, including those where pitfall trapping was not conducted. A 1.5 km circular buffer was then calculated around each center point, and all breeding sites within this buffer were identified for each study polygon in 2015 (Fig. A1). This buffer encompassed the estimated maximum migration distances for adult wood frogs between breeding pools and upland habitat (Regosin et al. 2003; Baldwin et al. 2006*b*), as well as the average dispersal distances for YOY wood frogs (Berven and Grudzien 1990), thus ensuring that all potential breeding sites near the pitfall arrays were identified. Potential breeding sites ranged in size (surface area) from 0.0037 to 2.093 ha (Table A1). Breeding sites were identified in the spring (late April and early May) of 2015 by searching the entire 1.5 km radius around each study site, identifying any aquatic features with potential to act as breeding sites, and performing egg mass surveys to confirm breeding activity. Breeding sites were defined as any aquatic feature where wood frog eggs were detected.

Egg mass counts were conducted in 2015 at all confirmed breeding sites to estimate reproductive effort (breeding population size). Egg mass counts are a commonly used proxy for the size of breeding wood frog populations since the number of breeding females at a site is correlated with the number of egg masses deposited (each breeding female deposits one egg mass) (Crouch and Paton 2000). A "population" in this study was defined as all wood frogs using all breeding sites within the 1.5 km search radius of each study site. A "breeding aggregation" refers specifically to the number of breeding females (inferred from the number of egg masses) at individual breeding sites. Therefore, we classified each study site as a single population, which could be composed of multiple breeding aggregations, depending on the number of breeding sites.

Egg mass surveys were conducted in early May 2015. During surveys, two observers waded around each breeding site and visually identified masses. The two observers started at the same location and searched in opposite directions around the perimeter of the pool until they met. After meeting, observers searched the opposing member's side of the wetland to ensure masses had not been missed. Masses were marked with flagging tape to avoid recounting during subsequent surveys. Search time for egg mass counts was commensurate with wetland size. After the wetland had been searched, egg masses were counted by visual inspection or feeling beneath the water surface if masses were layered (Baldwin et al. 2006*a*). Two egg mass counts were conducted at each wetland between May 6 and May 21, 2015 (Table A1); this ensured masses from individuals who bred after the initial survey were not missed.

All standing water of each breeding site was searched with the exception of two larger permanent beaver ponds in C1 (Table A1) where springtime water depths >1.0 m restricted search effort to emergent vegetation zones within 6.0 m of shore. However, due to the tendency of wood frogs to breed in communal aggregations and for resulting egg masses to be localized, we are confident that all egg masses were identified during surveys.

The permanency of breeding sites was based on Alberta's Wetland Classification System (ESRD 2015). Sites were classified as seasonal (dries during spring or summer most years), semi-permanent (inundated year-round, except during drought years), or permanent (holds water year-round). Wetland permanency was based on 3 years (2014–2016) of observations of breeding site hydrology.

Proximity to breeding sites

Euclidean distance of each pitfall array to the nearest breeding site was measured and used as an index of breeding site proximity using the "Generate Near Table" tool in ArcMap 10.3 (ESRI 2016). Wood frogs show high breeding site fidelity (Berven and Grudzien 1990; Vasconcelos and Calhoun 2004) with the location of breeding sites influencing upland distributions outside of the breeding season. Sites were only included in proximity analysis if (1) they supported breeding aggregations of >3 egg masses or (2) they retained water past May 31. For example, in study sites D1 and C1, several small sites (ATV ruts on access trails, Fig. A3) were identified that supported 1–3 egg masses but dried rapidly following egg deposition (before May 31); these sites were not included in proximity analysis.

Estimating soil wetness

As an estimate of wetness at pitfall arrays, the mean predicted depth-to-water (DTW) was used from the wet areas mapping (WAM) model. WAM is an airborne LiDAR-based terrain moisture model that predicts expected flow channels and associated water accumulation (depth to water) patterns at 1 m resolution of digital elevation (Murphy et al. 2008; White et al. 2012). DTW is defined as the depth to the expected water table; fully saturated soil or surface water is predicted when DTW equals zero, whereas higher values indicate increasing levels of dryness (Murphy et al. 2008). The main adjustable parameter in the WAM model is the flow initiation threshold (FIT), which represents the catchment area over which water is expected to accumulate (White et al. 2012). FIT values within the WAM model range from 0.5 to 16 ha. Lower FIT values (0.5 and 1 ha) provide a more optimistic prediction of wet areas that might be typical of wetter, early spring conditions, whereas higher FIT values (8 and 16 ha) mimic drier, late summer conditions (White et al. 2012).

In the boreal region of northwest Alberta, seasonal or semi-permanent wetlands and small streams, as well as temporary aquatic "non-wetland" features (e.g., ephemeral draws or pools), are highly variable with respect to hydrology, and may contain standing water for only a brief period after spring snowmelt or heavy rainfall (ESRD 2015). WAM is a static model, meaning that model outputs (such as DTW) do not vary among years and thus do not consider interannual or seasonal conditions that may influence the location, extent, and permanence of wet areas within a forested landscape. Despite this limitation, the effectiveness of the DTW index has been verified in several regions of Alberta, including EMEND sites (White et al. 2012) and it may serve as a tool for identifying potential terrestrial habitat for anuran amphibians.

