Forest Harvesting Generates Attractive Breeding Habitat for Male Eastern Gray Treefrogs (*Dryophytes versicolor*) at their Poleward Range Edge

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Abstract

Climate change and anthropogenic disturbance are changing many species' ranges. Anthropogenic habitat modification typically restricts species ranges, but at poleward range edges it could create warmer microclimates that offset marginal climatic conditions. I hypothesized that clearcutting is creating warmer, more favourable breeding habitat at the expanding, poleward range edge of the Eastern Gray Treefrog (*Dryophytes versicolor*). Using an autodetection tool and passive acoustic monitoring, I found higher calling activity at recently clearcut ponds compared to forested ponds. Structural equation modelling revealed significant direct effects of warmer air and pond surface temperatures on calling activity. Reduced canopy cover, leading to higher pond surface temperatures, were the key mediators between harvesting and increased calling activity. Clearcut ponds were 1.9±0.5 degrees warmer than forested ponds during the breeding season, which could facilitate faster tadpole development. However, I found no difference in tadpole food resources (periphyton production) between clearcut and forested ponds. These findings demonstrate how microclimate and anthropogenic disturbance influence breeding habitat at a poleward range edge. However, we still require crucial information on pond preference of females, tadpole development, and juvenile survival as a measure of fitness, and to determine whether anthropogenic habitat modification is facilitating this range expansion.

Land Acknowledgement

I respectfully acknowledge that the research for this project took place on the traditional lands of the Anishinaabe, and the territories of the Fort William First Nation, Signatory to the Robinson Superior Treaty of 1850, and the Lac Des Mille Lacs First Nation, Signatory to Treaty 3.

I am grateful for the opportunity to live, learn, and work on this land. I recognize that a land acknowledgement is just one part of the broader work of reconciliation. This is an ongoing process, and I am committed to continuing to learn from and support Indigenous communities.

Through this acknowledgement, I honour the relationship of Indigenous Peoples with these lands and recognize their knowledge and stewardship.

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1 Introduction

Ecological dynamics at range edges determine whether species' ranges expand or contract. Understanding these dynamics is especially important because many species are shifting their ranges in response to recent climate change (Parmesan et al. 1999, Parmesan and Yohe 2003, Hickling et al. 2006, Parmesan 2006, Thomas 2010, Chen et al. 2011, Lenoir et al. 2020), but often in directions opposite to climatic expectations (Pinsky et al. 2020, Lawlor et al. 2024). Species range limits often reflect niche limits (Hargreaves et al. 2014, Lee-Yaw et al. 2016), which can be determined by various biotic and abiotic factors (deRivera et al. 2005, Sexton et al. 2009, Chen et al. 2011, Algar et al. 2013, Wisz et al. 2013). Niche limitation, whether due to low habitat quality or availability, means that edge populations live in marginal conditions. Poleward edges track more closely with marginal abiotic conditions and organisms' thermal limits, suggesting abiotic limitation, compared to equatorward edges, which tend to be mediated by biotic interactions (Paquette and Hargreaves 2021, Moore et al. 2023). Species whose poleward range is restricted by marginal conditions can increase range-edge occupancy or expand their range if environmental conditions change, their niche evolves, or they seek out less marginal microhabitats.

Climate and habitat quality both exert pressure at species' range margins and influence their dynamics (Hill et al. 2001, Warren et al. 2001, Platts et al. 2019). For example, areas that are suitable climatically may still be marginal if they lack quality habitat (Hill et al. 1999, Warren et al. 2001); concomitantly, species may be restricted to higher quality habitats in marginal climatic conditions (Oliver et al. 2009). Also, climate and habitat are not independent, as key habitat features, like food resources, are

themselves climate dependent (Arbeiter et al. 2016). Habitat structure can also offset the effects of marginal climate by generating more favourable microclimates (Algar et al. 2018, Zellweger et al. 2019, Higgins et al. 2024). Organisms may thus seek out more thermally favourable microhabitats (Bennie et al. 2013, Lawson et al. 2014, Pateman et al. 2016), especially under thermal extremes, to avoid reaching their thermal limits (Sunday et al. 2014, Pinsky et al. 2019). While thermal refuges are often considered in terms of cool microhabitats to avoid overheating (Huey et al. 2009, Sunday et al. 2014, Cheng et al. 2023), warmer refugia are also important in mediating cold conditions (Tourani et al. 2023), which are often prevalent at poleward range edges (Auge et al. 2023).

Forest harvesting, whether for logging or land-use conversion (e.g. the creation of agricultural land), creates open habitats with warmer daily temperatures due to reduced canopy cover (Chen et al. 1993). Although anthropogenic habitat modification often reduces habitat quality, it may create more thermally favourable habitat for some species, allowing for expansion into previously unsuitable areas. For example, Frishkoff et al. (2019) found that three *Anolis* lizard species at low elevations (where mean annual temperature is high) used cooler forest habitats but switched to warmer pasture microhabitats at higher elevations (colder mean annual temperatures). Similarly, two frog species both swapped from forest to disturbed habitat at higher elevations, with the rate of switching dependent on their thermal niche (Frishkoff et al. 2015). Together, these results suggest that the presence of warmer microhabitats may facilitate increased occupancy or range expansion at the cold range edge.

For oviparous organisms that do not exhibit parental care, the selection of breeding site is a key decision that adults make for offspring survival and thus their fitness. Organisms should therefore choose breeding (or oviposition) sites that are advantageous for offspring survival and development. Although there are notable examples of parental care in amphibians (Crump 2015, Machado and Macedo-Rego 2023), most do not exhibit parental care, and many are selective about breeding habitat conditions (Kiesecker and Skelly 2001, Touchon and Worley 2015, Buxton and Sperry 2017, Smith and Harmon 2019, Dimitrie and Benard 2023). For those that breed in aquatic environments, tadpole development rates increase with warmer temperatures, reducing the time to metamorphosis (Newman 1998). Adult amphibians may, therefore, select warmer breeding habitats that benefit offspring development (Hocking and Semlitsch 2007, 2008). However, adult survival may also affect breeding site selection, especially in iteroparous species. In many frog and toad (anuran) species, males call to attract females, which can be energetically costly (Taigen and Wells 1985), and increase their predation risk (Ryan et al. 1981, 1982). Males may therefore select breeding ponds in areas with abundant food supplies that allow them to replenish resources, or those with lower predation risk. Females incur energetic costs for egg production (Hayward and Gillooly 2011) and gravid females may also pay a locomotory cost via reduced mobility (Magnhagen 1991). Thus, when selecting breeding sites, individuals need to consider both benefits to their offspring and potential costs to adult survival.

Harvesting is a major anthropogenic disturbance in the boreal forest, altering habitats for many taxa, including amphibians. On average, 121,000 ha are harvested in Ontario, Canada per year (2009 - 2019; Ontario Ministry of Northern Development,

69 Mines, Natural Resources and Forestry 2021), and harvesting practices have changed the
70 composition of Canada's Boreal Forests (Bergeron and Fenton 2012). In particular, clear-
71 cutting followed by planting seedlings is common practice (Brandt et al. 2013,
72 Pohjanmies et al. 2017). Harvesting reduces canopy cover and creates warmer, drier
73 daytime microclimates than in forests (Chen et al. 1993, Rittenhouse et al. 2008, De
74 Frenne et al. 2019). These microclimates increase the risk of desiccation for adult
75 amphibians and can lead to increased mortality and reduced growth (Todd and Rothermel
76 2006, Todd et al. 2014). While responses are species-specific (e.g. Patrick et al. 2006), in
77 general amphibian abundance is reduced in early successional, clearcut habitats
78 (deMaynadier and Hunter Jr. 1995). The reduced abundance may also be due to increased
79 predation pressure with reductions in habitat complexity (Todd et al. 2008, Chang and
80 Todd 2023, Hagnier et al. 2025), though there are limited studies on this for amphibians.
81 The altered habitat may also affect the dispersal of juveniles from ponds post-
82 metamorphosis (Patrick et al. 2006, Rittenhouse et al. 2008, Popescu and Hunter Jr.
83 2011).

84 Although harvesting may increase risk for adults and juveniles, it could improve
85 habitat for tadpoles. Warmer, open canopy ponds can increase tadpole development rates
86 (Newman 1998, Skelly et al. 2002, Schiesari 2006, Hocking and Semlitsch 2008), which
87 may be especially beneficial when the growing season is short. Furthermore, warmer
88 temperatures and increased solar radiation can lead to higher periphyton growth,
89 increasing food resources for tadpoles (Feminella et al. 1989, Skelly et al. 2002, Burrows
90 et al. 2021a). However, there are trade offs: changes to tree species composition may alter
91 leaf litter inputs, which can reduce the quality of tadpole resources (Williams et al. 2008,

92 Stoler and Relyea 2011). As adults seek to maximize their fitness, they need to balance
93 these potential benefits of warmer breeding ponds within harvested areas for their
94 offspring with the costs of traversing through and calling in low quality habitat
95 (clearcuts).

96 Here, I test the hypothesis that human disturbance, specifically forest harvesting,
97 creates attractive breeding habitat for male Eastern Gray Treefrogs (*Dryophytes*
98 *versicolor*, Hylidae; gray treefrogs hereafter; Figure 1.1c) at their northern range edge.
99 Gray treefrogs reach the northern edge of their broad distribution in Northwestern
100 Ontario and Manitoba (Canada; Figure 1.1b), and anecdotal evidence suggests that their
101 range is expanding and occupancy is increasing at their northern range edge near Thunder
102 Bay, Ontario, Canada. Given extensive forest harvesting in this region over the past
103 century (Brandt et al. 2013), it is possible that increased availability of warmer breeding
104 habitats has contributed to this expansion, especially since experiments closer to the
105 range core demonstrate that gray treefrogs breed in artificial ponds in clearcuts placed
106 close to the forest edge (Hocking and Semlitsch 2007), where warmer temperatures
107 quicken tadpole development (Hocking and Semlitsch 2008). However, whether these
108 effects apply in natural systems, or whether they are strong enough to mediate marginal
109 conditions at the range edge is unknown. Here, I use passive acoustic monitoring and
110 auto-detection algorithms to determine calling activity of male gray treefrogs at ponds in
111 forested and recently harvested areas across the breeding season and use structural
112 equation modelling to identify the key habitat features that mediate the impacts of
113 harvesting on calling activity.

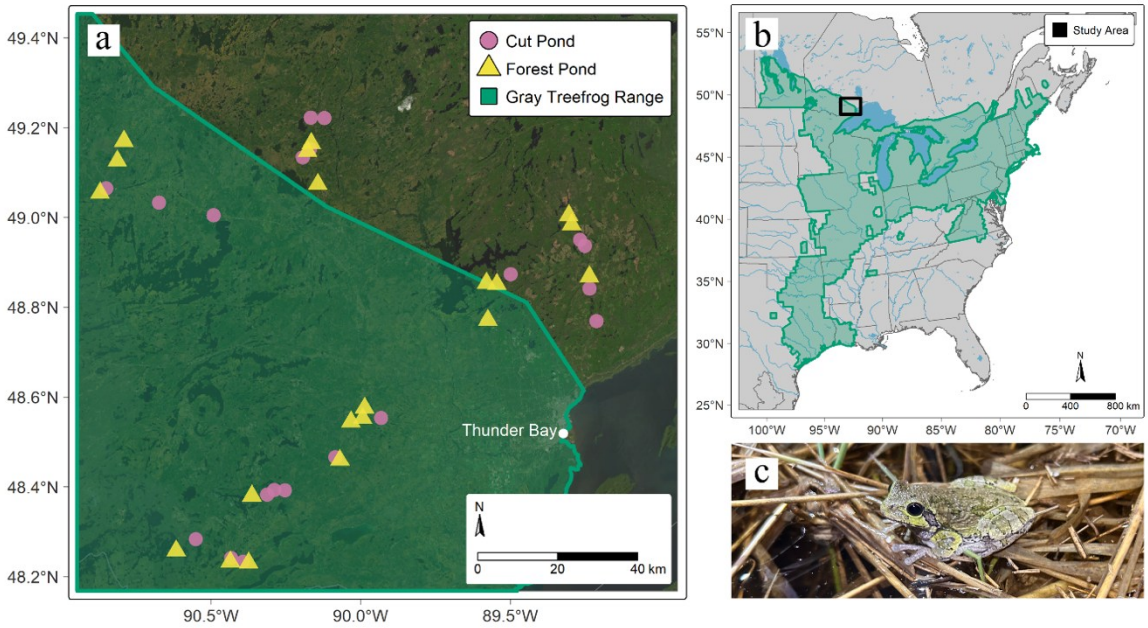

Figure 1.1 (a) Breeding ponds in clearcuts (pink circle) and forests (yellow triangle) studied at the northern range edge (green) of the Eastern Gray Treefrog (*Dryophytes versicolor*). (b) Range of the gray treefrog (green) across Eastern North America (IUCN 2020), including the study region (black square). (c) Gray treefrog image by Amy Klassen.

2 Methods

2.1 Study Region & Site Selection

Field work was conducted around the city of Thunder Bay (48.382, -89.246 DD; Figure 1.1a) in northwestern Ontario, Canada, at the northern range edge of gray treefrogs (Figure 1.1b). The study region is located in the Boreal Transition Zone between the Boreal Forest region, which is dominated by coniferous (softwood) and mixed forests, and the Great Lakes-St. Lawrence Forest region, which is dominated by mixed hardwood forests (Perera et al. 2011). There is also extensive forest harvesting in the region (Brandt et al. 2013) with around 28% (~ 14 M ha) of the managed boreal forest in Ontario and Quebec being logged since ~1976 (Mackey et al. 2024). There is an average of 121,000 ha harvested in Ontario per year (2009 - 2019; Ontario Ministry of Northern Development, Mines, Natural Resources and Forestry 2021), and across the three managed forests covering the study area (Lakehead, Dog-River Matawin, Black Spruce), there were 11,678.2 ha harvested per year (2013 - 2023; data from the Ontario Ministry of Natural Resources and Forestry 2025a under the Open Government License - Ontario).

In 2025, I sampled 40 breeding ponds in the Thunder Bay, ON region (Figure 1.1; Table 6.1; Figure 6.1) spanning 0.97° (108 km) latitude. Twenty ponds were within clearcuts between 2-13 years of age (mean ± SE: 7.6 ± 0.5 yr), and twenty were within forests that had not been cut for at least twenty years to align with increased canopy cover (5-10 years) and basal area recovery post harvest (20-30 years; Bartels et al. 2016) while maximizing sample size due to a lack of mature forests in the area. To be included, ponds had to meet the following criteria. Clearcut ponds could be along a gravel road (no paved roads due to salting) or an old logging road, but they had to be entirely within a cut and

not along a forest edge. Forested ponds could not be along a road; there had to be 3 meters of shrubs or trees between the pond and the road (Figure 2.1). Forested ponds did not require a closed canopy; they just could not be bordered by recent anthropogenic disturbance. Due to the limited availability of accessible ponds within the age restrictions, random sampling was not possible. The age of the stands was determined using the boreal disturbance database (Remmel et al. 2023) based on the most recent disturbance. Time since cutting could not be determined for all forested sites, as not all locations had historical data within the boreal disturbance database, especially due to lower resolution with older disturbances. However, based on tree size and the inclusion of harvesting events dating back 50 years in the database (Remmel et al. 2023), it is a conservative assumption that forested areas were at least 20 years post-harvest.

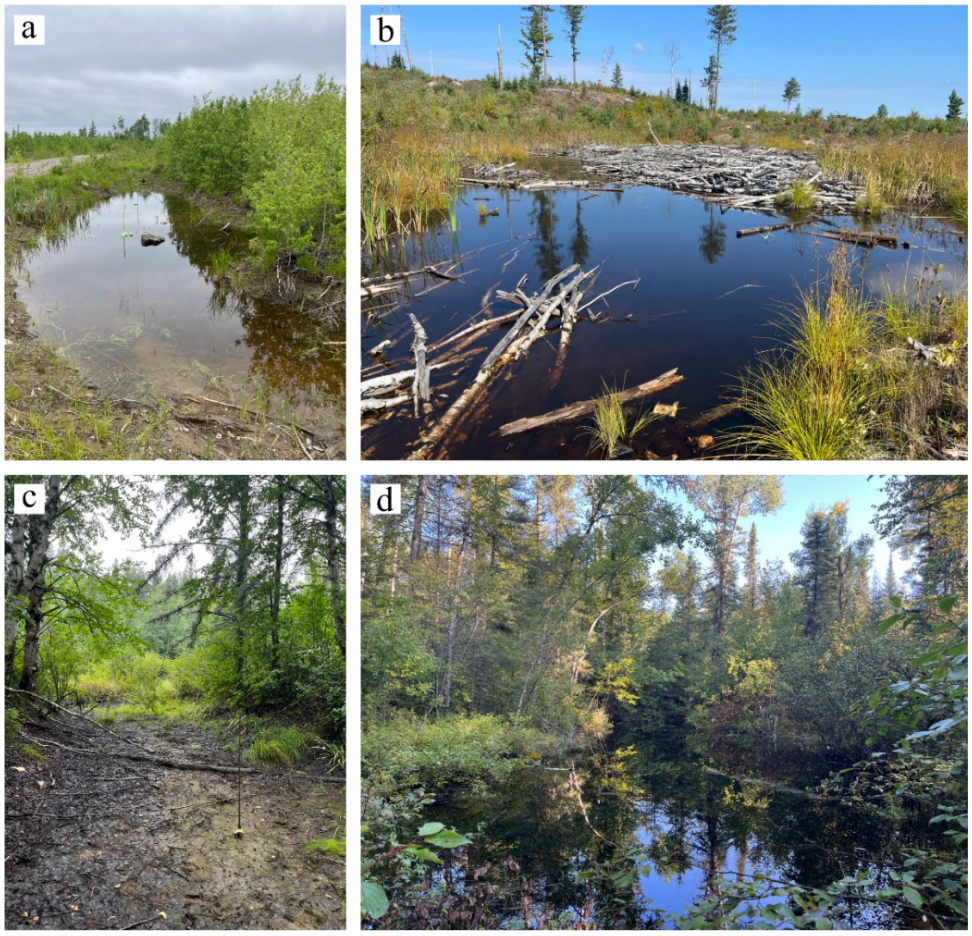

Figure 2.1 Breeding ponds in clearcuts (a, b) and forests (c, d). The Upsala Cut 1 (a) pond in a clearcut beside a road and the Sand Cut 3 (b) pond in the middle of a clearcut. The Graham Forest 2 (c) pond after it dried, with the image facing the shrubs that separate the pond from a nearby road, and the Sand Forest 3 (d) pond surrounded by forest.