Mean DTW was calculated using the focal statistics tool in ArcMap 10.3 (ESRI 2016) from 20 m circular buffers around each pitfall array that prevented overlapping buffers between adjacent arrays. A set of univariate general linear mixed models (GLMMs) was run separately for early and late season captures, and the best supported model (i.e., FIT value) for each season was assessed using Akaike Information Criterion corrected for small sample sizes (AICc) (Table A2). For early season, almost all FIT models ranked lower than a null model (no DTW effect included) except FIT 0.5 ha. The difference in support between the 0.5 ha model and the null model, however, was marginal (ΔAICc < 2). For late season, the 8 ha FIT was the best supported model, and therefore, was used for all final analyses to keep the moisture index consistent between early and late season models.

Statistical analysis

Wood frog captures were standardized to "catch per unit effort" (CPUE) ((total frog captures at array/# of trap nights) $\times$ 100). "Trap nights" is defined as the number of nights pitfall arrays were actively trapping multiplied by the number of pitfall traps open during that period. GLMMs with a Gaussian response were used to test which variables had the greatest influence on adult wood frog captures among different study sites (see below for treatment of YOY captures). Wood frog captures (CPUE) were pooled across all trapping sessions for adult frogs only and used as the final response variable. Pitfall arrays therefore acted as independent units of observation. CPUE values were natural log transformed to meet regression

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assumptions; normality and homoscedasticity were assessed visually using boxplots and Shapiro–Wilk tests. Transformed data met all assumptions aside from three outliers with high capture numbers that were retained in all models to maintain sample size.

All models included forest treatment variables of retention level and forest cover type. Inclusion of other predictors, including breeding site proximity, and predicted soil moisture (mean DTW), as well as their interaction terms, were first examined as univariate GLMMs to assess their individual importance. Significance of individual predictors was determined using log-likelihood ratio tests where nested candidate models were compared with a null model with only random effects (study area); models were evaluated as having good fit if they explained significantly more variation in adult wood frog captures than this null model with no fixed effects. Fixed effects included retention level, forest type, soil moisture, breeding proximity, and interaction terms. All statistical analyses were conducted in R version 3.2.5 (R Development Core Team 2016).

YOY frogs represent a distinct and highly vagile life history stage; differences in the number and permanency of breeding sites (i.e., permanent, semi-permanent, or seasonal wetlands) among study sites meant some study sites had few or no YOY, while others had many. Given this high variation, data from YOY frogs were not analyzed statistically.

Results

Capture summary

In 2014, 114 wood frogs were captured over 1148 trap nights between July 14 and August 25 (86 adults, 28 YOY). In 2015, 847 wood frogs (482 adults, 365 YOY) were captured over 5170 trap nights between May 10 and August 24 across four study sites (Table 1). In 2015, both adult and YOY capture rates varied among study sites and seasons. For all study sites, adult capture rates were higher early versus late in the season (Table 1; Fig. 2). In 2015, YOY captures were higher in the two conifer sites (C1 and C2) compared with the two deciduous stands (D1 and D2). YOY captures at three sites (D2, C1, and C2) reflected the fact that some or all breeding habitats at these sites retained water long enough for tadpoles to metamorphose (Table A1). Only one YOY was captured in the second deciduous stand (D1) as a result of drying of all breeding habitats prior to larval metamorphosis.

There were a total of 8 recaptures in 2014, and 28 recaptures in 2015, all of which were adult age class. All except one recapture occurred at the pitfall array of original capture. In the lone exception, a single adult female (weight = 13.0 g, SUL = 50 mm) in C1 was captured at a different pitfall array 88 m from the array of original capture. In no instances were frogs documented moving between adjacent harvest treatments.

GLMMs and seasonal capture rates

In 2015, the final model for early season captures for adult wood frogs included only the study design variables of retention level ($p = 0.463$) and forest cover type ($p = 0.762$), with neither variable significantly explaining variation in capture rates (Table 2). No consistent trends were apparent in adult capture rates across retention levels in either forest type during early season sampling in 2015. For late season capture of adults, the final model included three variables: retention level, which alone was not significant ($p = 0.523$); the significant variable of forest type ($p = 0.031$); and the significant interaction between these variables ($p = 0.025$; Table 2). With respect to forest type, abundance was significantly higher in the two conifer study sites compared with deciduous sites during the late season (Fig. 2). Based on the model coefficient for forest type ($\beta = -0.177 \pm 0.067$), relative abundance of adult wood frogs is expected to be 16% higher in conifer sites relative to deciduous sites. The significant interaction indicates that there was an effect of retention that depended on forest type. During late season, relative abundance decreased with retention level in deciduous-stand sites, with slightly higher capture rates observed in clearcuts and 20% retention relative to 50% retention and uncut controls (Fig. 2). In contrast, conifer sites saw increases in relative abundances with retention level during late season, with capture rates slightly higher in 50% retention and controls relative to clearcuts and 20% retention. The interaction effect, however, was weak, and differences in capture rates among retention levels in both deciduous and conifer stands were relatively small. Based on the model coefficient ($\beta = -0.004 \pm 0.002$), relative abundance of adult wood frogs is expected to increase by 0.4% with each % increase in retention in conifer forests, or decrease by 0.4% with each % decrease in retention in deciduous forest.

Breeding site proximity had no significant effect on adult wood frog capture rates in either season and was not included in either of the final models. Soil moisture was significant in the initial univariate models for only the late season ($\beta = -0.084 \pm 0.035$; $p = 0.032$), with higher capture rates observed at pitfall arrays with higher predicted moisture (lower DTW; Table A3). This translates into an expected 8% increase in relative abundance per 1 m decrease in DTW (an increase in predicted soil moisture). Soil moisture was not independent of forest type, with conifer sites having higher predicted moisture than deciduous sites (Fig. A4). Moisture and the associated interaction terms with forest type were therefore excluded from the final model.

Breeding sites and reproductive effort

The number of breeding sites varied considerably among the four study sites, as did wetland permanency and associated wood frog reproductive effort (number of egg masses) (Fig. A4; Table A1). Site D1 had eight breeding sites (seven seasonal and one semi-permanent) that dried prior to successful emergence of metamorphs. Egg mass counts at these sites ranged from 2 to 27, $\bar{x} = 11.1 \pm 8.8$. In contrast, site D2 had a single semi-permanent breeding site containing two egg masses. Although this represents a relatively small breeding population, the site never completely dried and produced YOY. Site C1 was characterized by two large permanent beaver ponds (1.68 and 2.093 ha) within a valley that bisected the terrestrial sampling sites. Both beaver ponds lasted the entire summer and supported the majority of wood frog breeding in C1, with 269 egg masses counted in the

Table 1. Wood frog (*Lithobates sylvaticus*) captures at study sites sampled at EMEND in 2014 and 2015.

					Counts			Capture rates (CPUE)		
Year	Season	Study site	Forest cover	Trap nights	Adult	YOY	Total	Adult	YOY	Total
2014	Late	D1	Deciduous	604	49	7	56	8.11	1.16	9.27
		C1	Conifer	544	37	21	58	6.80	3.86	10.66
2015	Early	D1	Deciduous	744	109	0	109	14.65	0	14.65
		D2	Deciduous	604	65	0	65	10.76	0	10.76
		C1	Conifer	736	70	0	70	9.51	0	9.51
		C2	Conifer	486	99	0	99	20.37	0	20.37
	Late	D1	Deciduous	688	40	1	41	5.81	0.15	5.96
		D2	Deciduous	608	26	23	49	4.28	3.78	8.06
		C1	Conifer	664	48	201	249	7.23	30.27	37.50
		C2	Conifer	640	58	107	165	9.06	16.72	25.78

*Only two study sites (D1 and C1) were sampled in 2014 and sampling was restricted to later summer (July–August). In 2015, two additional study sites were added (D2 and C2) for a total of four study sites. Sampling was conducted throughout the spring and summer (May–August) in 2015. **Note:** Values include actual counts and standardized capture rates (captures/100 trap nights) for adult, young-of-the year (YOY), and total captures (adults + YOY). Trap nights denote the cumulative number of nights all trapping arrays were open within each study site.

northern pond (GBN) and 285 masses in the southern pond (GBS). Six smaller seasonal breeding sites located closer to upland pitfall arrays supported comparatively low reproductive effort (range: 1–10 masses); all dried before metamorphosis could occur. Site C2 contained a single semi-permanent breeding site that was not surveyed for egg masses in 2015, but had 37 masses in 2016.

Discussion

Retention level and forest type

We hypothesized that wood frog abundance would be positively related to the extent of deciduous canopy cover, as a deciduous overstory would create a greater abundance of preferred forest microhabitats such as leaf litter and woody debris. Therefore, we predicted that deciduous sites would have higher wood frog abundance relative to conifer sites overall, and that in deciduous sites there would be a greater abundance of wood frogs in unharvested controls and 50% retention, relative to 20% retention and clearcut treatments. Conversely, we predicted lower relative abundance of adult wood frogs in conifer sites relative to deciduous sites, but expected to observe higher abundance in lower retention (20%) and clearcuts, as post-harvest aspen regeneration and understory development would provide more suitable refuge and foraging habitats compared with mature conifer (controls) and 50% retention stands.

Although we did observe effects of harvest retention and forest type on wood frog abundance, our observations were not concordant with our initial predictions, and were dependent on season. During early season, there was no consistent pattern in adult wood frog abundance across retention levels in either forest type or between forest types in general. In late season, however, the relationship between adult wood frog abundance and retention level differed between sites dominated by deciduous versus coniferous forest. In deciduous sites, late season capture rates generally decreased with retention level, whereas in conifer sites, capture rates increased with retention level. This interaction, however, was weak, as differences in capture rates between retention levels were relatively small and marked by high variability among pitfall arrays within treatments. Based on the model coefficient ($\beta = -0.004 \pm 0.002$), relative abundance of adult wood frogs would only be expected to increase by 0.4% with each % increase in retention in conifer forests, or conversely, to decrease by 0.4% with each % increase in retention in deciduous forests.

In deciduous sites, we predicted that relative abundance would increase with retention level, with adult wood frog abundance expected to be lower in response to a lack of mature (60–80 years) deciduous canopy cover in sites with lower retention (20% and 0% (clearcuts)). In fact, early season capture rates in clearcut and 20% retention treatments were comparable to those in 50% retention and unharvested controls. In the late season, capture rates were actually higher in lower retention treatments relative to 50% retention and controls. In conifer sites, we predicted adult abundance would decrease with amount of retention, owing to early aspen regeneration that provided more suitable upland conditions (e.g., greater surface cover and associated microclimate) in low retention stands relative to higher retention and mature (unharvested) conifer stands. Although there was no significant difference in capture rates across retention types during the early season, capture rates generally increased with retention level during the late season, contrary to predictions.