All ponds had to have emergent vegetation within or along their edge for gray treefrogs to call from (Dodd 2023). In general, running water was avoided, but three sites were in slow-running water, such as a forested wetland next to a lake margin (Sand Forest 1; Site locations in Appendix 6.1) or flooded areas with a low flow blocked by beaver dams (Boreal Forest 2, Glimmer Forest). Selected ponds were a minimum of 800 m apart. Ponds were initially at least 25 cm deep to reduce the risk of drying out, and I avoided large ponds with diameters over 100 m. I also only selected ponds where there were no spraying operations during 2025. Spraying with glyphosate-based herbicides is common

after clearcutting (Man et al. 2011) and gray treefrogs avoid breeding ponds that have been sprayed (Takahashi 2007). Spraying can have negative impacts on amphibians (Howe et al. 2004, Relyea and Jones 2009, Williams and Semlitsch 2010), though negative effects may be lower or negligible at the concentrations likely to be experienced in these habitats (Wojtaszek et al. 2004).

2.1.1 Quantifying Calling Activity

At each clearcut and forest pond, I installed an autonomous recording unit (ARU; AudioMoth) on a tree (Figure 2.3) close to, and facing, the pond (within 15 m). ARUs were placed 2.5 ± 0.9 m farther from clearcut ponds (mean ± SE: 6.4 ± 0.8 m) than forest ponds (3.9 ± 0.5 m; $t(30.3) = 2.64$, $p = 0.013$) due to a lack of available trees around clearcuts to install ARU's. Although calls can travel more easily through open habitat (Yip et al. 2017), even at forested ponds there was little to no vegetation between the ponds and ARUs, and given the short distances from ponds, this was unlikely to have confounded measures of calling activity. The ARUs sampled a 2-minute recording every 30 minutes from 19:00 to 02:30 (16 nightly files), aligning with gray treefrogs' peak calling times (Dodd 2023). AudioMoths were equipped with Firmware V1.11.0 and recorded at a 48 kHz/16-bit sampling rate with medium gain. I recorded from the night of May 26 to the night of June 30 (includes July 1 0:00 to 2:00) to align with the main breeding season in Thunder Bay, ON (Dodd 2023, Lockhart 2024). At two forested ponds (Glenwater For 2, Sand For 2), the ARUs experienced technical issues and did not record during the breeding season.

To analyze the audio data, I used the repeat interval-based bioacoustic identification tool (RIBBIT; Lapp et al. 2021), which is one of the few bioacoustic tools

available for detecting anurans' trilling mating calls. RIBBIT divides an audio file into a series of time windows (~1-2 sec) and analyzes each window to detect calls based on a user-specified pulse repetition rate and frequency band. The score is calculated for each time window from the amplitude signal as the maximum power spectral density within the user-specified pulse repetition range for the given species. In the original formulation, a score is produced for each window, and if that score in any window exceeds a user-specified species-specific threshold, the species is scored as present (for full details, see Lapp et al. 2021). For the species of choice, the user defines the signal frequency band, the pulse repetition rate range, the window length, and other desired settings, such as removing noise-band frequencies from overlapping species (see Appendix 6.2 for a list of RIBBIT parameters). While originally developed to detect presence / absence only, I modified RIBBIT to create a measure of calling activity.

2.1.2 Determining a Calling Activity Index

To develop a calling activity index with RIBBIT, I randomly selected 200 two-minute audio files from 18 breeding ponds in the Thunder Bay region, which had been collected as part of a wider bioacoustic monitoring program in 2024. None of the recordings were collected from ponds that were used in my main analyses. To maximize the prevalence of gray treefrogs, only files recorded from May 25 to June 25 between 21:00 and 00:00 (Eastern Daylight Time) were included. As a measure of calling activity for each file, I manually counted the gray treefrog calls (Figure 2.2) by listening to each file and examining the spectrogram in Raven Pro (v1.6.5; K. Lisa Yang Center for Conservation Bioacoustics at the Cornell Lab of Ornithology 2025). I used the number of calls in a file rather than the standard anuran survey scoring system (0-3 scale) used by

the North American Amphibian Monitoring Program (NAAMP) (Sargent 2000, Nelson and Graves 2004) because the latter can be subjective and can vary between listeners. When frogs were chorusing, overlap of calls was high, making identification of individual calls more difficult. In these situations, to count individual calls, I scanned for visual variations in individual frequencies and start times and listened for when new calls started. I then used these 'true' measures of calling activity to evaluate a set of indices extracted from the same 200 files using R Statistical Software (v4.5.2; R Core Team 2025) and a modified version of RIBBIT (Lapp et al. 2021) with parameters tuned for the Thunder Bay, ON region (Lockhart 2024; Table 6.2).

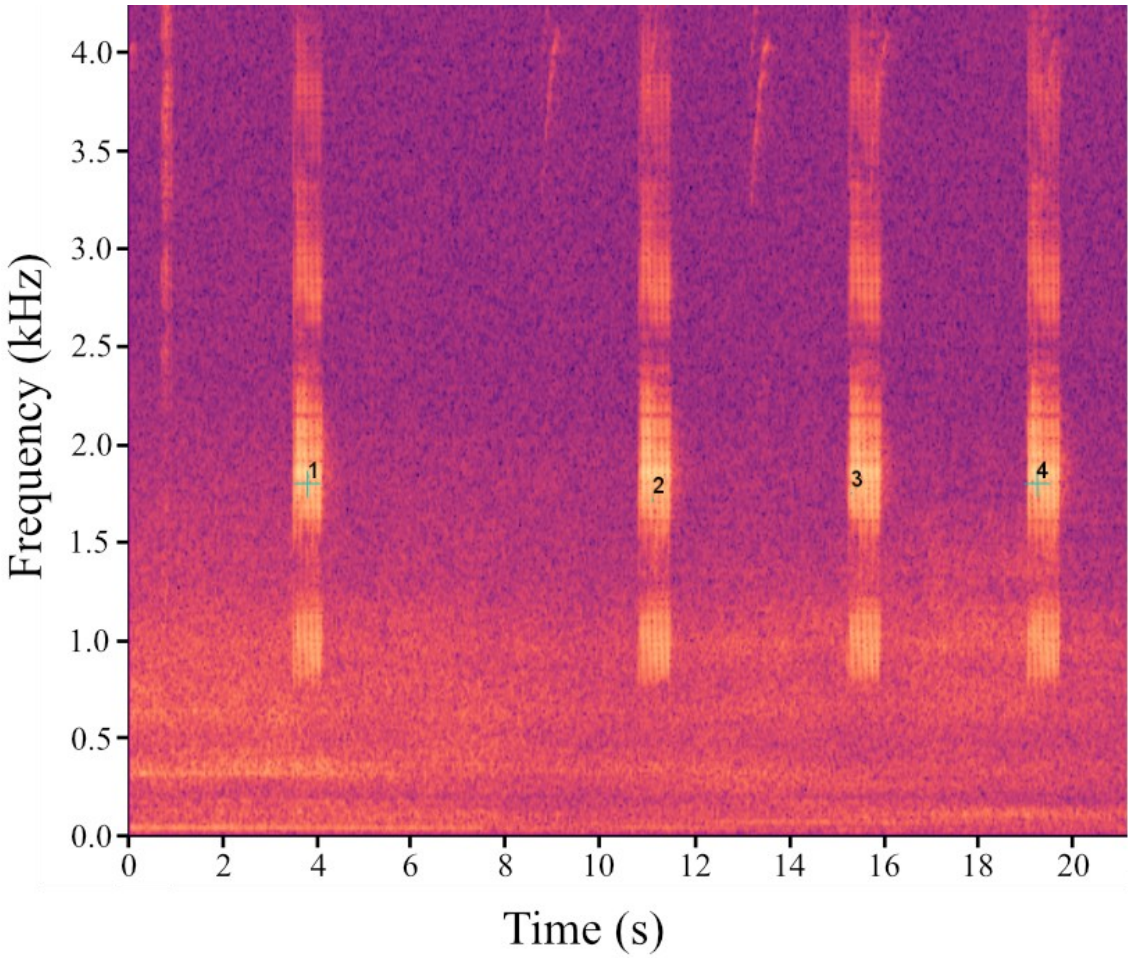

Figure 2.2 Spectrogram of four Eastern Gray Treefrog (*Dryophytes versicolor*) calls. Frequency (kHz) versus time (s), where the intensity of the colour indicates amplitude (orange is louder, purple is quieter). The audio file was recorded at the breeding pond Sunshine Cabin in the Thunder Bay, ON region from June 2, 2024, at 22:30 EDT. The values on the spectrogram (1 to 4) indicate the selections of gray treefrog calls with Raven Pro (v1.6.5; K. Lisa Yang Center for Conservation Bioacoustics at the Cornell Lab of Ornithology 2025).

For each file, I calculated the maximum, minimum, and median window scores. I also calculated the sum of all window scores and the proportion of window scores with a detection. I did not use the mean window score because this is equivalent to the sum of scores, as all files had the same number of windows. I compared each of these measures to each other and to the manually counted number of calls using correlation.

2.1.3 Cumulative Calling Activity

To analyze each audio file collected from the ARUs, I used RIBBIT to determine the proportion of windows above the detection threshold, as described above (see results section 3.1.1). To obtain a measure of calling activity across the breeding season (May 26 to June 30), i.e. cumulative calling activity, I summed calling activity for all files within this period for each site. As each site had the same number of files recorded within this timeframe, no weighting or adjustments were required. This measure of cumulative calling activity integrates both the intensity of calling per night and the length of the breeding season at each pond.

I manually confirmed presence and absence of gray treefrogs at each site to reduce the potential for false positives to skew results. I manually checked all files with a gray treefrog detected in at least one window in order of decreasing calling activity score until a gray treefrog was heard or all files with a detection were checked. For sites with fewer than five files with gray treefrog detections, I checked the five files with the highest scores.

2.1.4 Chorusing

In many frog species, breeding activity is highest during periods of chorusing, where a large number of males call together (Ryan et al. 1981, Murphy 2003, Dougherty et al. 2022) and female gray treefrogs tend to select from a cluster of males rather than lone males (Stratman et al. 2021), suggesting increased female presence at choruses. To account for these key periods, I also evaluated chorusing intensity in three ways. Firstly, I recomputed cumulative calling activity (May 26 to June 30) but summed only those files in which at least 75% of windows were above the treefrog detection threshold. Secondly,

I extracted the upper quartile of files across all sites based on calling activity and summed the proportion of windows for each site across the breeding season. Finally, for each site, I extracted the five nights with the highest calling activity (proportion of windows) and again summed the proportion of windows across the breeding season. I compared these chorusing measures with each other and the cumulative calling activity using correlation.

2.2 Habitat Characteristics

2.2.1 Temperature & Humidity

At each pond, on the same tree as the ARU, I installed an M-RSA solar radiation shield (Figure 2.3) containing a HOBO MX2301A, which recorded hourly air temperature (T_{air}) and relative humidity.

Figure 2.3 Installation of an autonomous recording unit (ARU; green square) at breast height, and a solar radiation shield (white) above it containing a temperature logger for T_{air} and relative humidity.

I used a HOBO pendant Temp/Alarm (UA-001-08) or a HOBO MX2201 to measure the surface (T_{surf}) and bottom (T_{bottom}) water temperatures of each pond. I randomized the temperature logger type for both the pond surface and bottom. Temperature loggers were fixed to a bamboo stake (Figure 2.4) as close to the centre of the pond as possible given safety considerations and soil/substrate conditions. The centre of the pond was selected to avoid pond edges that would likely dry early during the season and limit data collection. Surface temperature loggers were secured within an open-ended piece of white PVC pipe to function as a radiation shield, with a section of pool noodle for flotation (Figure 2.4). For analysis of all temperature types (T_{air}, T_{surf}, T_{bottom}), I used nighttime (19:00 to 02:00 EDT) temperatures during the breeding season (May 26 to June 30; includes 00:00 to 02:00 EDT for July 1) to align with calling activity.

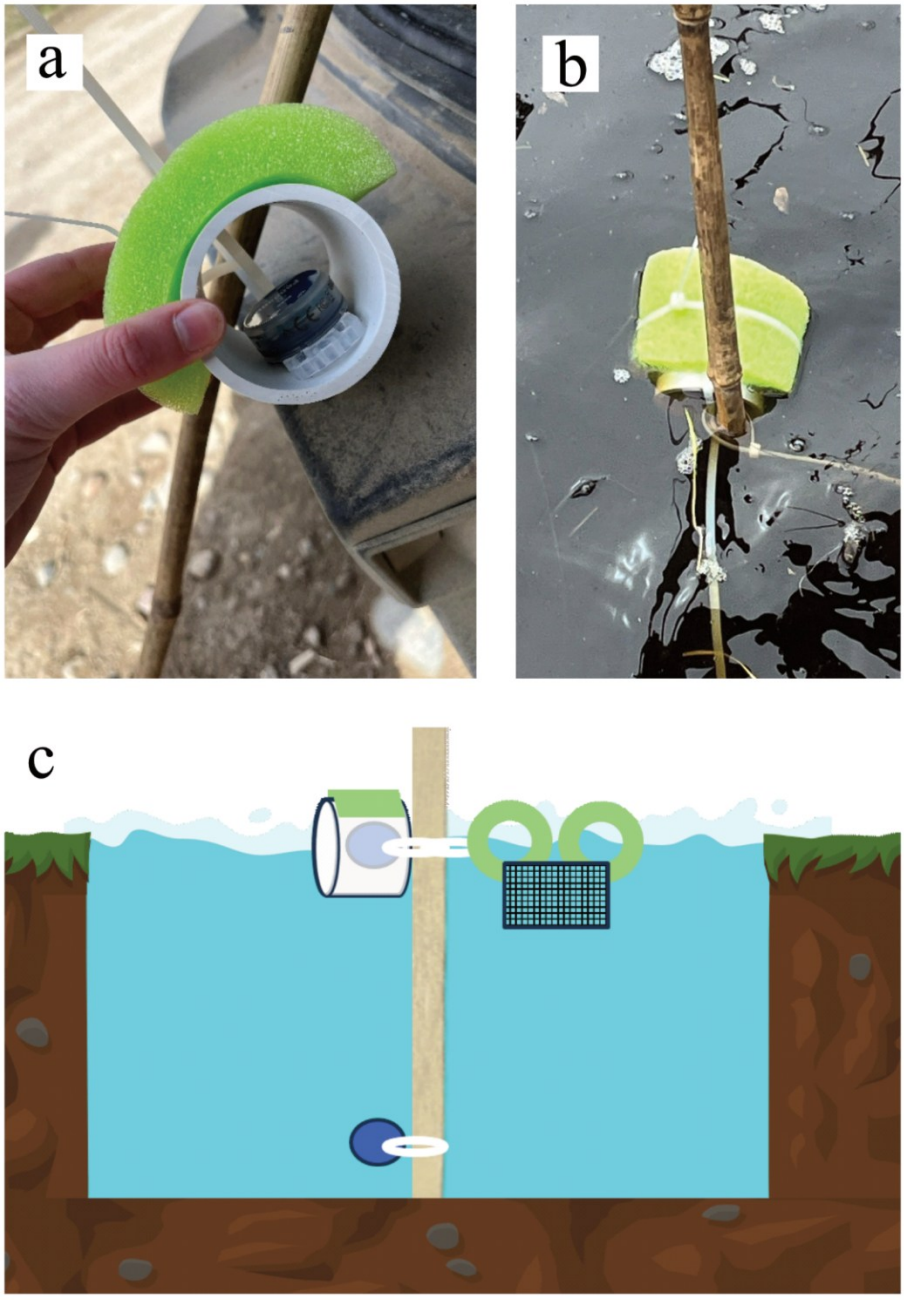

Figure 2.4 Water temperature logger setup. Surface temperature (T_{surf}) logger within radiation shield (a) installed in a pond (b). Diagram (c) of setup in a pond with a bamboo stake with the T_{surf} logger in the radiation shield, the bottom temperature (T_{bottom}) logger attached to the stake near the bottom of the pond, and the periphyton sampler to the right of the stake.

2.2.2 Missing Temperature Data

During the field season, there were several issues with temperature loggers, resulting in missing data (Table 2.1). Due to presumed wildlife interference, the T_{surf} and T_{bottom} loggers from two forest ponds (Glimmer Forest and Graham Forest 1) were not recovered from the field. In one clearcut and four forest ponds (Table 2.1), the T_{surf} logger shifted to the bottom of the pond, presumably due to environmental (e.g. wildlife, debris, weather) interference. One clearcut and three forest ponds (Table 2.1) had instances where the T_{bottom} logger came loose from the bottom position and floated to the surface.

Table 2.1 Percentage of nighttime (19:00 to 02:00 EDT) water temperature data during the breeding season (May 26 to June 30) for each site that is missing due to changes in logger position. Sites with missing audio data (Glenwater Forest 1, Sand Forest 2) are excluded from the table. Interpolated data is bolded; data excluded from analysis are in red.