These results may be explained, in part, by the levels of forest regeneration at our study sites. Timber harvest treatments were applied at EMEND 17 years previous to measures of wood frog responses, thus likely providing sufficient time for recovery of habitat features impacted during harvest. Reduced abundance of wood frogs and other forest-associated amphibians following timber harvesting is often attributed to the loss of canopy cover, and other forest elements, such as leaf litter and woody debris that provide shade and habitat for refuge and foraging (DeMaynadier and Hunter 1995,

Fig. 2. Comparison of wood frog (*Lithobates sylvaticus*) capture rates across retention levels for adult (top, A and B), and YOY (bottom, C and D) wood frogs during early season (May—June) and late season (July—August) sampling at four study sites at EMEND in 2015 (D—deciduous stands, C—conifer stands). Values shown are mean ± standard deviation. No YOY wood frogs were captured in the early season.

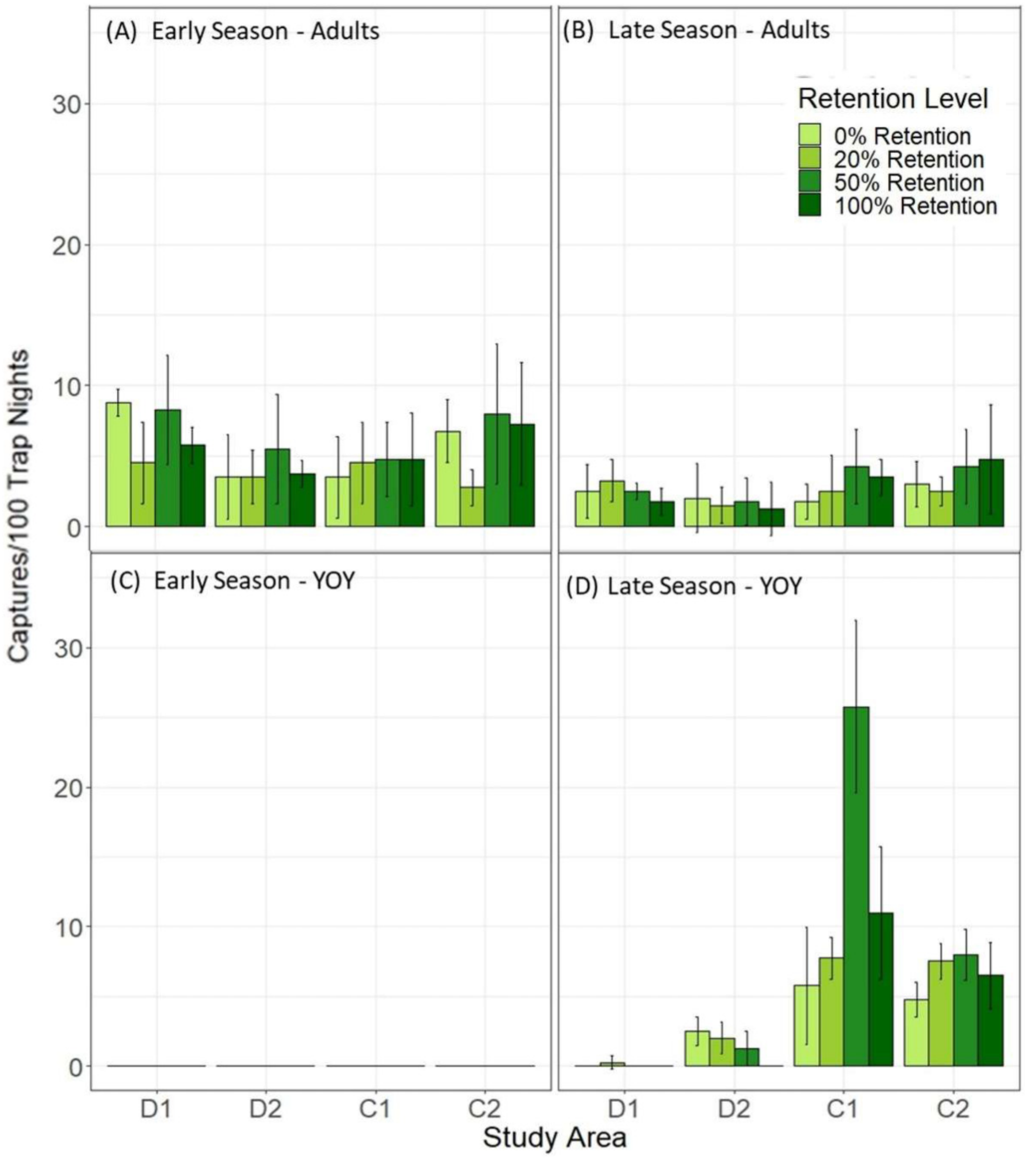

Table 2. Model results describing adult wood frog capture rates for early (May–June) and late (July–August) season sampling in 2015.

Season	Predictor	Coefficient	Standard error	*t* value	*p* value
Early	Retention	0.001	0.001	0.735	0.463
	Forest	−0.048	0.157	−0.304	0.762
Late	Retention	0.001	0.001	0.640	0.523
	Forest type	**−0.177**	**0.067**	**−2.660**	**0.031**
	Retention × forest	**−0.004**	**0.002**	**−2.100**	**0.025**

Note: Final models included only predictors and interactions that were statistically significant; these are bolded in the table.

1998, 1999; Semlitsch et al. 2009), which could be mitigated by retention of mature trees. Early, post-disturbance forest succession in the boreal mixedwood typically involves a transition from shade-tolerant broadleaf species (trembling aspen, balsam poplar) to conifer species (Lieffers et al. 1996; Macdonald and Fenniak 2007; Gradowski et al. 2010). At EMEND, post-harvest clearcuts and lower retention treatment stands are dominated by trembling aspen in both deciduous and conifer-dominated forests (Craig and Macdonald 2009). Therefore, leaf litter and canopy may have already compensated for the removal of mature trees in clearcut and lower retention treatments. The forest floors of study sites were generally characterized by high understory plant cover, including a mix of woody shrubs, grasses, and forbs. Further, though not formally sampled in all study sites, coarse woody debris was abundant in all retention levels and forest types, suggesting there was ample cover for wood frogs.

Forest type alone also had a significant effect on adult wood frog abundance, but only during the later summer months (July and August), when capture rates were significantly higher in the two conifer sites versus the two deciduous sites. This result differs from previous research suggesting wood frogs prefer deciduous forest over conifer forest (Roberts and Lewin 1979; Browne et al. 2009). For example, in northeastern Alberta, Constible et al. (2001) found greater relative abundance of wood frogs at lakes surrounded by deciduous forests (Owl River) compared with those dominated by conifer forest (Mariana Lake), a difference the authors attributed to potential variation in breeding site quality between the two study areas.

Convergence of habitat in deciduous and conifer sites from mature trees (preharvest) to early successional stands dominated by young trembling aspen helps explain comparable densities of wood frogs across sites. Prior to harvesting, conifer-dominated stands consisted predominantly (>70%) of mature trees, particularly white spruce (Volney et al. 1999; Macdonald and Fenniak 2007). In conifer sites at EMEND, the forest floor of undisturbed, control stands was dominated by moss and lichens and did not have the leaf litter layer characteristic of control stands at deciduous sites (M. Robinson, personal observation). These observations are consistent with preharvest data at EMEND showing deeper litter layers in unharvested deciduous-dominated sites relative to coniferous sites (Macdonald and Fenniak 2007).

Soil moisture

We predicted relative abundance of wood frogs would be related to local soil moisture, since wood frogs seek out moist microhabitats during post-breeding movements (Baldwin et al. 2006*b*; Rittenhouse and Semlitsch 2007*a*). We therefore expected abundance to be higher at sites with higher predicted soil moisture, irrespective of retention treatment or forest type. In agreement with these predictions, we found that soil moisture, as predicted by the DTW index, had a significant effect on capture rates during late, but not early season sampling sessions; adult wood frog captures were higher in areas predicted to have wetter soil conditions (i.e., lower DTW) in the late season. Variation in soil moisture among sites may also help explain the difference in abundance during the late season between deciduous and conifer forests.

These findings are not surprising given the association of wood frogs with moist microhabitats observed in other studies (Roberts and Lewin 1979; Rittenhouse and Semlitsch 2007*a*; Freidenfelds et al. 2011). For example, Freidenfelds et al. (2011) found that radio-tracked wood frogs freely traversed recent clearcuts in Maine, USA, but were often located in pools, puddles, and other moist refugia. The authors suggested that availability of standing water and moist areas in clearcuts may benefit migrating amphibians, and that the absence of such features may help explain wood frog avoidance of clearcuts in other studies. Previous studies also suggest that wood frog movements may only be limited during certain times of their active season in post-harvest environments. Late spring and early summer, when adult capture rates were highest, correspond to post-breeding movements of wood frogs from breeding sites into upland foraging habitat. This period also coincides with wetter forest floor conditions (more standing water) observed at study sites and greater cumulative rainfall, relative to July and August (M. Robinson, personal observation). Similarly, Popescu et al. (2012) found higher captures of both adult and juvenile (YOY) wood frogs in unharvested and partial cut treatment stands relative to clearcuts over a 6-year post-harvest study period, but differences were only observed during summer and fall months (June to September), and not during the spring migration period (April to May).

Previous studies have found that wood frogs move opportunistically during periods of rainfall (Rittenhouse and Semlitsch 2007*b*, 2009; Taylor and Paszkowski 2017). For all sites combined, we recorded our highest capture rates of adult wood frogs during, or shortly after (1–2 days) periods of rainfall during both the early and late seasons. During the early season, captures may have represented adult frogs migrating to forested summer habitats. During late season, however, high captures during or shortly after rain events may have represented movements within upland summer habitats by frogs foraging or seeking new refuge microhabitats.

Breeding site proximity

Abundance of adult wood frogs was predicted to be positively related to breeding site proximity, with capture rates expected to decline as the distance to the nearest breeding site increased. Contrary to expectations, there was no effect of breeding site proximity on abundance during either the early or late season. This result was unexpected given previous research findings in Alberta showing declining densities of wood frogs and other amphibians with increasing distance from wetlands, lakes, and other potential breeding habitats (Roberts and Lewin 1979; Hannon et al. 2002; Macdonald et al. 2006; Okonkwo 2011).