Site	Habitat Type	Missing T_{surf} (%)	Missing T_{bottom} (%)
Adrian Lake Cut	Clearcut	0.0	0.0
Boreal Cut 1	Clearcut	0.0	0.0
Boreal Cut 2	Clearcut	0.0	0.0
Boreal Cut 3	Clearcut	0.0	0.0
DL Cut	Clearcut	0.0	0.0
DRT Cut 1	Clearcut	0.0	0.0
DRT Cut 2	Clearcut	0.0	0.0
DRT Cut 3	Clearcut	0.0	0.0
Glenwater Cut	Clearcut	0.0	0.0
Hwy 527 Cut 1	**Clearcut**	**9.4**	0.0
Hwy 527 Cut 2	Clearcut	0.0	0.0
Hwy 527 Cut 3	Clearcut	0.0	0.0
Hwy 527 Cut 4	Clearcut	0.0	0.0

Site	Habitat Type	Missing T_{surf} (%)	Missing T_{bottom} (%)
Pipeline Cut	Clearcut	0.0	0.0
Sand Cut 1	Clearcut	0.0	0.0
Sand Cut 2	Clearcut	0.0	0.0
Sand Cut 3	Clearcut	0.0	0.0
Sapawe Cut	Clearcut	0.0	22.2
Sideen Cut	Clearcut	0.0	0.0
Upsala Cut 1	Clearcut	0.0	0.0
Boreal Forest 1	Forest	0.0	0.0
Boreal Forest 2	Forest	0.0	0.0
DL Forest 1	Forest	0.0	0.0
DL Forest 2	Forest	0.0	0.0
Dorion Forest	Forest	37.2	0.0
DRT Forest 1	Forest	48.3	22.2
DRT Forest 2	Forest	0.0	0.0
DRT Forest 3	Forest	0.0	0.0
Gilbride Forest	Forest	0.0	0.0
Glenwater Forest 2	Forest	0.0	0.0
Glimmer Forest	Forest	100.0	100.0
Graham Forest 1	Forest	100.0	100.0
Graham Forest 2	Forest	0.0	81.6
Hwy 527 Forest 1	Forest	0.0	0.0
Hwy 527 Forest 2	Forest	0.0	0.0
Sand Forest 1	Forest	62.2	62.2
Sand Forest 3	Forest	0.0	0.0
Sapawe Forest	Forest	41.6	0.0

I identified data from loggers that had shifted position using field notes and visual inspection of temperature traces (Figure 2.5) and subsequently removed the data (referred to as missing data). An incorrect T_{surf} logger position was identified when the T_{surf} trace began to match the T_{bottom} trace, and vice versa when the T_{bottom} logger was floating. In addition to the mispositioning of water temperature loggers, three radiation shields (with the T_{air} loggers) fell off the trees; however, no obvious changes in air temperature were detected from the temperature traces, so the data will be used in the analysis without corrections. To evaluate the extent of the missing data, I calculated the percentage of missing data from the nighttime breeding season (19:00 EDT May 26 to 02:00 EDT July 1; Table 2.1). As missing temperature data (for reasons other than pond drying) could bias mean temperature estimates, I did not use sites with T_{surf} and T_{bottom} positioning errors aside from one site, Hwy 527 Cut 1. Due to the small proportion of data missing from Hwy 527 Cut 1 (9.4%; Table 2.1), I decided to interpolate the missing data, using the strong relationships between temperature variables, to maximize my small sample size of ponds. I interpolated missing T_{surf} data by modelling it as a function of T_{air} and/or T_{bottom} with an interaction of time of day. As temperature changes diurnally and the rate of change over time may differ between the water and air, I used time of day as a predictor where I converted the hour of the day to radians ($\theta = 2\pi t/24$) and fit as a sine ($\sin\theta$) and cosine ($\cos\theta$) wave to account for the cyclic nature of the time of day. I used data from the rest of the season (May 16 to September 16), and I tested eight linear models to select the best model fit I used the model with the lowest AICc ($T_{surf} \sim T_{bottom} * T_{air} * (\text{Sin(Time of day)} + \text{Cos(Time of day)})$; Table 2.2) to interpolate missing data (Figure 2.5).

Table 2.2 Fit of predictive linear model of T_{surf} for interpolation using T_{bottom}, T_{air}, and time of day for site Hwy 527 Cut 1. The model with the lowest AICc (bolded) was used for interpolation of missing T_{surf} data.

Model	**R^2**	**AICc**
Tsurf ~ Tbottom	0.188	12,277.29
Tsurf ~ Tair	0.789	9,559.09
Tsurf ~ Tbottom + Tair	0.791	9,538.80
Tsurf ~ Tbottom * Tair	0.794	9,518.97
Tsurf ~ Tbottom * (Sin(Time of day) + Cos(Time of day))	0.727	10,090.58
Tsurf ~ Tair * (Sin(Time of day) + Cos(Time of day))	0.866	8,646.35
Tsurf ~ Tbottom + Tair * (Sin(Time of day) + Cos(Time of day))	0.885	8,347.51
Tsurf ~ Tbottom * Tair * (Sin(Time of day) + Cos(Time of day))	**0.911**	**7,834.75**

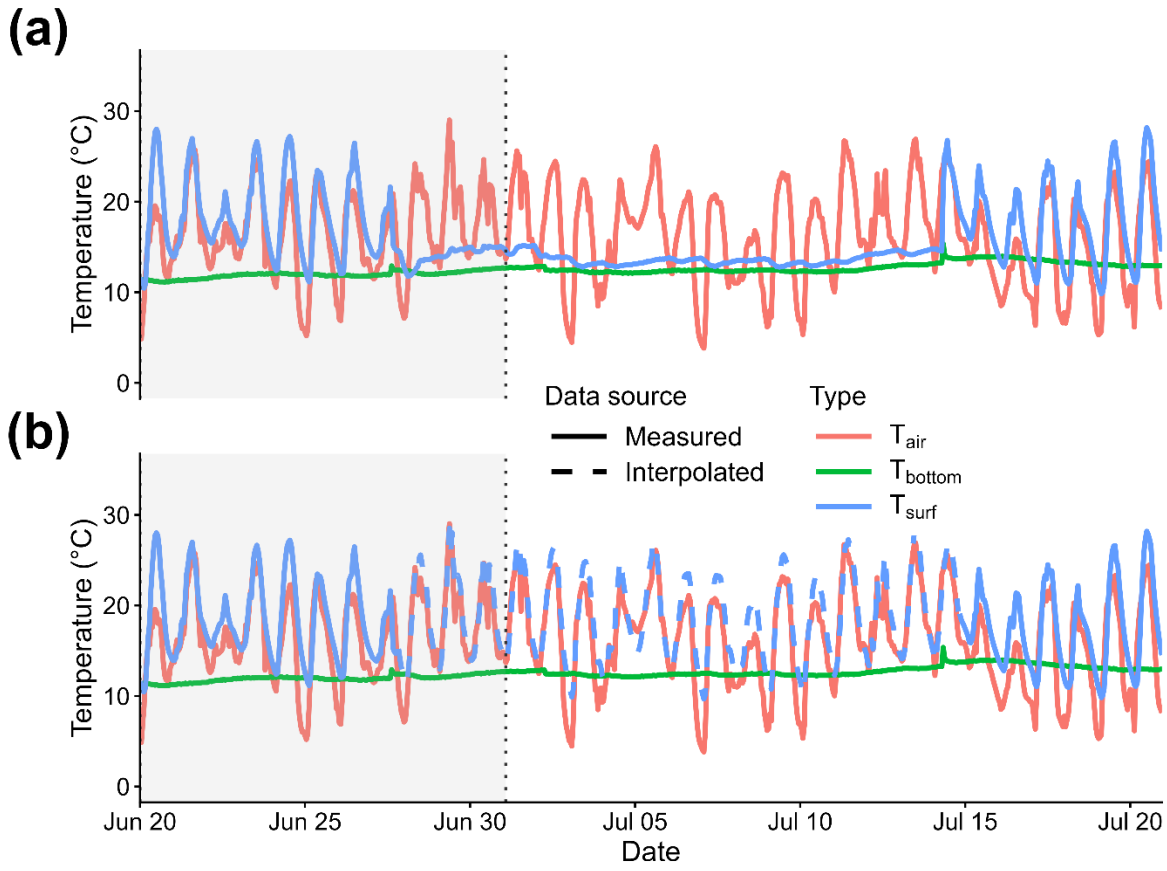

Figure 2.5 Hourly temperature traces of site Hwy 527 Cut 1 from June 20 to July 20. The raw temperature trace (a) was visually scanned to determine when the T_{surf} logger first sank, which was determined to be on June 28 and was fixed in the field on July 14. The data between June 28 and July 14 were removed and replaced with (b) interpolated values (dashed line) by using T_{air}, T_{bottom} and time of day ($T_{surf} \sim T_{bottom} * T_{air} * (\text{Sin}(\text{Time of Day}) + \text{Cos}(\text{Time of Day}))$). The shaded area shows the breeding season where nighttime temperatures were used to calculate mean temperatures.

2.2.3 Pond Surface Area and Depth

Pond depth was manually measured at the stake with the temperature loggers during each site visit (~monthly). For seven sites, if the stake had become detached from the bottom, or the pond dried at that location but still had water elsewhere, it was reinstalled, and the new location's depth was recorded; if the stake was missing, the depth was measured at the estimated location. Pond surface area was measured in July using a

Nikon Forestry Pro II Laser Rangefinder/Hypsometer by measuring each pond's major (long) and minor (short) axes and calculating surface area assuming ponds were oval:

$$\text{Area} = \pi * \text{radius of major axis} * \text{radius of minor axis}.$$

The pond size for Sand Forest 1 was not measured, as size was difficult to estimate, as it was a forested wetland next to a lake margin. As the water level had dropped at some ponds by July, the edge of the pond during the breeding season was estimated using visual indicators of water level, such as marks on trees or in the soil that indicate the spring water level.

2.2.4 Hydroperiod

I used field notes and visually inspected the temperature traces for ponds that dried to determine when they first dried and determine their hydroperiod (Figure 2.6). Drying events were inferred if, for example, surface and bottom temperatures became equal or matched the air temperature.

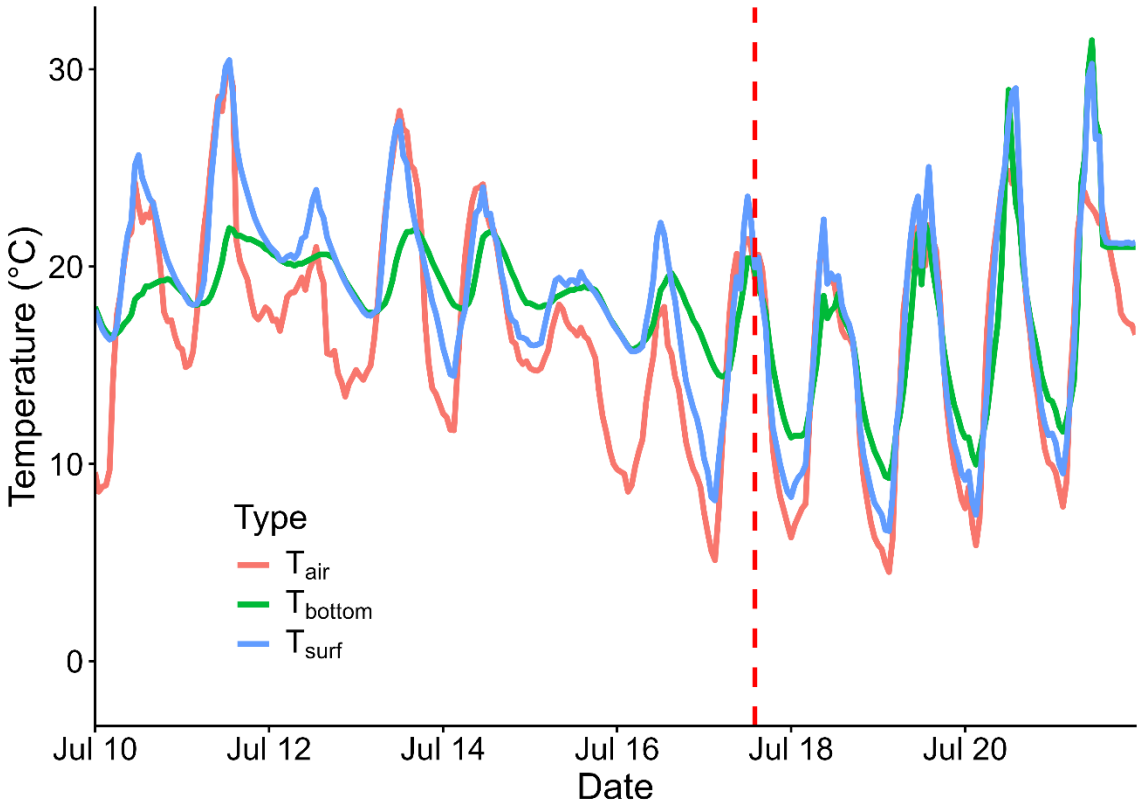

Figure 2.6 Hourly temperature traces for Upsala Cut 1 from July 10 to 21. The red vertical line indicates the inferred drying date (July 17) based on visual inspection of the temperature trace. In this case, the inference was made because the T_{bottom}, T_{surf}, and T_{air} showed similar temperature traces.

2.2.5 Canopy Cover, Tree Species and Size

The canopy cover and tree species size and composition around breeding ponds were measured in July. Tree measurements were performed in each cardinal direction (N, E, S, W) around each pond. I measured canopy cover using a convex spherical densiometer, using the correction to reduce overlap from Strickler (1959); canopy cover was additionally recorded at the center of the pond where the water temperature loggers were installed. I calculated the mean canopy cover across all the measurements. The tree species and diameter at breast height (DBH) were measured at each of the four sampling points using 2.5 m x 10 m transects perpendicular to the pond's edge (100 m^2 total). DBH was only measured for trees larger than five cm in diameter, and trees had to exceed

breast height (1.3 m) to be considered a ‘tree’. This included many small trees and shrubs. I also counted the number of woody stems with DBH less than five cm in each transect. I calculated basal area for large trees within each transect using DBH, assuming circular trunks. For the East transect of Boreal Forest 2, only seven meters were accessible due to safety hazards. As a result, weighted sums for basal area of large trees and the number of small trees were calculated to account for the short transect.

Although the vast majority of habitat characteristics were measured in July, three measures were taken in September, due to logistical issues: tree height in Sideen Cut East and Boreal Cut 2, and pond size of Boreal Cut 3. Additionally, at two sites, the tree-species transects were remeasured (these were among the first sites I measured), as I realized I had likely misidentified sapling white spruce. I remeasured all four transects for Hwy 527 Cut 3 and the West transect for Sand Cut 3.

2.2.6 Tree Diversity

As tree species composition affects leaf litter inputs to ponds, influencing tadpole food resources (Stoler and Relyea 2011) and adult habitat, I measured tree species diversity around the breeding ponds in two ways. First, I calculated the inverse Simpson’s index (high values = high diversity) using the vegan package (Oksanen et al. 2025) in R (R Core Team 2025) from the combined counts of large and small trees. Secondly, I used the same tree counts to calculate the proportion of coniferous trees around each pond, as leaf litter inputs vary considerably between coniferous and deciduous trees (Stoler and Relyea 2011).

2.2.7 Distance to Trees

As the distance adult treefrogs have to travel through clearcuts may influence pond selection (Hocking and Semlitsch 2007), I measured the distance from each pond to tree cover using QGIS v3.34 (QGIS Development Team 2023). I first identified the centre of each pond using a combination of Google Earth basemaps (resolution < 1 m; Google 2025), Sentinel-2 imagery (resolution 10 m; European Space Agency 2025), and Planet Basemaps Viewer (resolution 3 m; Planet Team 2025) from 2025. I then quadrisected the area surrounding each pond along its N-S and E-W axes and measured the distance to the nearest forest stand (>20 years, minimum area of 1 ha) in each quadrant, then found the mean distance across all four quadrants (Figure 2.7). Forest stand age was determined using Planet Basemaps Viewer (3 m resolution) and the Boreal Disturbance Database (Remmel et al. 2023). Some forested sites were surrounded by mature trees to the visible edge; these were given distances of zero.

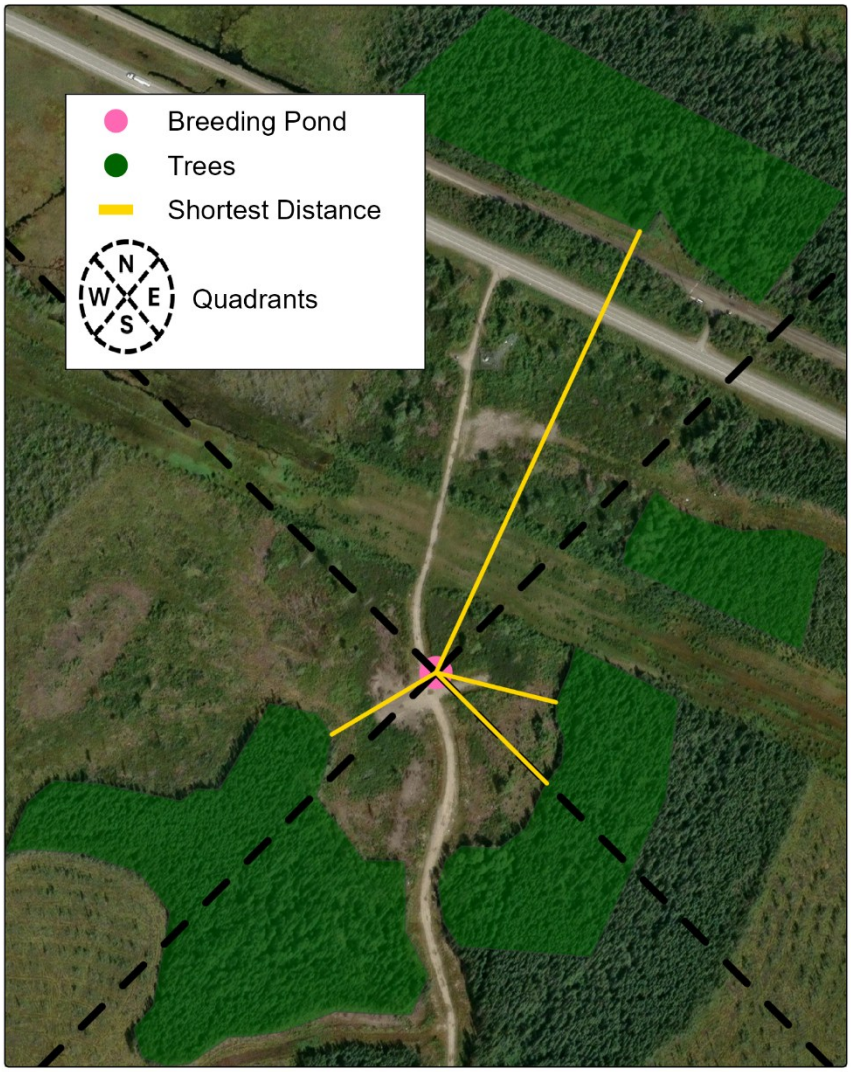

Figure 2.7 Distance to trees diagram for Upsala Cut 1, showing the pond center with the 90° quadrants radiating outward. The distance is measured between the pond center and the closest tree polygon in each quadrant.

2.2.8 Periphyton

Periphyton is composed of a variety of organisms that live attached to surfaces in the water, and as a food resource, it can influence tadpole growth and survival (Hocking and Semlitsch 2008, Stoler and Relyea 2011, Van Meter et al. 2011). Periphyton was sampled following a slightly modified version of (Skelly et al. 2002). I placed a glass slide in a fibreglass mesh bag to prevent grazing. Two cable ties were placed around the slide edges to keep the mesh off the slide itself (Figure 2.8). The cable ties only touched

the edges of the glass slides to allow for periphyton growth on the main faces of the slide. The glass slides were held lengthwise and hung below two pieces of pool noodles so that the slides were 10 cm below the water surface (Figure 2.8), aligning with the same depth selected by Hocking and Semlitsch (2008). 2 slides were attached to the stake with the water temperature loggers, and an additional stake with another 2 slides was placed elsewhere in the pond. These were installed early in the breeding season (June 6-12) and removed at the estimated time when tadpoles reached metamorphosis (August 15-21). This was based on the earliest known emergence of juveniles from a pond in the region (August 13). They were installed for 70 days, except for the Sandstone Lake (locations in Figure 6.1)group of sites (n = 5), which were removed after 69 days due to weather constraints.