These results may be explained by variation in the density of breeding sites and the availability of other wet areas (discussed above) among the four study sites. Population studies for aquatic-breeding amphibians are often centered around a single focal breeding site (e.g., lake, wetland, vernal pool), with populations defined as the individuals sampled at the breeding site and within a defined area of surrounding upland habitat. We frequently captured frogs at large distances from known breeding sites (range of pitfall array distance from nearest breeding site used in proximity analysis: 74.7–961.2 m), confirming that adult wood frogs may use forested upland habitat far removed from breeding sites. Two of our study sites (D1 and C1) had a relatively high number of breeding sites (eight at each site) compared with D2 and C2, each of

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which contained only one. Because most breeding habitats at D1 and C1 supported relatively small breeding aggregations (≤3 egg masses), and were therefore not included in proximity analysis, the relatively high number of breeding habitats compared with upland trapping sites may have obscured any effect of breeding site locations on upland densities.

Variation in breeding habitat, reproductive effort, and YOY

Due to the nature of the EMEND design, we were unable to control for the number, type, and location of breeding habitats at our study sites. This precluded a controlled comparison of YOY metrics (e.g., production, dispersal distances) among sites. We did observe breeding at a variety of permanent and temporary aquatic habitats across our four study sites (Table A1; Fig. A1), and differences in YOY captures reflected variation in the size and permanency of breeding sites. The sites with the highest YOY captures both contained permanent breeding sites (two beaver ponds in C1, and a single permanent wetland in C2). In comparison, YOY captures were relatively low at the two deciduous sites, which were supported by smaller, more temporary breeding habitats. At D1, we documented relatively high reproductive effort (88 total egg masses) across eight breeding sites; however, all sites dried prior to larval metamorphosis, resulting in only a single YOY capture. In comparison, D2 contained only a single, small breeding site (area = 33.7 m^2; max depth = 70 cm), but it retained water until at least August 31, allowing successful recruitment of metamorphs (23 captures of YOY). These findings underscore the importance of considering the number and type of potential breeding sites within harvest areas for maintaining local amphibian populations. For wood frogs, even a single, small seasonal or semi-permanent wetland can make a considerable contribution to local populations in at least some years.

Conclusion

Our results further highlight the disparity in responses of amphibian populations to timber harvesting and forest management in North America. While previous studies in Alberta that focused on large lakes and wetlands have shown that wood frogs are tolerant of recent disturbance from harvesting (Constible et al. 2001; Hannon et al. 2002; Macdonald et al. 2006), studies from other parts of North America have found that negative effects of harvesting can persist for several years (e.g., >6 years in Maine, USA) (Popescu et al. 2012). Our study may represent a particularly accurate characterization of the variation in breeding and non-breeding habitat suitability for wood frogs in early successional post-harvest forests in the boreal mixedwood, as we incorporated a variety of factors such as breeding site distribution and ground moisture. We recognize that our study examined abundance of wood frogs at the scale of retention harvest treatments (~4–10 ha) implemented in the EMEND research area, whereas timber harvest blocks in the boreal mixedwood are typically much larger (>100 ha). Likewise, retention harvest in Alberta reflects a variety of dispersed and clumped patterns, depending on the desired targets of forest companies. Yet, as a whole, we detected a weak effect of retention harvesting on adult wood frog abundance in 17-year post-harvest forests, and that the effect was dependent on season and forest type. Our results suggest that habitat changes associated with early forest regeneration may help provide suitable upland habitat for wood frogs, in both deciduous- and (previously) conifer-dominated forests. Further, availability of wet areas may help mitigate the effects of habitat change associated with forest harvesting and subsequent regeneration, especially during drier summer months.

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The data that support the findings of this study will be openly available on the Dryad online repository at doi:10.5061/dryad.mcvdnck30 following publication of this manuscript.

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Competing interests

The authors declare that there are no competing interests. The funding agencies had no role in the design of the study; in the collection, analyses, or interpretation of data; or in the preparation of the manuscript.

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Appendix A

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Table A1. Summary of breeding sites identified at four study sites at EMEND in 2015, including coordinates (latitude and longitude; coordinate system: WGS84 standard), wetland surface area, max depth, egg mass survey dates, total egg masses, drying date, permanency, and whether site was used in breeding site proximity analysis.

Study site	ID	Coordinates (wetland center) Latitude	Longitude	Surface area (m^2)	Max depth (cm)	Survey date 1	Survey date 2	Total masses	Drying date	Permanency	Proximity analysis (yes/no)
	EA53	56.750560	−118.324545	16.5	40	May 8	May 22	2	May 30	Seasonal	No
	CA4	56.749467	−118.321710	47.1	40	May 8	May 13	2	May 30	Seasonal	No
	A1	56.744977	−118.324005	82.1	29	May 6	May 13	4	May 30	Seasonal	Yes
	CA2	56.748804	−118.319872	13.7	35	May 8	May 13	10	May 30	Seasonal	Yes
D1	EMD8	56.750873	−118.329757	74.9	40	May 8	May 15	10	June 10	Seasonal	Yes
	A2	56.745426	−118.323154	175.1	31	May 6	May 13	17	May 30	Seasonal	Yes
	EA1	56.750386	−118.338309	72.0	46	May 7	May 15	17	July 7	Semi-permanent	Yes
	EMD7	56.752834	−118.336254	215.2	30	May 7	May 22	27	June 10	Seasonal	Yes
D2	I1	56.823548	−118.366577	33.7	70	May 9	May 25	2	–	Permanent	Yes
	EA115	56.786490	−118.362921	27.5	13	May 13	–	1	May 25	Seasonal	No
	EA144	56.798237	−118.376447	28.0	30	May 14	–	1	May 25	Seasonal	No
	G2	56.799587	−118.375482	73.5	40	May 14	–	2	May 25	Seasonal	No
C1	EA148	56.797511	−118.372245	83.4	30	May 14	–	3	May 25	Seasonal	No
	G3	56.799727	−118.375012	43.4	40	May 14	–	3	May 25	Seasonal	No
	EA152	56.798112	−118.372333	201.5	60	May 14	–	10	June 15	Seasonal	Yes
	GBN	56.799749	−118.369691	16 750	>100	May 14	–	269	–	Permanent	Yes
	GBS	56.789321	−118.370211	20 930	>100	May 14	–	285	–	Permanent	Yes
C2	*HP1	56.802247	−118.330674	232.8	53	–	–	*37	–	Semi-Permanent	Yes

*Egg mass survey was not possible at the single breeding site in C2 in 2015. Total egg mass count shown was from the following year (2016) and used in concert with pool permanency as basis of inclusion in proximity analysis.

Table A2. Results of GLMMs comparing seven different flow initiation threshold (FIT) values for depth-to-water on adult wood frog capture rates across four study sites at EMEND in 2015.

Season	DTW model	DF	LogLik	AICc	ΔAICc	w_i
Early	DTW 0.5	4	−22.421	53.521	0	0.232
	NULL	3	−23.890	54.180	0.659	0.167
	DTW 16	4	−22.840	54.358	0.837	0.153
	DTW 1	4	−23.195	55.068	1.547	0.107
	DTW 8	4	−23.213	55.104	1.584	0.105
	DTW 2	4	−23.326	55.329	1.809	0.094
	DTW 4	4	−23.501	55.681	2.160	0.079
	DTW 12	4	−23.715	56.109	2.588	0.064
Late	DTW 8	4	−6.194	21.066	0	0.315
	DTW 4	4	−6.810	22.299	1.233	0.170
	DTW 0.5	4	−7.062	22.803	1.736	0.132
	DTW 12	4	−7.346	23.370	2.304	0.099
	NULL	3	−8.496	23.391	2.325	0.098
	DTW 2	4	−7.548	23.774	2.708	0.081
	DTW 16	4	−7.854	24.385	3.319	0.060
	DTW 1	4	−8.161	25.000	3.933	0.044

Note: Captures were converted to "catch per unit effort" (CPUE) ((total adult captures at array/# of trap nights) × 100) and used as the final response variable. Individual pitfall arrays at each study site acted as independent units of observation. CPUE values were Ln-transformed to meet regression assumptions of normality and equal variance. DF, degrees of freedom; LogLik, log likelihood ratio; AICc, Akaike information criterion corrected for small sample size; ΔAIC_c, delta AIC_c; w_i, Akaike weight.

Table A3. Results of initial GLMMs explaining early and late season adult wood frog capture rates at four study sites sampled at EMEND in 2015.

Season	Model	Predictor	Coefficient	Standard error	*t* value	*p* value
Early	Retention	Retention	0.001	0.001	0.735	0.463
	Forest	Forest	−0.048	0.157	−0.304	0.762
	Moisture	Moisture	−0.057	0.049	−1.14	0.259
	Breeding	Breeding	0.013	0.053	0.252	0.803
	Retention × forest	Retention × forest	−0.001	0.002	−0.657	0.787
Late	Retention	Retention	0.001	0.001	0.640	0.523
	Forest	Forest	−0.177	0.067	−2.660	**0.031**
	Moisture	Moisture	−0.084	0.035	−2.420	**0.032**
	Breeding	Breeding	−0.033	0.039	−0.850	0.407
	Retention × forest	Retention × forest	−0.004	0.002	−2.100	**0.025**

Note: Captures were converted to "catch per unit effort" (CPUE) ((total adult captures at array/# of trap nights) × 100) and used as the final response variable. Individual pitfall arrays within each study area acted as independent units of observation. CPUE values were Ln-transformed to meet assumptions with normality and equal variance. *p* values in bold indicate statistical significance of a predictor at $\alpha = 0.05$.

Fig. A1. Location of breeding sites across four study sites sampled at EMEND in 2015. Marker size is proportional to wetland surface area. The number of egg masses counted at each breeding site is shown next to individual markers on four inset maps (right). Empty polygons represent other timber harvest treatment areas not sampled in the current study. The matrix areas (white) surrounding the EMEND research forest consist of a patchwork of mixedwood forest stands of varying age and harvest histories, interspersed with lakes, rivers, wetlands, and streams. Both the base map and polygons showing EMEND harvest treatments are from the EMEND database and were ultimately provided by Mercer Peace River Pulp Ltd. (1999). Map projection: NAD83, UTM Zone 11U.