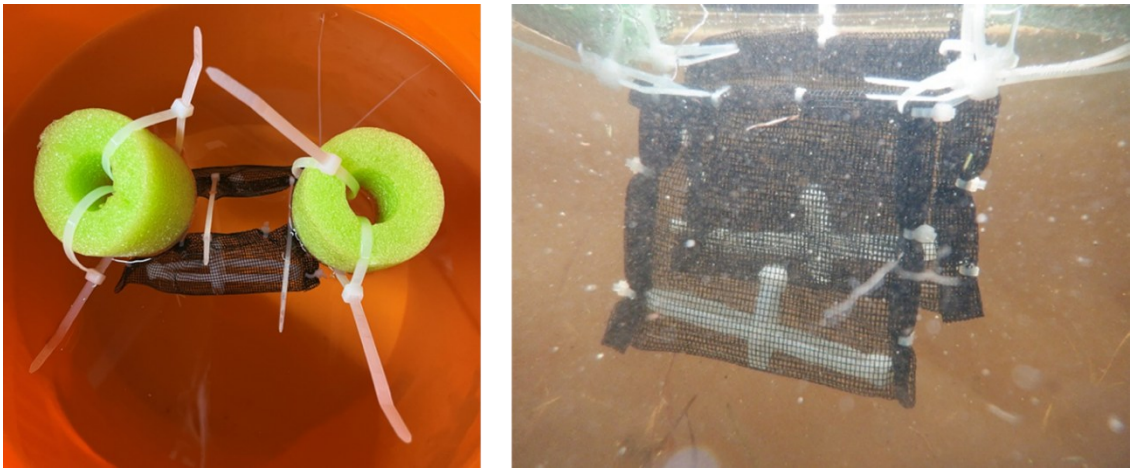

Figure 2.8 Glass slides for periphyton collection enclosed in mesh bags to prevent grazing, with pool noodles for flotation. Lab testing (Left) versus field installation (Right).

Two slides were used for chlorophyll α analysis (one from the centre stake containing temperature loggers and one from the other stake); the other two slides were used for biomass. For the chlorophyll α samples, I scraped the periphyton content from each slide using a toothbrush and razor blade (Figure 2.9). The slides were then rinsed

with distilled water, and the resulting slurry was vacuum filtered through cellulose filters (1.2 µm pore size). Pressure during filtering did not exceed 7 PSI to avoid rupturing algal cells. These samples were promptly covered with aluminum foil to prevent sunlight exposure, which can degrade chlorophyll pigments. Biomass slides were collected and placed into sealed containers to prevent moisture loss. Both sets of samples were stored in a cooler until return to Lakehead University (<12 hours) where they were stored in a -23°C freezer until analysis. The Lakehead University Environmental Lab conducted the chlorophyll α analysis and biomass measurements.

Figure 2.9 Periphyton was scraped off the glass slides with a razor blade and toothbrush (Left). The periphyton was rinsed off the slides with distilled water and vacuum-filtered onto filter paper (Middle). Once filtered, the filter paper was removed and stored prior to analysis (Right).

Chlorophyll α samples were extracted with 10 mL of 90% acetone. Samples were vortexed until the filters dissolved. Absorbance readings were measured at 630 nm, 647 nm, and 664 nm. The minimum absorbance at 750 nm was used to correct for turbidity. For the biomass samples, they scraped the slides and measured the wet weight. Following Ash-Free Dry Mass (AFDM) methods, the samples were dried at 105 °C overnight, and then the dry weight was recorded. The samples were then placed in a muffle furnace at

600 °C for 12-16 hours to measure the loss on ignition to determine organic matter content, calculated as the difference in mass before and after loss on ignition.

Some ponds dried before samples could be collected. At two sites (DRT Forest 3, DL Forest 2), the second stake had dried, so both slides at the center were used for chlorophyll α, and no biomass samples were collected. For Adrian Lake Cut, there was an issue with chlorophyll α filtration and only biomass was collected. For the Hwy 527 Cut 1 sample, high turbidity resulted in a negative chlorophyll α value, and the sample was excluded from subsequent analysis.

2.3 Analysis

All statistical analysis and data preparation were performed in the statistical software R version 4.5.2 (R Core Team 2025).

2.3.1 Comparing Clearcuts and Forests

I tested for differences in cumulative calling activity and pond and habitat characteristics between ponds in clearcuts and forests. I used Welch's t-tests if the data were normally distributed and the other test assumptions were met. If the data were non-normal, they were log-transformed to obtain a normal distribution. However, if there were zeros in the data set, a Wilcoxon-Mann-Whitney test was performed instead. As calling activity and chorusing intensity contain zero's, I square root transformed them to obtain a normal distribution for analysis.

2.3.2 Spatial Autocorrelation

I tested for spatial autocorrelation in the residuals of the calling activity ~ habitat type (clearcut or forest) relationship with a Moran's I correlogram using the spdep package (Bivand et al. 2026). Distance-based neighbours were selected using fixed 20 km

distance bands, based on the distribution of distances between sites (Figure 2.10). Distances were calculated via a distance matrix using the geosphere package (Hijmans 2024). Weights were calculated with the style "w".

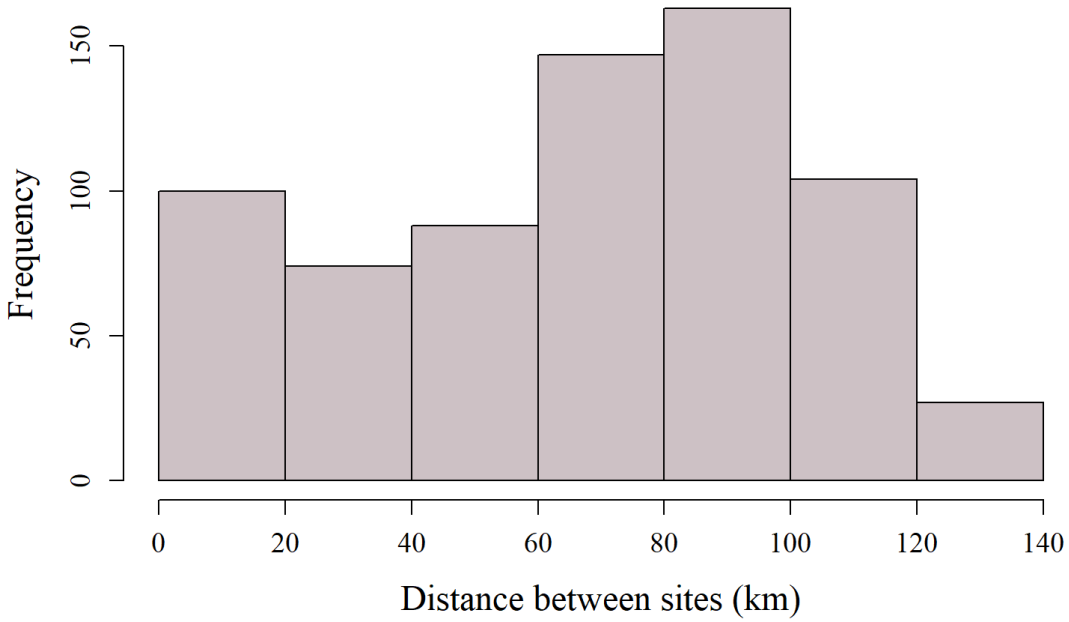

Figure 2.10 Distribution of distances between breeding pond sites (n = 38) studied around Thunder Bay, ON.

The residuals for calling activity did not exhibit spatial autocorrelation at any distance class (Figure 2.11; 0-20 km distance band: *Moran's I* = -0.130, $p = 0.864$). Therefore, I did not consider spatial autocorrelation further.

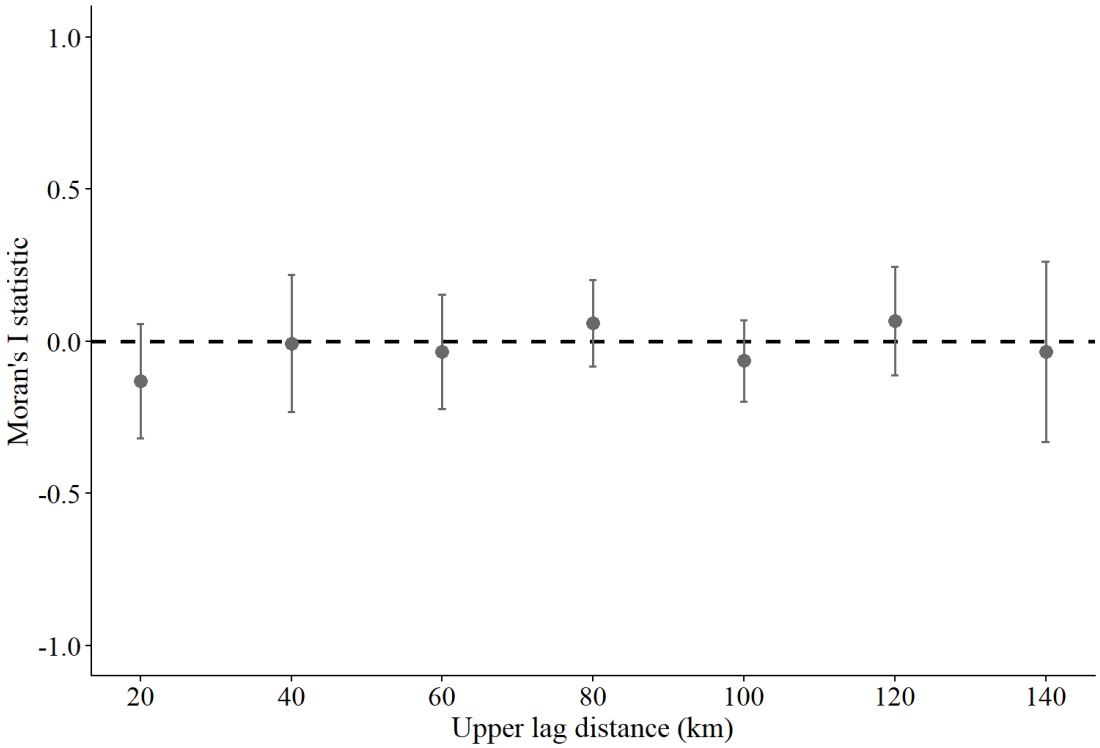

Figure 2.11 Correlograms for spatial autocorrelation testing of the residuals (n = 38) for the linear model of cumulative calling activity ~ habitat type. The correlogram is of Moran's I coefficient ± 2 SD (error bars) at 7 neighbourhoods or distance classes (20 km). The black dotted line shows the expected value of Moran's I with no spatial autocorrelation. Grey indicates no significant ($p > 0.05$) spatial autocorrelation, and red indicates significant spatial autocorrelation ($p < 0.05$).

2.3.3 Structural Equation Modeling

To evaluate pathways linking harvesting, habitat change and calling activity, I fit a structural equation model (SEM; Grace 2006, Lefcheck 2016). I first developed a directed acyclic graph (DAG; Shipley 2000) to represent hypothesized causal pathways linking forest harvesting and calling activity (Figure 2.12). The DAG included vegetation characteristics (canopy cover, number of small trees, Simpson's inverse diversity index for trees, proportion of coniferous trees), distance to trees (a landscape feature), and microclimate (T_{surf}, T_{air}, water vapour). As relative humidity is highly temperature dependent, I used water vapour density (WVD) in the SEM, as WVD is less temperature dependent and more relevant for amphibian evaporative water loss (Wygoda and Kersten

2013). To calculate WVD, I first calculated the saturation vapour pressure using the air temperature, and then the actual vapour pressure from the saturation vapour pressure and relative humidity. I then used the actual vapour pressure and air temperature to calculate the WVD using the ideal gas law equation. In addition to variables predicted to be impacted directly or indirectly by forest harvesting, I also included pond surface area (log-transformed), as more males may be present in certain ponds simply due to their larger size.

The effect of forest harvesting on the microclimatic variables (T_{air}, T_{surf}, WVD) is predicted to be mediated by reduced canopy cover (Figure 2.12). Other tree characteristics are predicted to directly influence calling activity. At greater distances from a patch of trees, specifically in clearcuts, there may be a greater risk of predation and desiccation. The basal area calculated for large trees was not included because it was significantly correlated with distance to trees ($r = -0.611$, $t_{30} = -4.23$, $p < 0.001$) and canopy cover ($r = 0.859$, $t_{30} = 9.22$, $p << 0.001$). To reduce the number of variables in the SEM, I performed a PCA on the number of small trees, the reciprocal Simpson's index, and the proportion of coniferous trees, and used the first principal component in the SEM, which captured 47% of the variance (Table 2.3). This component loaded strongly and positively on the number of small trees (0.65) and was negatively associated with the reciprocal Simpson's index (-0.28) and the proportion of conifers (-0.71). Low principal component scores indicate coniferous-dominated or mixed forest areas with few small trees and high tree diversity.

532 Table 2.3 Eigenvectors and summary statistics for the principal component analysis of the
533 number of small trees, proportion of coniferous trees, and the inverse Simpson index.

Variable	**PC1**	**PC2**	**PC3**
Number of Small Trees	0.66	0.38	-0.65
Proportion of Conifers	-0.72	0.05	-0.7
Inverse Simpson's Index	-0.23	0.92	0.31
Eigenvalue	1.42	1.02	0.56
Proportion of Variance	0.47	0.34	0.19
Cumulative Proportion	0.47	0.81	1

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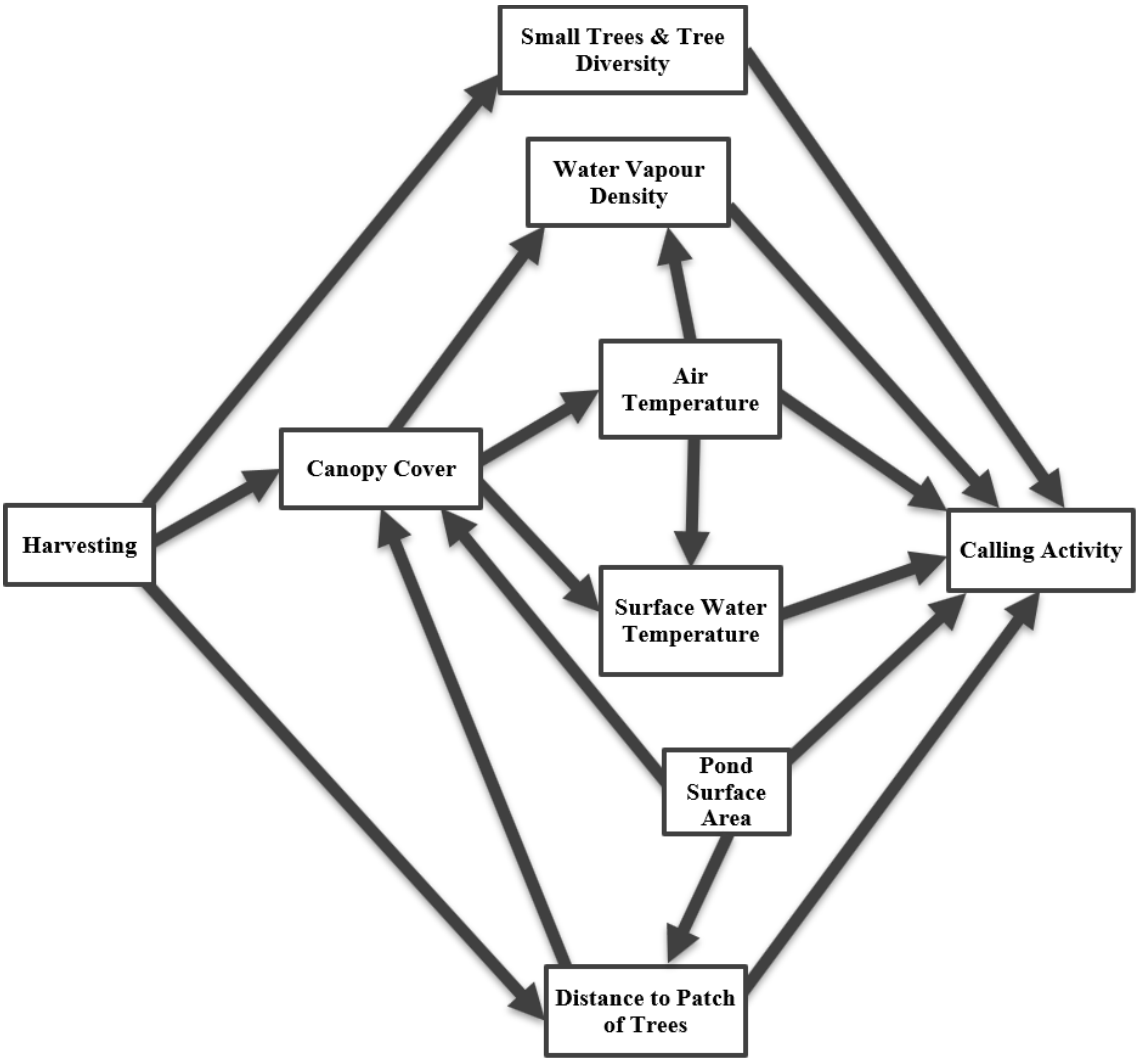


Figure 2.12 Hypothesized directed acyclic graph of hypothesized impacts of harvesting on the calling activity of male Eastern Gray Treefrogs (*Dryophytes versicolor*).

The SEM (Figure 2.12) was fit using the piecewiseSEM package (Lefcheck 2016, Lefcheck et al. 2025) which fits the model as a series of linear models, one for each endogenous variable (i.e. has an arrow pointing to the variable). I evaluated the SEM using directed separation tests and overall fit using the *C* statistic (Shipley 2013, Lefcheck 2016). Lastly, I calculated the standardized path coefficients.

3 Results

3.1 Quantifying Calling Activity

3.1.1 Determining a Calling Activity Index

All the calling activity indices were strongly correlated with the number of gray treefrog calls manually counted in a file and with each other (Figure 3.1). The proportion of windows over the threshold ($r = 0.88$, $t_{198} = 25.77$, $p << 0.001$; Figure 3.1) and the sum of window scores ($r = 0.86$, $t_{198} = 23.42$, $p << 0.001$) had the highest correlations with the number of calls. The median ($r = 0.84$, $t_{198} = 21.72$, $p << 0.001$; Figure 3.1), maximum ($r = 0.77$, $t_{198} = 16.99$, $p << 0.001$), and minimum window scores ($r = 0.76$, $t_{198} = 16.46$, $p << 0.001$) had slightly to moderately weaker correlations. The proportion of windows and the sum of window scores were highly collinear ($r = 0.97$, $t_{198} = 55.00$, $p << 0.001$; Figure 3.1). I used the proportion of windows above the threshold for subsequent analyses, as it had a slightly higher correlation with the manually counted calls than the sum of window scores, and it also has the advantage of returning zero when gray treefrogs are absent. Hereafter, I refer to the proportion of windows above the threshold as "calling activity".

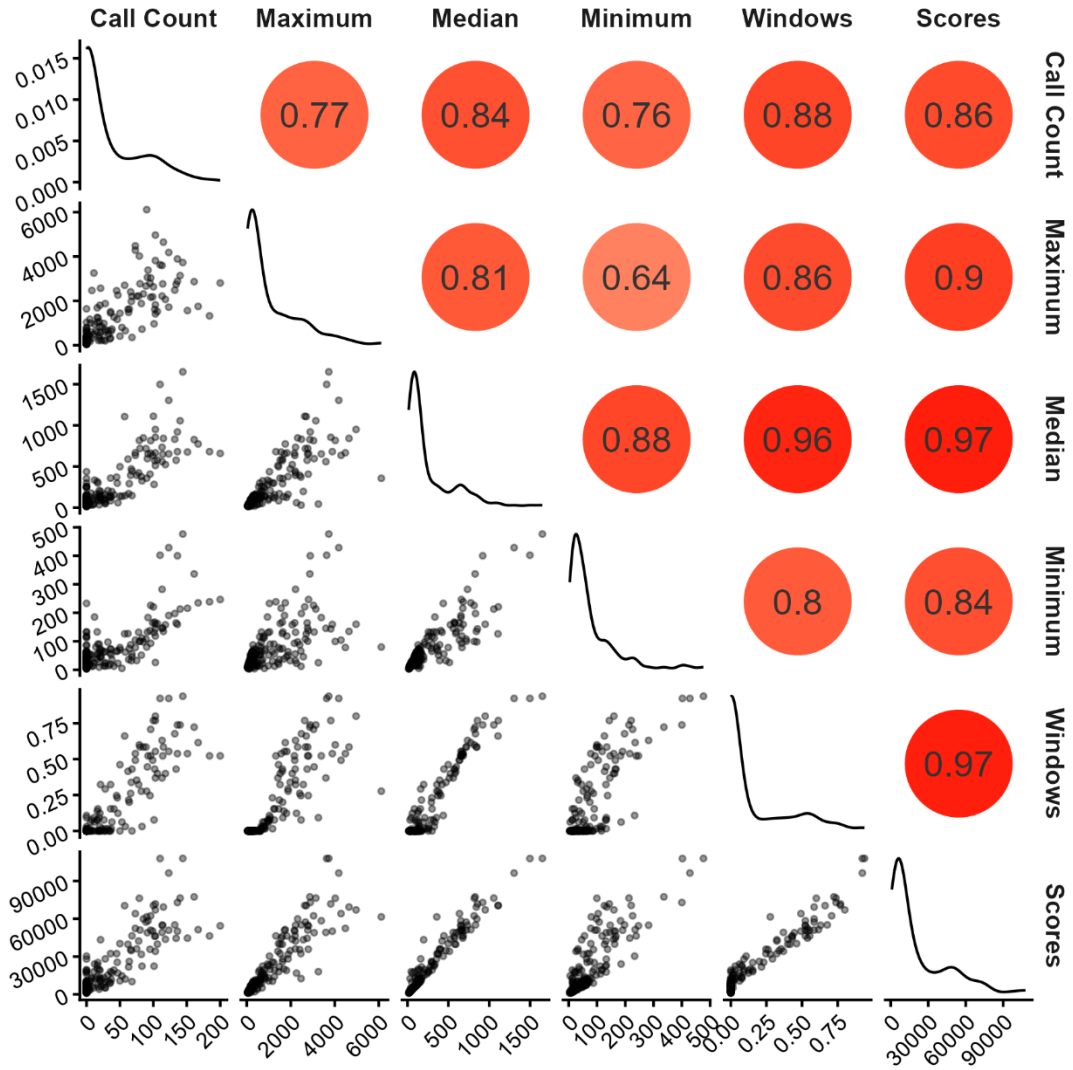


Figure 3.1 Comparison of counted calls and calling activity indices (n = 200). Upper: Correlogram between indices, displaying the correlation coefficient, and colour indicates correlation strength and direction (red = 1, white = 0, blue = -1). Diagonal: Density plot of the distribution of values. Lower: Scatterplots between indices. Call count is the manually counted gray treefrog calls in a 2-minute file. Maximum, median, and minimum are derived from the RIBBIT (Lapp et al. 2021) scores for each file. Windows is the proportion of windows above the gray treefrog detection within a file. Scores refers to the sum of all RIBBIT scores within a file.

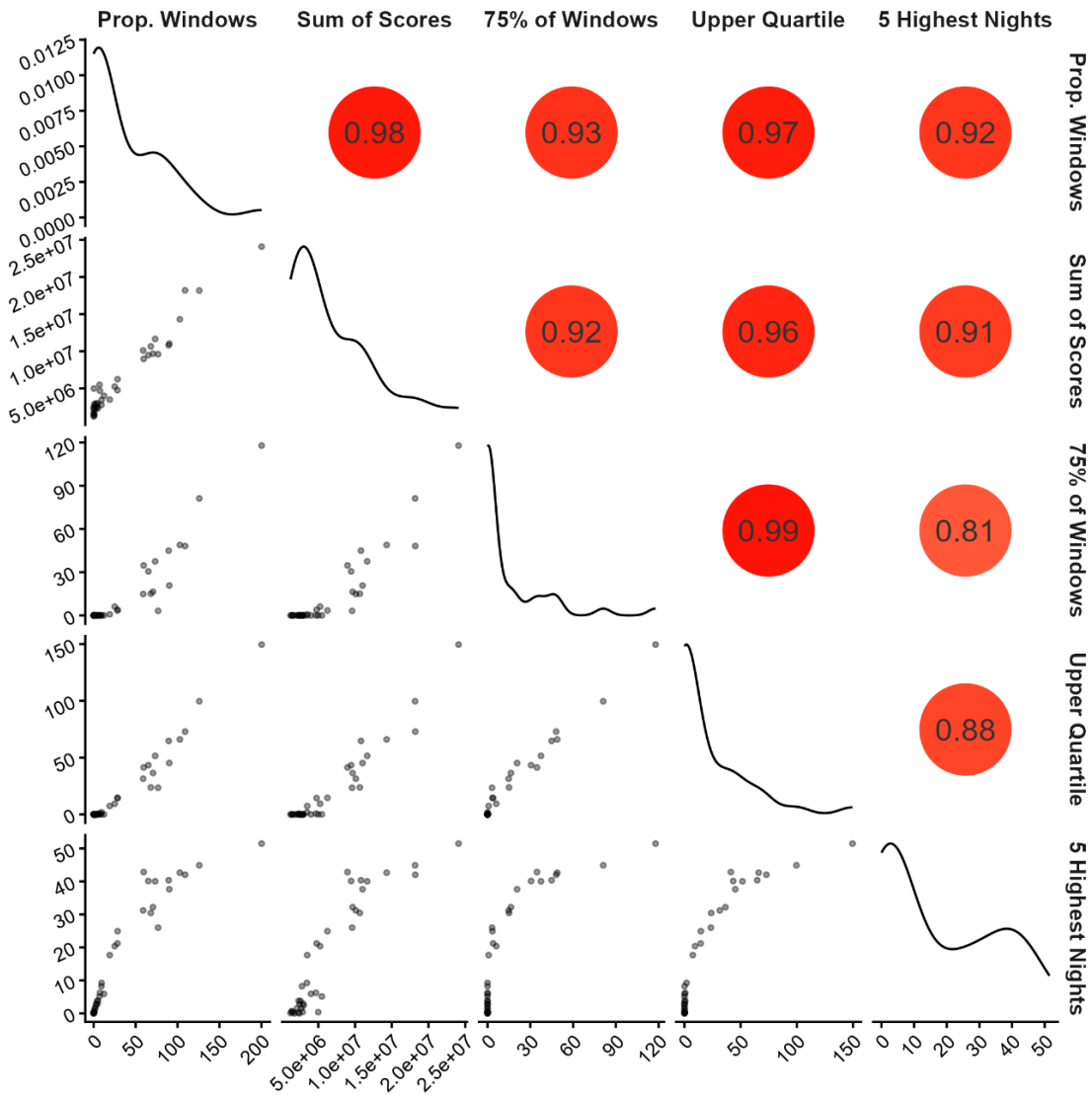
3.1.2 Cumulative Calling Activity and Chorusing

I used 21,888 two-minute recordings (729.6 hrs) from the breeding season to measure cumulative calling activity across 38 ponds. 3,887 files had at least one window

above the RIBBIT score threshold for gray treefrog calls. 36 of 38 ponds had gray treefrog detections with RIBBIT. 604 files contained chorusing across 17 breeding ponds.

The different measures of chorusing were all highly correlated with the two best performing measures of calling activity, proportion of windows and the sum of scores (Figure 3.2). This is not surprising, as the data used to quantify chorusing are a subset of those used for calling activity. I selected the cumulative proportion of windows in files with >75% window detections as the preferred measure of chorusing because it can be determined without incorporating information from other files, which is the case for the other two chorusing measures (five nights with the highest scores and the upper quartile of files). Hereafter, I refer to the cumulative proportion of windows in files with >75% window detections as 'chorusing intensity'.

From my manual listening to the files with the highest RIBBIT results for each site, I determined that 29 ponds had gray treefrog calls. Seven ponds that had detections with RIBBIT were deemed false positives via manual listening. These ponds had low calling activity in general (mean ± SE: 2.6 ± 1.3), and none of them contained chorusing.



586

587 Figure 3.2 Comparison of calling activity and chorusing indices for clearcut and forest
588 data (n = 38). (Upper) Correlogram between indices, displaying the correlation
589 coefficient, and colour indicates correlation strength and direction (red = 1, white = 0,
590 blue = -1). (Diagonal) Density plot of the distribution of values. (Lower) Scatterplots
591 between indices. Windows is the proportion of window scores above the gray treefrog
592 detection within a file. The Sum of Scores is the sum of all RIBBIT (Lapp et al. 2021)
593 scores within a file. 75% of windows is the summed proportion of windows for files that
594 have >75% of window scores above the gray treefrog detection threshold. The upper
595 quartile is the summed proportion of windows with detection for the top 25% of files (not
596 including zeros). The 5 highest nights is the summed proportion of windows for the five
597 highest nights of calling for each site.

3.2 Calling Activity in Clearcuts and Forests

Both cumulative calling activity and chorusing intensity were significantly higher at clearcut ponds than forest ponds (Figure 3.3; Table 3.1). Gray treefrog calling was more prevalent in clearcuts than forests (manual listening: 19/20 clearcut ponds, 10/18 forest ponds; $X^2 = 6.12$, df = 1, $p = 0.013$), as was chorusing (13/20 clearcut ponds, 4/18 forest ponds; $X^2 = 5.39$, df = 1, $p = 0.020$).

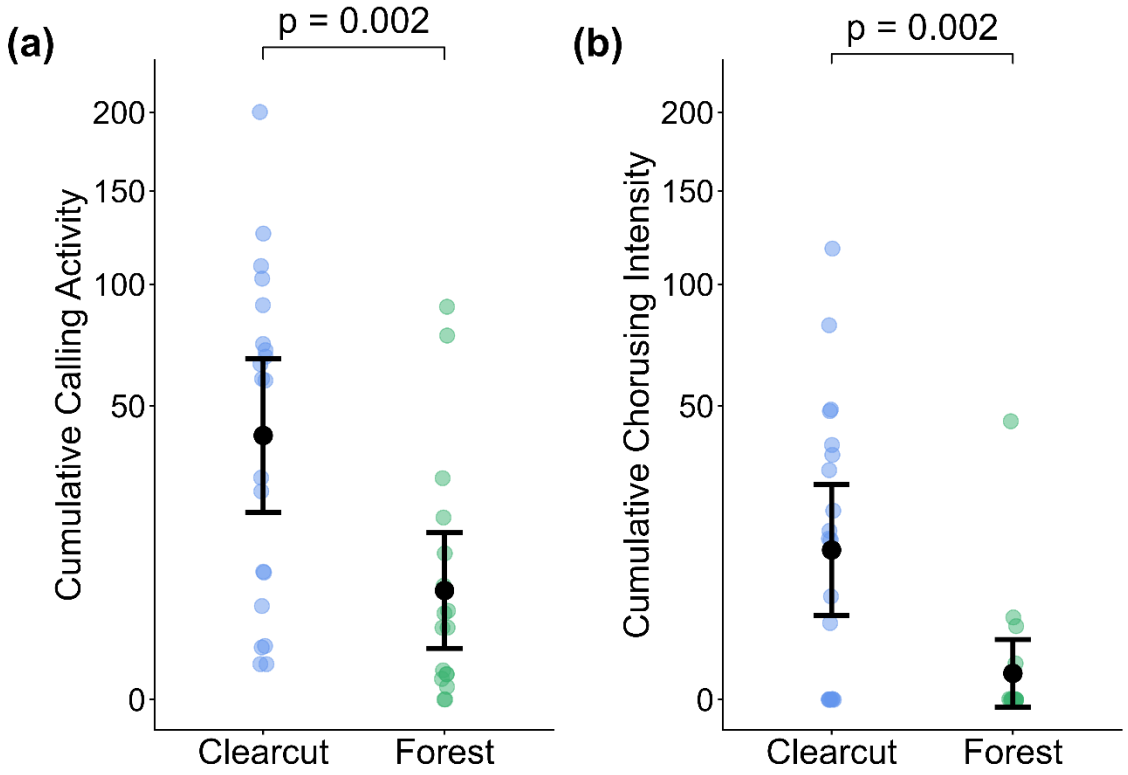


Figure 3.3 Cumulative calling activity and chorusing intensity of Eastern Gray Treefrogs (*Dryophytes versicolor*) in clearcuts (n = 20) and forests (n = 18) measured using RIBBIT (Lapp et al. 2021). (a) Cumulative calling activity measured over the breeding season as the summed proportion of windows with a RIBBIT score over the detection threshold. (b) Gray treefrog chorusing over the breeding season measured as the summed proportion of windows over the detection threshold for files that had > 75% of windows with a detection. Data is plotted on a square root scale (y-axis). Means are indicated with black circles with 95% confidence intervals for error bars. The bar above the plots displays the p-value from t-tests.

3.3 Comparing Clearcut and Forest Habitat

Unless otherwise specified, I used the 38 ponds with audio data to compare clearcut (n = 20) and forest ponds (n = 18); all sample sizes are specified in Table 3.1.

Table 3.1 Summary table of clearcut versus forest pond comparisons (t-tests and Wilcoxon-Mann-Whitney (WMW) tests). Clearcut and Forest columns display the values specified in the Summary Statistic column, which was dependent on the test performed. For variables where a logarithmic (pond surface area, chlorophyll ɑ, organic matter) or square-root (calling activity, chorusing intensity) transformation was applied for analysis, the raw values are displayed for the Mean (SE).

Variable	Summary Statistic	Clearcut	Forest	Clearcut Sample Size	Forest Sample Size	Test	Test Statistic	p-value	df
Calling Activity	Mean (SE)	55.3 (11.8)	14.3 (6.2)	20	18	t-test	3.38	0.002	34.2
Chorusing Intensity	Mean (SE)	23.8 (7.0)	2.9 (2.5)	20	18	t-test	3.50	0.002	28.1
T_{surf}	Mean (SE)	18.3 (0.3) °C	16.5 (0.5) °C	20	12	t-test	3.42	0.003	19.9
T_{bottom}	Mean (SE)	14.3 (0.6) °C	12.9 (0.8) °C	19	13	t-test	1.41	0.170	25.3
T_{air}	Mean (SE)	14.2 (0.2) °C	14.7 (0.1) °C	20	18	t-test	-1.85	0.073	33.9
WVD	Mean (SE)	8.5 (0.1) g/m³	8.8 (0.1) g/m³	20	18	t-test	-3.36	0.002	36.0
Pond Surface Area	Mean (SE)	371.1 (94.2) m²	427.1 (135.7) m²	20	17	t-test	-0.24	0.811	33.6
Initial Depth	Mean (SE)	62.8 (5.5) cm	54.8 (4.4) cm	20	18	t-test	1.14	0.263	34.9
Final Depth	Mean (SE)	40.9 (8.8) cm	24.4 (6.0) cm	20	18	t-test	1.55	0.131	32.8
Canopy Cover	Mean (SE)	7.6 (2.2) %	56.0 (6.4) %	20	18	t-test	-7.18	<0.001	21.1
Tree Distance	Mean (SE)	172.8 (22.7) m	8.7 (2.0) m	20	18	t-test	7.21	<0.001	19.3
Number of Small Trees	Median (IQR)	62.0 (36.5-103.5)	66.5 (38.2-84.0)	20	18	WMW test	184.50	0.907	
Basal Area of Large Trees	Median (IQR)	0.0 (0.0-1.5) m²/ha	22.1 (15.6-28.6) m²/ha	20	18	WMW test	4.00	<0.001	
Inverse Simpson Index	Mean (SE)	3.4 (0.4)	3.3 (0.3)	20	18	t-test	0.15	0.880	34.2
Proportion of Conifers	Median (IQR)	15.1 (3.1-34.1) %	31.2 (12.5-53.3) %	20	18	WMW test	127.50	0.128	
Chlorophyll α	Mean (SE)	0.3 (0.1) µg/cm²	0.2 (0.0) µg/cm²	11	11	t-test	1.01	0.324	19.9
Organic Matter	Mean (SE)	452.2 (118.0) µg/cm²	227.1 (65.9) µg/cm²	13	9	t-test	1.90	0.077	15.0

3.3.1 Temperature & Humidity

The mean nighttime T_{surf} of clearcut ponds was 1.9 °C ± 0.5 (SEM) warmer than forest ponds (Figure 3.4a; Figure 3.5; Table 3.1). The mean nighttime (19:00 to 02:00) T_{bottom} and mean nighttime T_{air} did not differ significantly between clearcut and forested ponds (Figure 3.4a; Table 3.1) however, in the evening leading up to calling (15:00 to 18:00) the T_{air} was significantly higher in clearcuts ($t(35.9) = 2.124$, $p = 0.041$; Figure 3.5). The nighttime air at clearcut ponds had lower mean WVD than forest ponds (Figure 3.4b; Table 3.1).