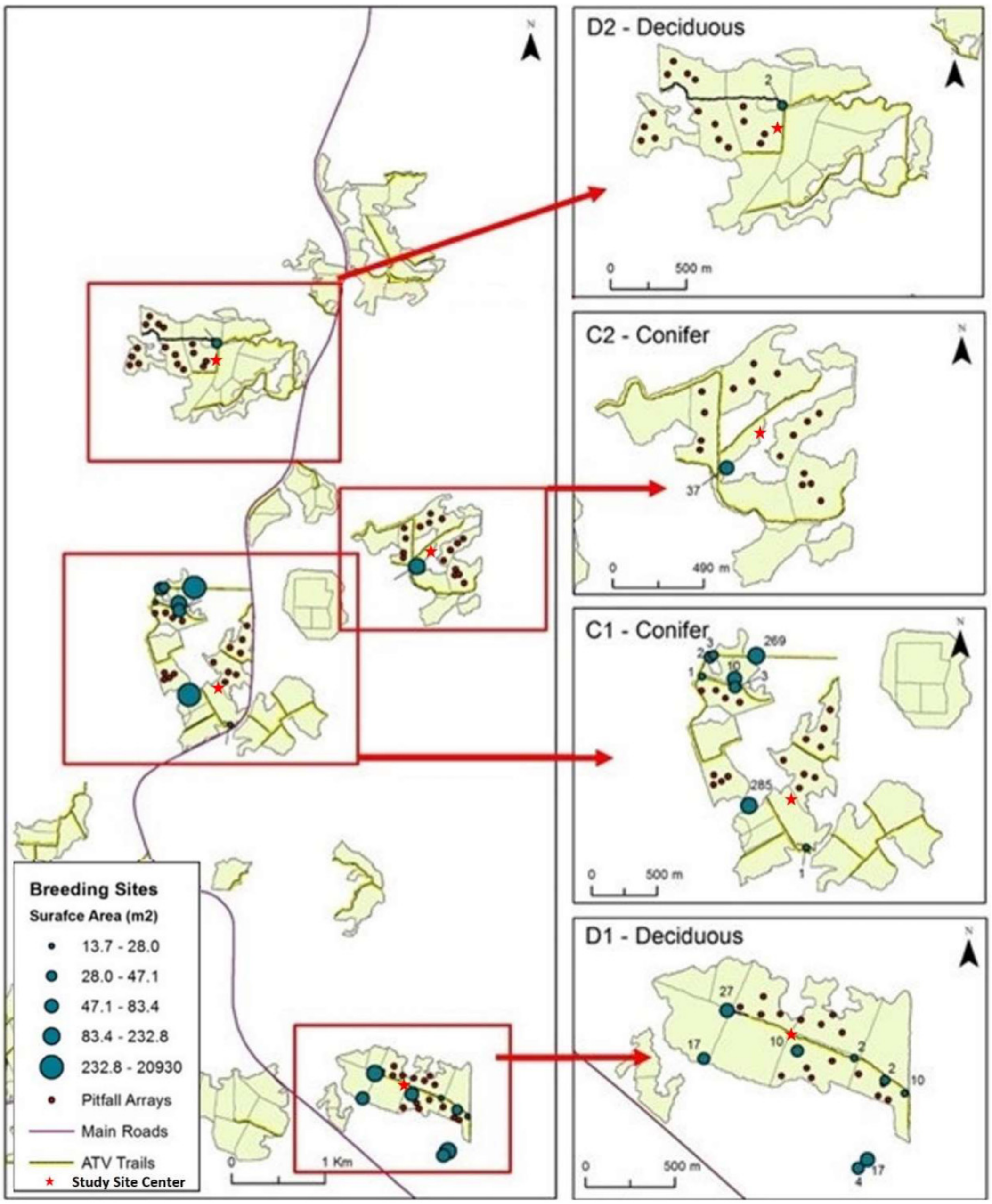

Fig. A2. Pitfall trapping array design used to live capture wood frogs. Photo of actual array (A) and design dimensions (B).

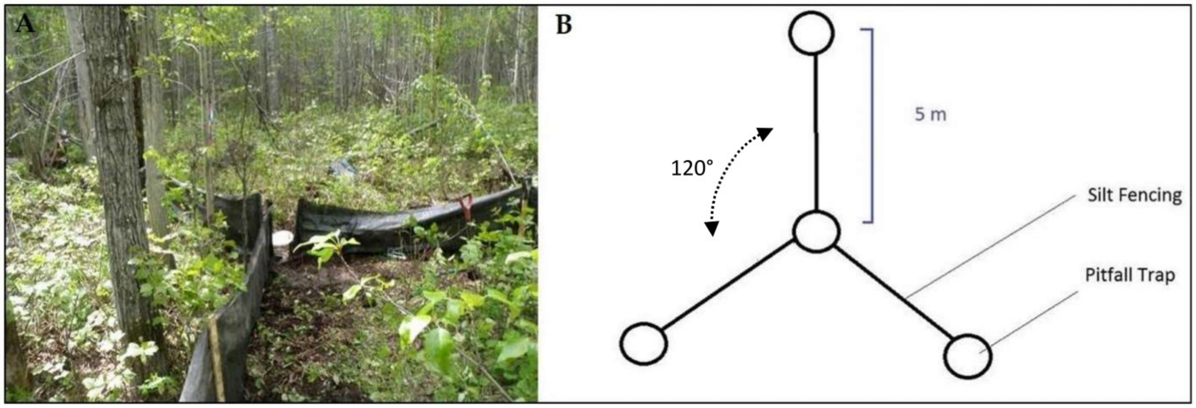

Fig. A3. Example breeding habitats across four terrestrial study sites at EMEND. (A) Seasonal (anthropogenic ATV ruts); study site D1. (B) Semi-permanent wetland; study site D2. (C) Semi-permanent wetland; study site C2. (D) Permanent wetland (beaver pond); study site C1.

Fig. A4. Mean predicted moisture among four study sites sampled at EMEND in 2015. Soil moisture was estimated based on the depth-to-water (DTW) obtained from the wet area mapping (WAM) model. DTW describes the predicted distance to the water table. Lower values indicate greater predicted wetness.