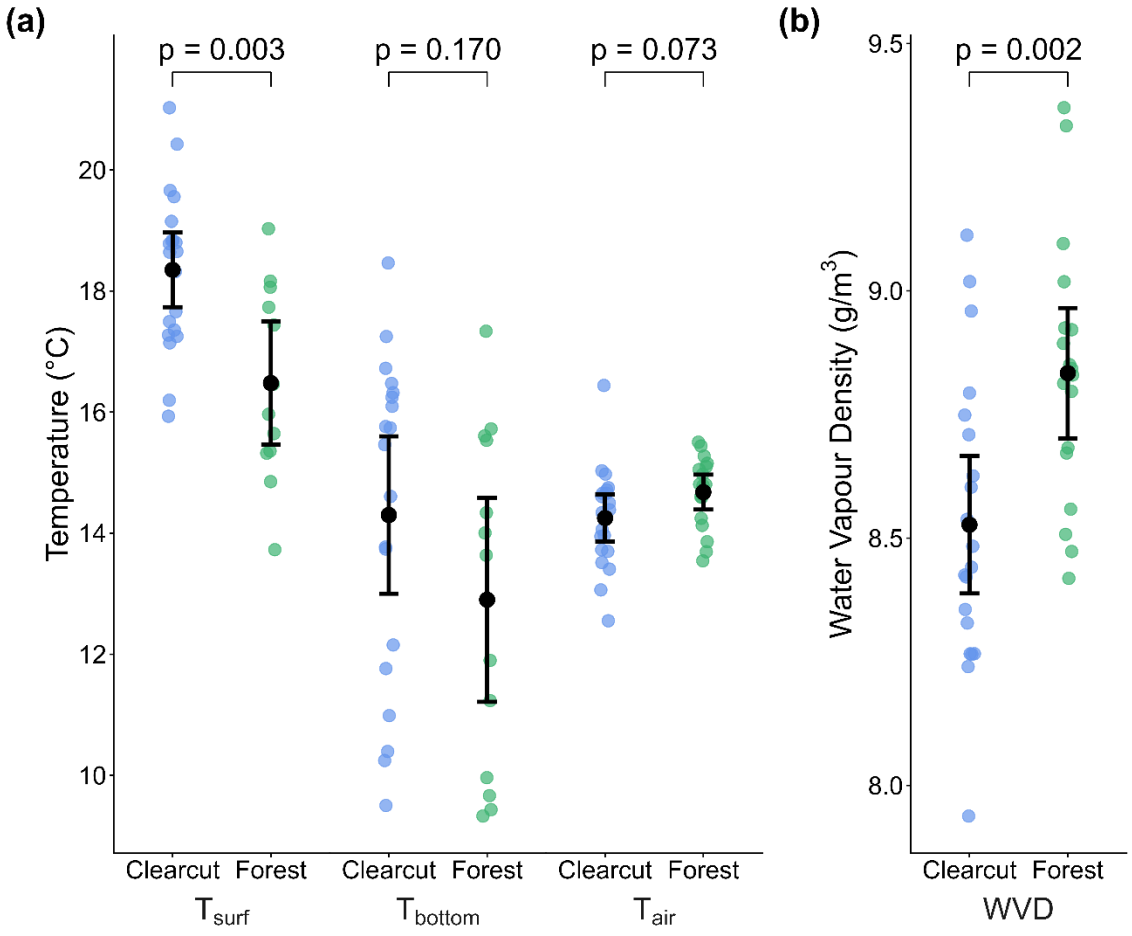


Figure 3.4 Mean nighttime (19:00 to 02:00 EDT) temperature (a) and water vapour density (b) at clearcut and forest ponds from the nights of May 26 to June 30, 2025. Sample sizes are found in Table 3.1. Means are indicated with black circles with 95% confidence intervals for error bars. Bars above indicate the p-value from t-tests.

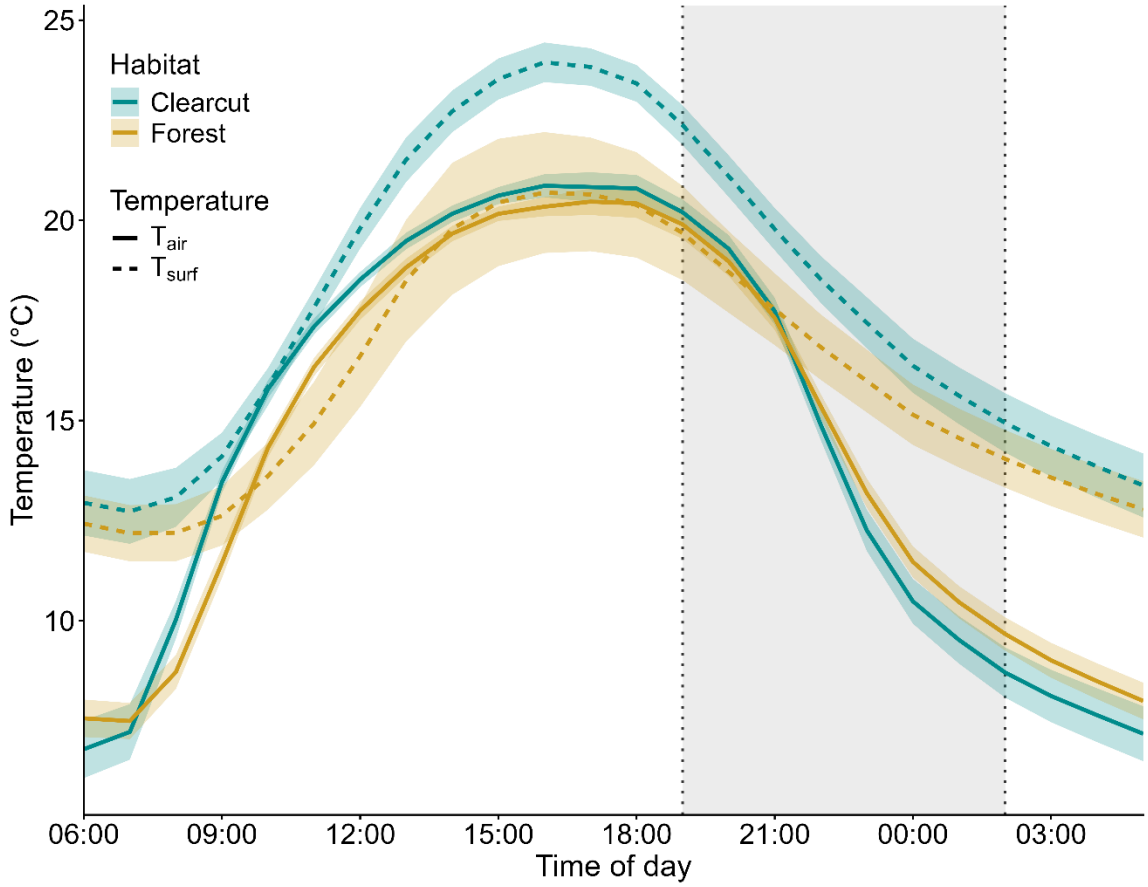


Figure 3.5 Mean hourly air (T_{air}; solid lines) and surface water (T_{surf}; dashed lines) temperature of clearcut (blue) and forest (yellow) ponds from May 26 to June 30. Shaded areas indicate 95% confidence intervals. The grey shaded area from 19:00 to 02:00 EDT indicates the temperature range used to calculate mean temperature, to align with the audio recordings used for calling activity.

3.3.2 Pond Size and Depth

Pond surface area was not significantly different between clearcut and forest ponds (Figure 3.6a; Table 3.1); the pond surface area measurement for Sand For 1 is missing due to difficulties with identifying pond margins. Surface area ranged from 36.1 to 1649.3 m^2 for clearcut ponds and between 33.0 and 2356.2 m^2 for forest ponds. Initial depth was not significantly different between clearcuts and forests (Figure 3.6b; Table 3.1) and ranged from 32 to 116 cm for clearcut ponds and between 30 and 98 cm for forest ponds. The final depth was not significantly different between clearcuts and forests (Figure 3.6c; Table 3.1), nor was the number of ponds that dried by the time of equipment

collection (September 8-18). Of these, five were forest ponds, and six were clearcut ponds ($X^2 \approx 0$, df = 1, $p \approx 1.0$). The final depth at clearcut ponds ranged from 0 to 121 cm, and for forest ponds, from 0 to 93 cm.

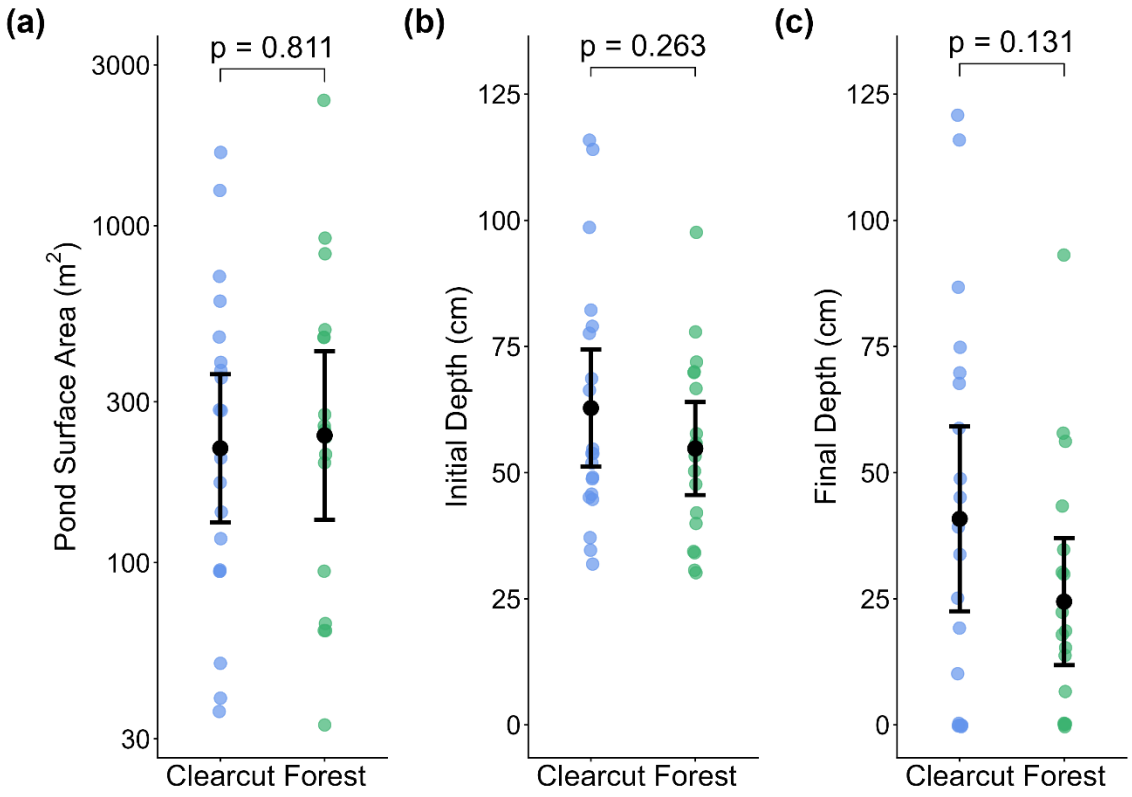


Figure 3.6 The (a) pond surface area (logarithmic scale (y-axis); clearcut: n = 20; forest: n = 17), (b) initial depth (clearcut: n = 20; forest: n = 18), and (c) final depth (clearcut: n = 20; forest: n = 18) of breeding ponds in clearcuts and forests. Means are indicated with black circles with 95% confidence intervals for error bars. Bars above display the p-values from t-tests.

3.3.3 Tree Characteristics

The mean canopy cover was 48.4 ± 6.7% higher around forest ponds than clearcut ponds (Figure 3.7a; Table 3.1). The mean distance to a stand of trees (minimum 1 ha) from the centre of the ponds was 164.1 ± 22.8 m further for clearcut ponds than forest ponds (Figure 3.7b; Table 3.1). The number of small trees around clearcuts did not differ significantly from that of forests (Figure 3.7c; Table 3.1). The basal area of large trees

(DBH > 5 cm) was larger around forested ponds than clearcut ponds (Figure 3.7d; Table 3.1). Both measures of tree diversity, inverse Simpson index and proportion of coniferous trees, did not differ significantly between clearcut and forested ponds (Figure 3.7e; Figure 3.7f; Table 3.1).

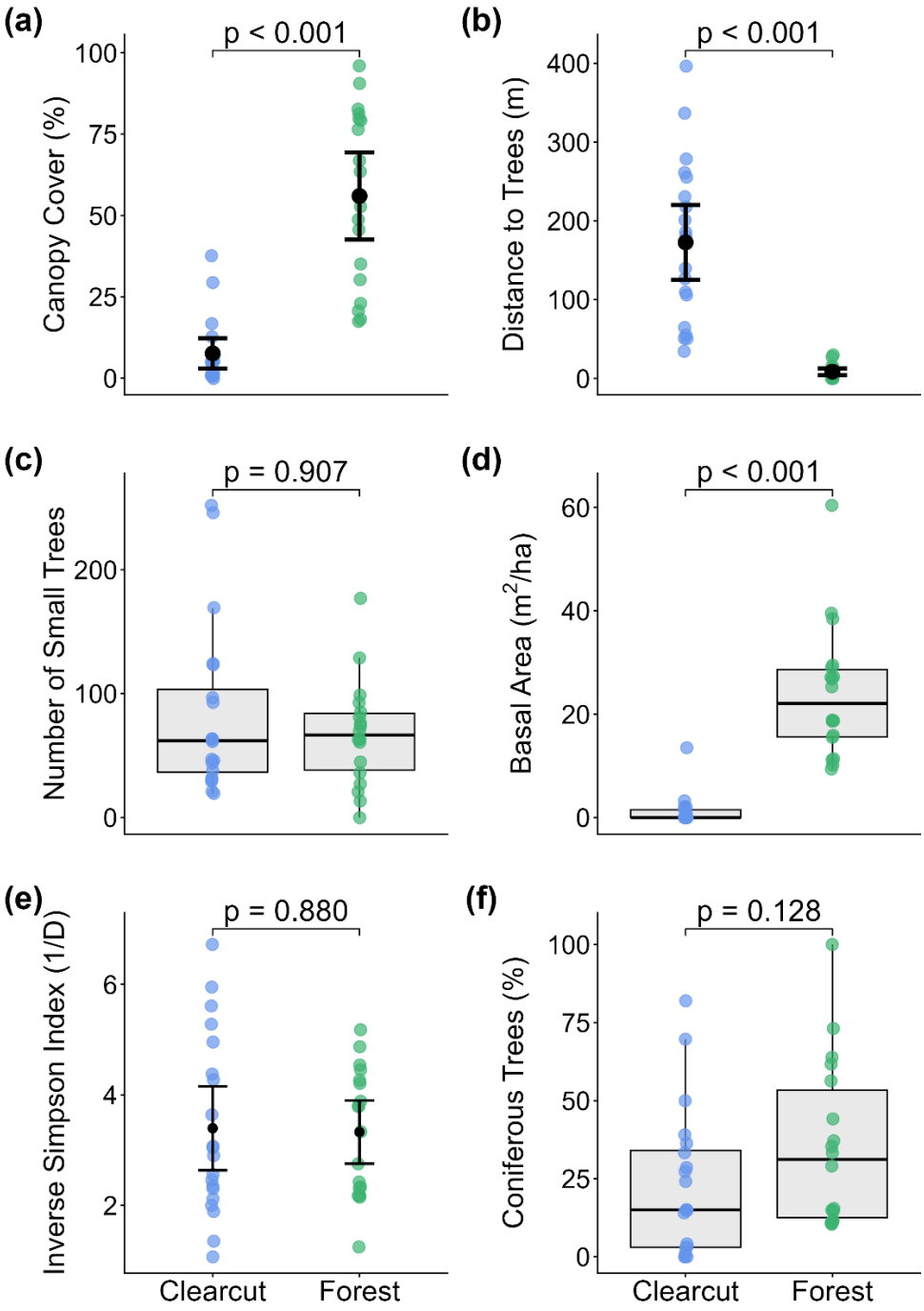


Figure 3.7 Tree characteristics around clearcut (n = 20) and forest (n = 18) breeding ponds. The variables can be grouped as vegetation characteristics (a: canopy cover; c: number of small trees; d: basal area of large trees), landscape characteristics (b: mean distance to a mature stand of trees), and tree diversity characteristics (e: inverse Simpson index; f: proportion of coniferous trees). For variables with normal distributions (a, b, e), the means are indicated with black circles with 95% confidence intervals for error bars. For non-normal distributions (c, d, f), the medians and interquartile ranges are displayed with boxplots. Bars above plots display the p-value from t-tests (a, b, e) or Wilcoxon-Mann-Whitney tests (c, d, f).

3.3.4 Periphyton

Chlorophyll α was not significantly different between clearcut and forest ponds (Figure 3.8a; Table 3.1). Nor did the organic matter differ significantly between clearcut and forest ponds (Figure 3.8b; Table 3.1).

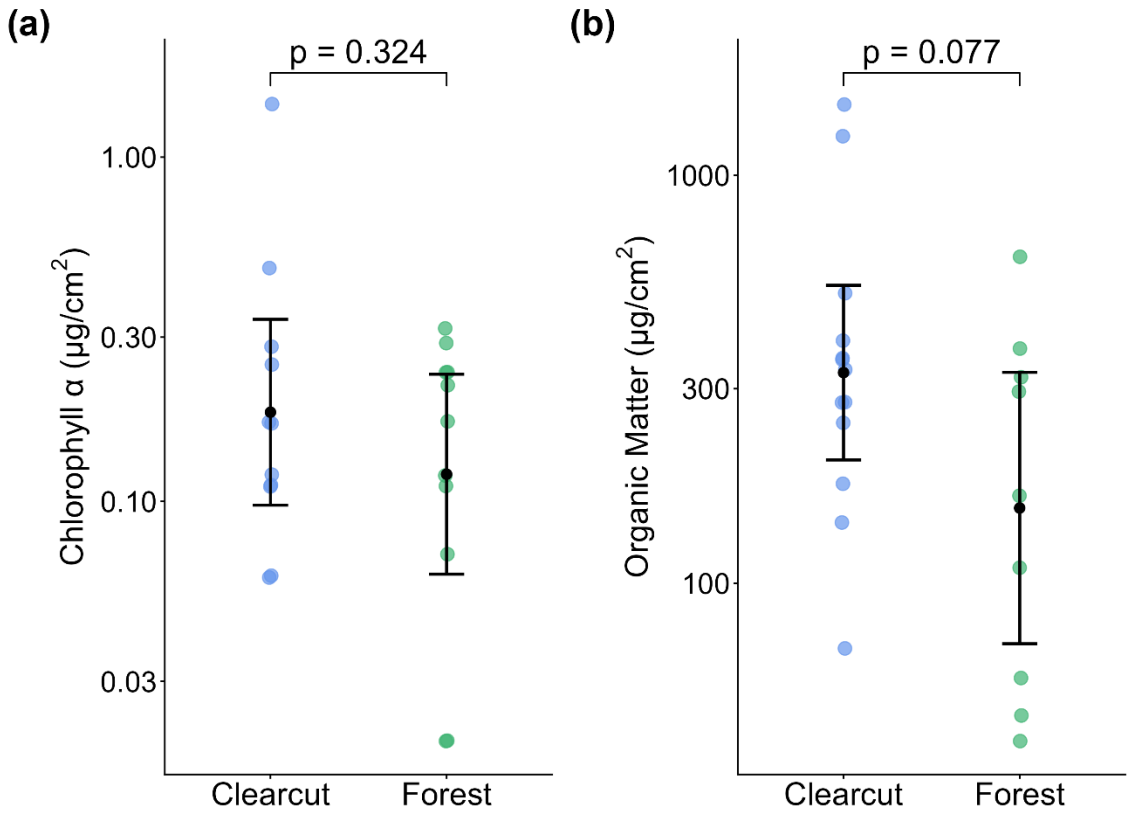
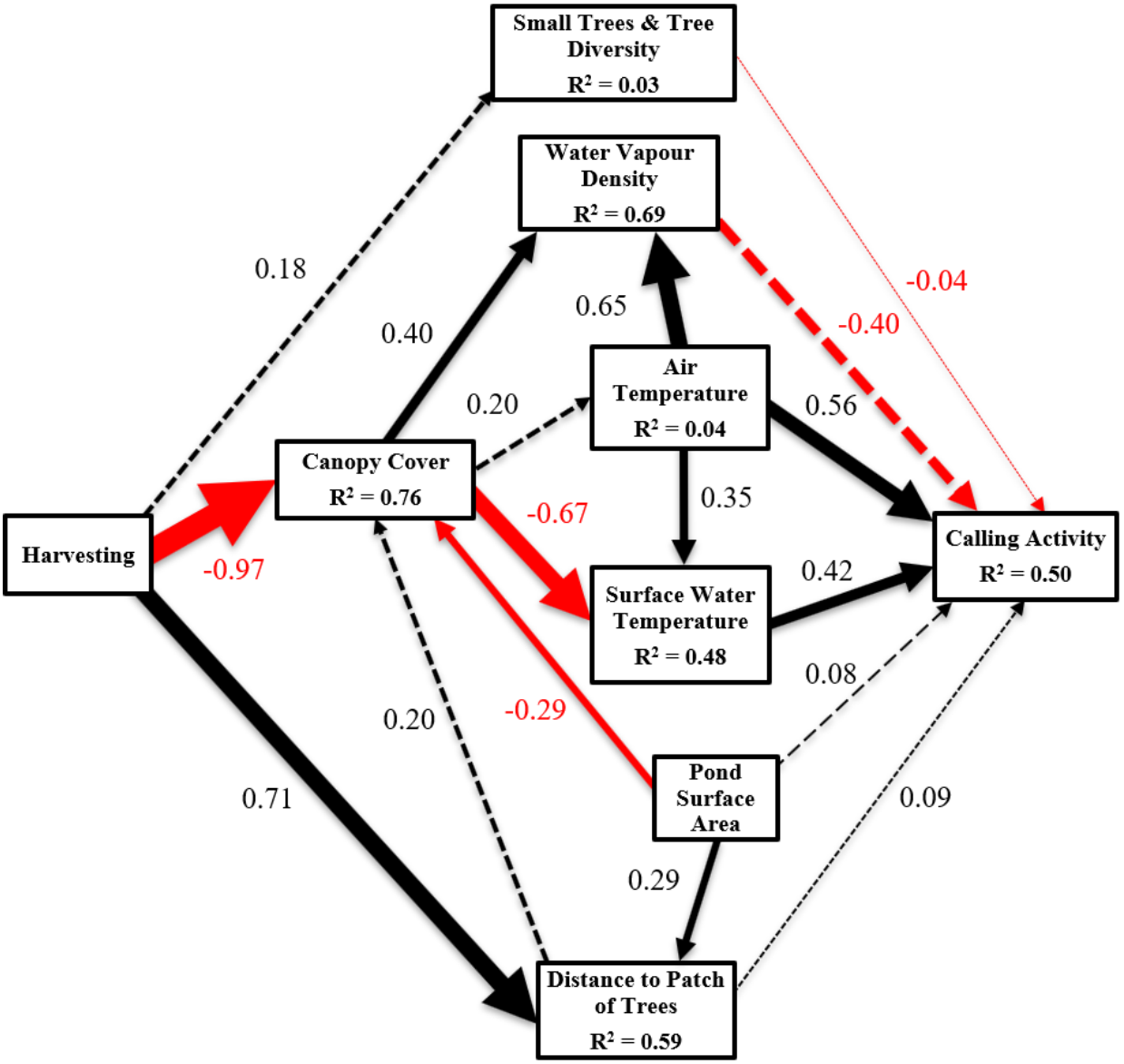


Figure 3.8 Periphyton content collected from glass slides placed 10 cm below the surface in clearcut (a: n = 11, b: n = 13) and forest ponds (a: n = 11, b: n = 9) for 70 days (69 days for the 5 'Sandstone Lake' sites). Periphyton content measured as (a) chlorophyll α and (b) organic matter on a logarithmic scale (y-axis). The means are indicated with black circles with 95% confidence intervals for error bars. Bars above plots display p-values from t-tests.

3.4 Structural Equation Modelling

After excluding sites with missing data, 32 breeding ponds (20 clearcuts, 12 forests) were used in the SEM (Figure 3.9; Table 3.2). The model fit the data well (C = 22.99, df = 36, p = 0.954); all tests of d-separation (conditional independencies) were non-significant (Table 3.2), indicating that there were no missing paths among the

variables incorporated in the SEM (Lefcheck 2016). Air temperature and surface water temperature had positive effects on calling activity (Figure 3.9; Table 3.2). Water vapour density had a marginal negative effect on calling activity. The distance to trees, pond surface area and the small tree and tree diversity component did not affect calling activity. In summary, the only significant effects on calling activity were temperature (Appendix 6.3: Figure 6.2; T_{air}, T_{surf}). Air temperature was not influenced by any other variables in the SEM. Surface water temperature was affected by the air temperature and canopy cover. Harvesting indirectly influenced calling activity via the canopy cover to Tsurf pathway (Figure 3.9; Table 3.2).



707

708 Figure 3.9 Structural equation model of the effects of forest harvesting and other
709 variables on gray treefrog calling activity. Paths with significant coefficients ($p < 0.05$)
710 are represented by solid lines. Positive relationships are shown in black, and negative
711 relationships are displayed in red. Arrow thickness is scaled by the magnitude of the
712 standardized coefficients, as shown next to the arrows. R^2 values are shown in a box
713 within the responding variable. Small Trees and Tree Diversity refers to the first
714 component calculated from the PCA.

Table 3.2 Structural Equation Model (SEM; Figure 3.9) path coefficients and summary statistics. Significant paths ($p < 0.05$) are bolded, and paths with positive standardized coefficients are in black text; negative standardized coefficients are shown in red text. Tree PC1 refers to the first principal component of tree diversity and the number of small trees. To improve normality prior to analysis, the pond surface area was log-transformed and calling activity was square-root transformed.

Path	Coefficient	SE	t-value	p-value	Standardized Coefficient
Harvesting → Canopy Cover	**-60.74**	**8.61**	**-7.06**	**<0.001**	**-0.97**
Harvesting → Tree Distance	**162.63**	**27.30**	**5.96**	**<0.001**	**0.71**
Canopy Cover → Tsurf	**-0.04**	**0.01**	**-4.90**	**<0.001**	**-0.67**
T_{air} → WVD	**0.26**	**0.04**	**6.10**	**<0.001**	**0.65**
T_{air} → Calling Activity	**2.82**	**1.13**	**2.49**	**0.020**	**0.56**
T_{surf} → Calling Activity	**0.98**	**0.37**	**2.65**	**0.014**	**0.42**
Canopy Cover → WVD	**0.00**	**0.00**	**3.75**	**<0.001**	**0.40**
WVD → Calling Activity	-5.08	2.88	-1.77	0.089	-0.40
T_{air} → T_{surf}	**0.78**	**0.30**	**2.59**	**0.015**	**0.35**
Pond Surface Area → Canopy Cover	**-18.82**	**6.53**	**-2.88**	**0.008**	**-0.29**
Pond Surface Area → Tree Distance	**69.58**	**28.08**	**2.48**	**0.019**	**0.29**
Tree Distance → Canopy Cover	0.05	0.04	1.39	0.176	0.20
Canopy Cover → T_{air}	0.00	0.00	1.14	0.264	0.20
Harvesting → Tree PC1	0.43	0.43	0.98	0.335	0.18
Tree Distance → Calling Activity	0.00	0.01	0.56	0.583	0.09
Pond Surface Area → Calling Activity	0.64	1.20	0.53	0.601	0.08
Tree PC1 → Calling Activity	-0.15	0.47	-0.31	0.759	-0.04

Table 3.3 Tests of d-separation and conditional independence considering the Structural Equation Model (SEM; Figure 3.9) structure. Tests (independence claims) are for each pair of variables that do not have arrows between them in the SEM. Significant paths ($p < 0.05$) are bolded. Tree PC1 refers to the first principal component of tree diversity and the number of small trees. To improve normality prior to analysis, the pond surface area was log-transformed and calling activity was square-root transformed.

Independence Claim	**df**	**t-value**	**p-value**
Harvesting → Calling Activity	24	1.71	0.100
Harvesting → T_{air}	29	-0.32	0.750
Harvesting → WVD	28	0.75	0.462
Harvesting → T_{surf}	28	0.83	0.412
Pond Surface Area → Tree PC1	29	0.54	0.594
Pond Surface Area → T_{air}	29	-0.10	0.920
Pond Surface Area → WVD	28	-0.02	0.984
Pond Surface Area → T_{surf}	28	-0.44	0.662
Canopy Cover → Tree PC1	27	0.56	0.581
Canopy Cover → Calling Activity	23	-0.79	0.437
Tree Distance → Tree PC1	28	-0.61	0.544
Tree Distance → T_{air}	27	0.63	0.533
Tree Distance → WVD	26	-0.15	0.885
Tree Distance → T_{surf}	26	-0.98	0.337
Tree PC1 → T_{air}	28	0.57	0.571
Tree PC1 → WVD	27	1.09	0.287
Tree PC1 → T_{surf}	27	0.04	0.968
WVD → T_{surf}	28	0.57	0.574

4 Discussion

While anthropogenic disturbance is typically thought to restrict species ranges, it can create warmer, open habitats that can be beneficial at poleward range edges (Lawson et al. 2014, Pateman et al. 2016, Auge et al. 2023), potentially offsetting marginal climate conditions (Frishkoff et al. 2015, 2019). At their poleward range edge, I found that male gray treefrogs had higher calling activity at ponds within recent clearcuts than within forests, despite adults' reliance on arboreal habitats, consistent with experimental results for gray treefrogs further south in their range (Hocking and Semlitsch 2007) and for their diploid sister species, Cope's Gray Treefrog (*Dryophytes chrysoscelis*; Felix et al. 2010). Ponds with warmer air and surface temperatures had higher calling activity, with surface temperature higher in clearcuts due to reduced canopy cover. These warmer ponds likely benefit tadpole development (Hocking and Semlitsch 2008). Furthermore, these benefits seem to outweigh the costs to adults of traversing open, disturbed habitat. Despite previous research showing that male gray treefrogs select open canopy ponds when they are close (<50 m) to forest edges (Hocking and Semlitsch 2007), I found no decline in calling activity as the distance of clearcut ponds from tree stands increased. The extensive recent history of harvesting in Northwestern Ontario's Boreal Forest (Brandt et al. 2013, Mackey et al. 2024) has likely increased the availability of attractive breeding habitat for gray treefrogs, potentially contributing to higher occupancy and recent range expansion.

Elevated calling activity in recent clearcuts implies that males perceive a benefit from selecting these ponds rather than those in more closed canopy forested areas. These benefits were predicted to be thermal. Consistent with this prediction, structural equation modelling revealed direct positive effects of both air and surface water temperature on

753 calling activity. Nighttime air temperature was not actually warmer in clearcuts; newly
754 regenerating clearcuts tend to have more variable temperatures than forested areas with
755 higher daytime, but colder nighttime, temperatures (Chen et al. 1993, Moore et al. 2005).
756 However, air temperatures were higher in clearcuts in the early evening hours leading up
757 to the start of nightly calling (Figure 3.5), which may be what adults are cueing from as
758 they move towards breeding ponds (Harding and Mifsud 2017). Warmer air temperatures
759 may also favour locomotion for adults to access ponds (Navas et al. 1999, Arnoldi et al.
760 2025).

761 Pond surface temperature was higher in clearcuts, and our SEM indicated a key
762 role for pond surface temperature in mediating the indirect effect of harvesting on calling
763 activity. Harvesting reduces canopy cover, which in turn increases incident solar radiation
764 and warms water bodies, especially the upper strata (Kiffney et al. 2003, Moore et al.
765 2005). Warmer ponds can increase tadpole development rates (Newman 1998, Hocking
766 and Semlitsch 2008), allowing them to metamorphose and leave ponds earlier. While
767 rapid maturation is not necessarily beneficial, as individuals may have, for example,
768 smaller body sizes (Newman 1998), it may be especially important at high latitudes
769 where breeding and development seasons are shorter. Males may, therefore, be selecting
770 breeding ponds that increase their fitness by providing beneficial environments that
771 increase offspring survival post-metamorphosis.

772 Warmer surface temperatures may also have thermal advantages for adult males.
773 Gray treefrogs are reported to call from either vegetation on the water's surface or from
774 overhanging branches (Harding and Mifsud 2017). In our study area, we almost
775 exclusively see males calling while in contact with the pond's surface (personal

776 observation). Calling from the water may allow adults to maintain warmer body
777 temperatures when air temperatures are cool (Höbel and Barta 2014); across our study
778 sites, the mean surface temperature was, on average, 3.3°C (95% CI: 2.7-3.9) warmer
779 than the mean air temperature. Warmer male body temperatures may be advantageous for
780 several reasons. Higher locomotory performance, which occurs as ectotherms warm (until
781 an optimum is reached; Angilletta 2009, Arnoldi et al. 2025), could be advantageous
782 within ponds during male-male aggressive interactions, or for predator escape. Calling
783 characteristics also vary with temperature in many amphibians, including gray treefrogs
784 (Gerhardt 1978). Pekny et al. (2026) recently proposed that this temperature dependence
785 means that information about the quality of breeding environments (i.e. temperature) is
786 encoded within males' calls and thus 'warmer' calls may be more attractive for females.
787 Direct tests of this hypothesis are lacking; however, experiments in gray treefrogs suggest
788 that females do not consistently prefer characteristics associated with warmer calls but
789 have a broad preference range and tend to select calls by males at temperatures similar to
790 their own (temperature coupling; Gerhardt 1978, Humfeld and Grunert 2015).

791 I also hypothesized that warmer pond temperatures in clearcuts may be beneficial
792 by increasing tadpole food resources. The reduced canopy cover and higher water
793 temperatures in clearcuts should allow for increased photosynthesis (Quinn et al. 1997).
794 However, periphyton content was not higher in clearcut ponds than in forest ponds,
795 though the sample size was limited. Differences in water chemistry, turbidity, and leaf
796 litter among the individual ponds may have affected periphyton more than solar radiation
797 alone. While some studies have found increases in periphyton after canopy removal
798 (Feminella et al. 1989, Skelly et al. 2002, Kiffney et al. 2003, Burrows et al. 2021b),

799 others report mixed effects (Richardson and Béraud 2014). Leaf litter has also been
800 shown to influence tadpole food resources (Williams et al. 2008, Stoler and Relyea 2011).
801 While I did not measure leaf litter content, I found no differences in the proportion of
802 conifers or tree diversity between clearcuts and forests. Although at different stages of
803 succession, all our ponds were within similarly managed forest areas, which may
804 contribute to this similarity. I would, however, expect lower leaf litter in clearcuts due to
805 fewer large trees than in forests and increased woody debris from harvest operations, but
806 our initial periphyton results suggest these do not have a large effect on periphyton,
807 though more extensive sampling is needed.

808 Increased calling activity in clearcut ponds suggests that benefits to males
809 outweigh potential costs. As the breeding season approaches, male gray treefrogs
810 abandon arboreal habitats to attend breeding ponds (Dodd 2023). Crossing open, recently
811 clearcut habitats could be more costly than accessing forest ponds. Clearcuts are
812 generally drier than forest habitats (Chen et al. 1993, Moore et al. 2005), aligning with
813 the lower water vapour deficit I found in clearcuts, which can increase desiccation risk in
814 amphibians. These costs may be mitigated by increased skin resistance and tolerance to
815 water loss in arboreal frogs (Young et al. 2005), the nocturnal activity of adults, which
816 means dispersing in cool temperatures, and their ability to rehydrate at breeding ponds.
817 However, juveniles dispersing away from breeding ponds may experience higher costs,
818 including mortality rates due to water loss, in clearcuts compared to forests (Rothermel
819 and Semlitsch 2002, Patrick et al. 2006, Todd and Rothermel 2006, Rittenhouse et al.
820 2009, Popescu and Hunter Jr. 2011). Adults may also face greater predation risk in open
821 clearcuts rather than in forest (Todd et al. 2008, Chang and Todd 2023, Hagnier et al.

2025) and will face higher energetic costs as they have to travel farther from arboreal habitats to reach ponds in recent clearcuts. Given the energetic demands of calling and breeding (Taigen and Wells 1985, Leach et al. 2024), this additional energetic output could impact breeding success. Consistent with there being a cost to travelling through clearcut habitat, Hocking and Semlitsch (2007) found that gray treefrogs near the centre of their range are unlikely to disperse more than 50 m into clearcuts to reach experimental breeding ponds. In contrast, I did not find an effect of distance to trees on calling activity, and I identified cases of chorusing as far as 268 m from trees. This discrepancy could reflect Hocking and Semlitsch's (2007) design, which involved multiple experimental ponds within the same clearcut, so there may have been little pressure to travel farther into the clearcuts, as suitable ponds were available close to the trees. Alternatively, it could reflect inherent differences between the attractiveness of experimental versus natural ponds, or a redistribution of the relative costs and benefits of clearcut versus forested ponds at the poleward range edge relative to the range core. The more open habitats created by harvesting could also be beneficial by allowing calls to carry farther than in more closed habitats (Yip et al. 2017). While many studies suggest reduced abundance of amphibians post-logging, responses tend to vary greatly among species (Asad et al. 2022) and time since harvest (Popescu et al. 2012). There have been cases of positive responses by other treefrog species to various forest-harvesting practices (Lemckert 1999, Vallan et al. 2004), though few studies examine why harvesting may be favourable to treefrogs.

The attractiveness of clearcut ponds at the northern range edge for male gray treefrogs could have broader-scale implications for the species' biogeography. Forest

harvesting has been ongoing in Ontario for at least the last century (Epp 2000), and 121,000 ha are harvested on average in Ontario per year (2009 - 2019 Ontario Ministry of Northern Development, Mines, Natural Resources and Forestry 2021), thereby increasing the attractive breeding habitat available to gray treefrogs. Gray treefrogs' use of this more thermally favourable breeding habitat at their range edge aligns with similar patterns in other taxa. For example, in cool climates, the Silver-Spotted Skipper butterfly (*Hesperia comma*) oviposited on bare ground, a warmer microclimate (Lawson et al. 2014), and the Speckled Wood butterfly (*Pararge aegeria*) used more physiologically favourable habitat for overwintering and larval development at the range edge (Pateman et al. 2016). Similarly, freshwater turtles (*Emydoidea blandingii; Chrysemys picta*) used warmer and less thermally variable microclimates, including during the nesting season, at their northern range edge (Auge et al. 2023). Similar patterns can be observed in adult habitat use in disturbed areas. In two species of *Craugastor* neotropical frogs (Frishkoff et al. 2015) and three species of *Anolis* lizards (Frishkoff et al. 2019), the organisms switched from using cooler forest habitat at low elevations to using warmer disturbed habitat at higher elevations. While gray treefrogs may not represent a shift in breeding habitat use, as experimental results suggest a clearcut preference further south in their range (Hocking and Semlitsch 2007), the increasing availability of clearcuts at the range edge may have facilitated increased occupancy and even range expansion, both of which have been suggested by natural history observations and anecdotal evidence for gray treefrogs in Northwestern Ontario over the past several decades.

Harvesting is not the only major disturbance within the Boreal and Boreal-Transitional forest that generates swaths of open habitat. Forest fires are a quasi-natural

disturbance (as they may also have anthropogenic causes), burning 84,110 hectares per year on average (2004 to 2024) in Ontario's Northern Boreal Forest (data from Ontario Ministry of Natural Resources and Forestry 2025b under the Open Government License - Ontario). While forest harvesting has been ongoing for more than a century (Epp 2000), it is a much more recent disturbance than forest fires. If forest harvesting is encouraging increased occupancy and even range expansion of gray treefrogs, it raises the question of why forest fires have not played the same role historically. It may be that only now, with greater amounts of open habitat and climate change, it is warm enough to allow further expansion or occupancy at the range edge. Or it may be that burned ponds are not preferential or as available to gray treefrogs. Forest harvesting in Canada's Northern Boreal Forest exceeds natural fire disturbance levels and increases fragmentation (Malcolm et al. 2025), making them more abundant and accessible to gray treefrogs. The construction of roads to access clearcuts could also facilitate dispersal. The roads create ditches that often hold water and have an open canopy on one side, which can form breeding ponds such as Upsala Cut 1 and four other clearcut ponds in this study. Forestry equipment can also create large ruts which can form ponds, as evident by Boreal Cut 1. Aside from pond creation, fires also tend to affect organisms differently than harvesting, especially in the earliest years post-disturbance (Schieck and Song 2006, Frank et al. 2025, 2026). Water chemistry also varies (Nitschke 2005), potentially affecting breeding habitat selection and tadpole growth. While gray treefrogs' use of burned ponds has not yet been studied, Cope's Gray Treefrog, which also breeds in open canopy ponds (Binckley and Resetarits 2007), do not tend to use burned breeding ponds (Schurbon and Fauth 2003, McDonald et al. 2018), and their tadpole performance was lower with burned

leaf litter treatments (McDonald et al. 2018). Responses to burned areas vary among amphibians; some may not change in abundance, while others increase (Hossack and Corn 2007). For example, Boreal Toads (*Bufo boreas*) colonized breeding ponds after a forest fire (Hossack and Corn 2007), which may be due to the warmer microhabitats of burned sites, especially warmer burrows (Hossack et al. 2009). Further research is needed on breeding habitat in burned sites, especially given the recent years of high-severity fires in Canada (Wang et al. 2025).

While my results suggest male gray treefrogs call more at ponds in clearcut areas, it is premature to conclude that clearcuts are beneficial for Eastern Gray Treefrogs, as we still lack key information. Most importantly, we do not know whether the higher calling activity translates to higher fitness. Studies in experimental ponds at the range core suggest that tadpoles develop faster and survival is higher in clearcut ponds (Hocking and Semlitsch 2008). However, it is possible this may differ in natural ponds and across the range. Additionally, negative impacts may also not emerge until later life stages. Juveniles of other amphibian species are thought to incur greater costs when leaving clearcut ponds than when leaving forest ponds (Patrick et al. 2006, Todd and Rothermel 2006, Rittenhouse et al. 2008, Popescu and Hunter Jr. 2011), and gray treefrog juveniles may not disperse farther than 100 to 200 m (Roble 1979, Johnson et al. 2007), which could be problematic given the distance to trees at a number of the breeding ponds in my study. It is possible, especially at ponds further into clearcuts, that this attractive breeding habitat may be an ecological trap (Hale and Swearer 2016), where it appears attractive to adults but does not increase offspring survival and fitness. My study design specifically selected ponds that were not undergoing spraying with glyphosate-based herbicides,

914 which can negatively impact amphibians (Howe et al. 2004, Relyea and Jones 2009,
915 Williams and Semlitsch 2010). Lastly, and crucially, we also lack key information on
916 females. I focused on males due to the infeasibility of sampling females, so it remains
917 unknown whether females select clearcut ponds for breeding. Female selection of
918 clearcut ponds at the range core (Hocking and Semlitsch 2007) and higher chorusing
919 intensity at clearcuts suggest the likelihood of female presence and breeding activity;
920 however, this remains untested in a non-experimental system. Further research is needed
921 to determine whether females also select breeding habitats in harvested areas and whether
922 these breeding ponds are beneficial to offspring or an ecological trap.

923 I found that forest harvesting is generating attractive breeding habitat for male
924 gray treefrogs at their poleward range edge. Ponds within clearcuts appear to be thermally
925 favourable, potentially via increased tadpole development rates (Hocking and Semlitsch
926 2008). These benefits appear to outweigh potential costs of traversing through these
927 disturbed habitats, especially desiccation due to the drier air. However, it is important that
928 the attractiveness of clearcut ponds to males is not interpreted as evidence that clearcuts
929 are beneficial for this species, as increased calling does not necessarily translate into
930 increased fitness. Further research should determine if these disturbed breeding habitats
931 are also preferred by females and if they are beneficial to offspring or an ecological trap.
932 Although other studies have similarly found increased use or abundance of a few
933 amphibian species in harvested areas (Lemckert 1999, Vallan et al. 2004, Hossack and
934 Corn 2007, Hocking and Semlitsch 2007, Asad et al. 2022), few studies have directly
935 studied the drivers of using clearcuts in natural ponds. The future work I have laid out

936 will aid in our understanding of whether these habitats are facilitating increased
937 occupancy or even range expansion in gray treefrogs.
938

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6 Appendix

6.1 Breeding Pond Locations

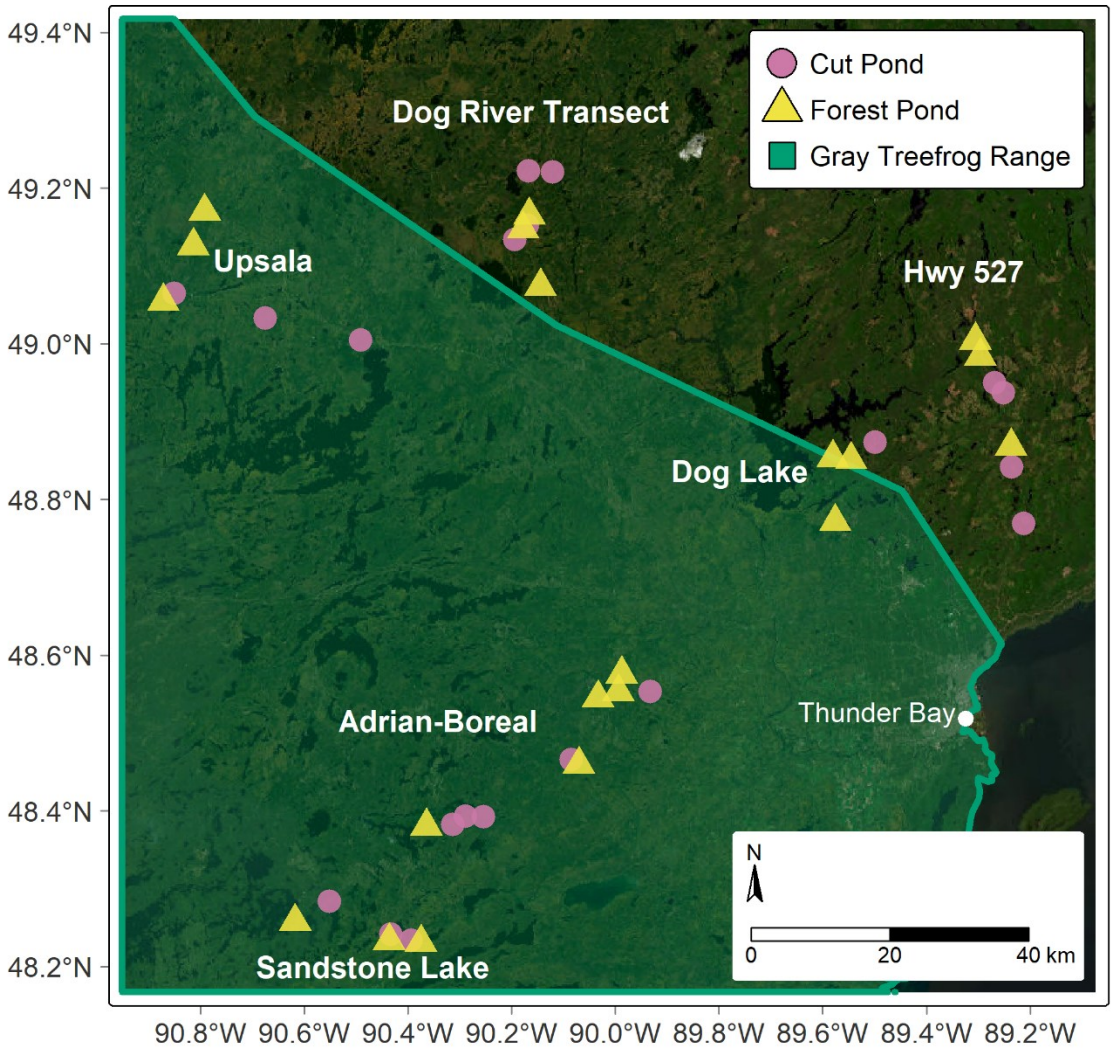

Figure 6.1 Clearcut and forest breeding pond locations around Thunder Bay, ON. Names of groups shown in white, which refer to sites in Table 6.1.

1379 Table 6.1 Clearcut and forest breeding pond locations and groups around Thunder Bay,
1380 ON.

Site	Habitat Type	Group	Latitude	Longitude
Adrian Lake Cut	Clearcut	Adrian-Boreal	48.469	-89.853
Boreal Cut 1	Clearcut	Adrian-Boreal	48.335	-90.207
Boreal Cut 2	Clearcut	Adrian-Boreal	48.339	-90.243
Boreal Cut 3	Clearcut	Adrian-Boreal	48.330	-90.269
Boreal Forest 1	Forest	Adrian-Boreal	48.387	-90.010
Boreal Forest 2	Forest	Adrian-Boreal	48.332	-90.321
Glenwater Cut	Clearcut	Adrian-Boreal	48.394	-90.023
Glenwater Forest 1	Forest	Adrian-Boreal	48.473	-89.915
Glenwater Forest 2	Forest	Adrian-Boreal	48.469	-89.956
Glimmer Forest	Forest	Adrian-Boreal	48.496	-89.904
DL Cut	Clearcut	Dog Lake	48.750	-89.350
DL Forest 1	Forest	Dog Lake	48.732	-89.401
DL Forest 2	Forest	Dog Lake	48.738	-89.436
Gilbride Forest	Forest	Dog Lake	48.655	-89.449
DRT Cut 1	Clearcut	Dog River Transect	49.087	-89.973
DRT Cut 2	Clearcut	Dog River Transect	49.156	-89.957
DRT Cut 3	Clearcut	Dog River Transect	49.151	-89.910
DRT Forest 1	Forest	Dog River Transect	49.006	-89.963
DRT Forest 2	Forest	Dog River Transect	49.083	-89.983
DRT Forest 3	Forest	Dog River Transect	49.099	-89.967
Sideen Cut	Clearcut	Dog River Transect	49.071	-90.002
Dorion Forest	Forest	Hwy 527	48.863	-89.126
Hwy 527 Cut 1	Clearcut	Hwy 527	48.620	-89.082
Hwy 527 Cut 2	Clearcut	Hwy 527	48.791	-89.085
Hwy 527 Cut 3	Clearcut	Hwy 527	48.805	-89.100
Hwy 527 Cut 4	Clearcut	Hwy 527	48.694	-89.090
Hwy 527 Forest 1	Forest	Hwy 527	48.721	-89.085
Hwy 527 Forest 2	Forest	Hwy 527	48.842	-89.121
Sand Cut 1	Clearcut	Sandstone Lake	48.188	-90.377

Site	Habitat Type	Group	Latitude	Longitude
Sand Cut 2	Clearcut	Sandstone Lake	48.199	-90.415
Sand Cut 3	Clearcut	Sandstone Lake	48.251	-90.526
Sand Forest 1	Forest	Sandstone Lake	48.230	-90.597
Sand Forest 2	Forest	Sandstone Lake	48.191	-90.421
Sand Forest 3	Forest	Sandstone Lake	48.184	-90.359
Graham Forest 1	Forest	Upsala	49.155	-90.605
Graham Forest 2	Forest	Upsala	49.113	-90.636
Pipeline Cut	Clearcut	Upsala	49.009	-90.511
Sapawe Cut	Clearcut	Upsala	49.055	-90.684
Sapawe Forest	Forest	Upsala	49.047	-90.708
Upsala Cut 1	Clearcut	Upsala	48.966	-90.330

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6.2 RIBBIT Parameters

Table 6.2 RIBBIT (Repeat Interval-Based Bioacoustic Identification Tool; Lapp et al. 2021) parameters used for acoustic detection of the Eastern Gray Treefrog (*Dryophytes versicolor*) in the Thunder Bay, Ontario, Canada region (Lockhart 2024).

Setting	Value
Window Length (s)	1.85
Window Sample Number	722
Signal Band Minimum Frequency (kHz)	1.94
Signal Band Maximum Frequency (kHz)	2.34
Noise Band Low Minimum Frequency (kHz)	0.35
Noise Band Low Maximum Frequency (kHz)	0.43
Noise Band High Minimum Frequency (kHz)	12.87
Noise Band High Maximum Frequency (kHz)	19.18
Minimum Pulse Repetition Rate (pulse/s)	15
Maximum Pulse Repetition Rate (pulse/s)	31
Gray Treefrog Detection Threshold	637.59

6.3 Calling Activity and Temperature

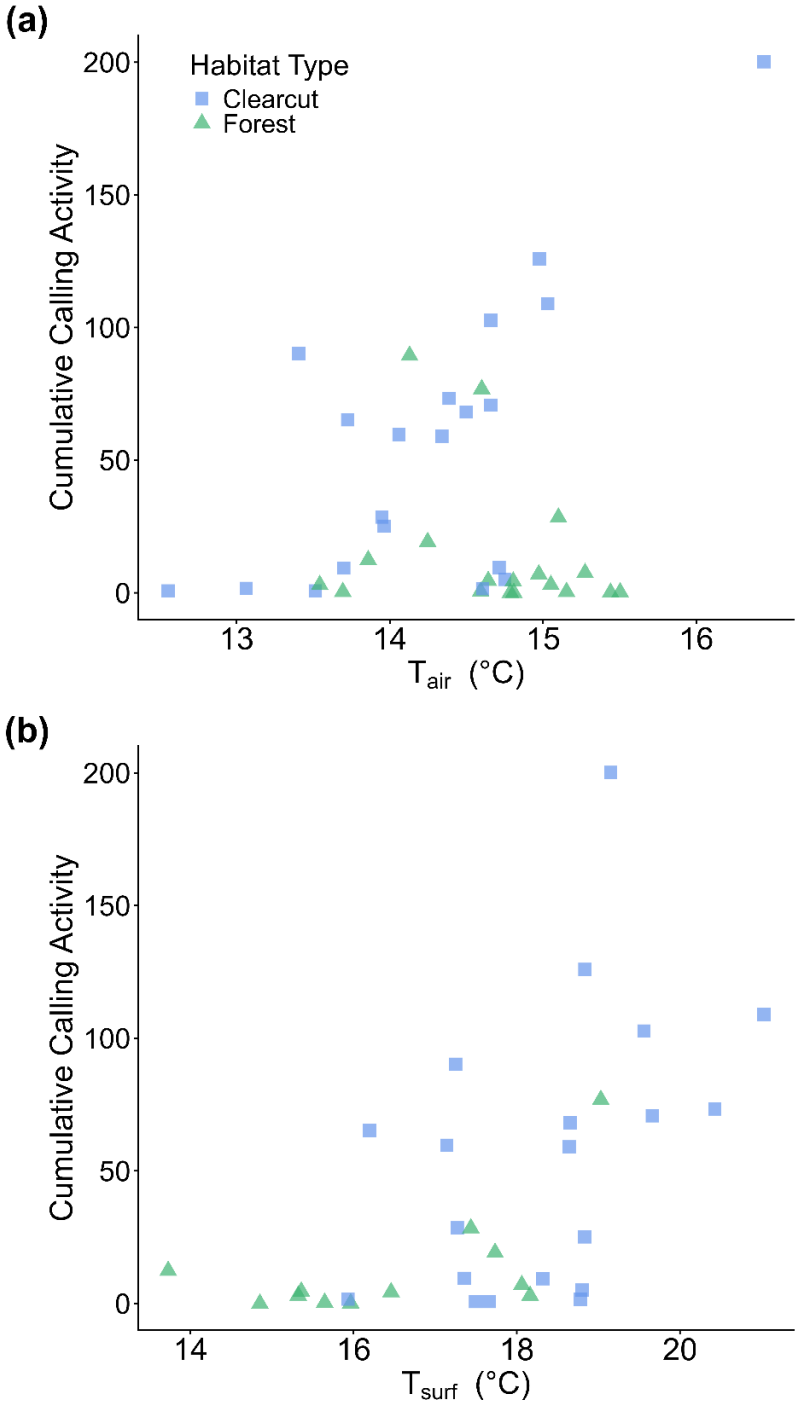

Figure 6.2 Scatterplot showing the association between cumulative calling activity of Eastern Gray Treefrogs (*Dryophytes versicolor*) over their breeding season (May 26 to June 30) and mean evening (19:00 to 02:00) (a) air temperature (T_{air}) and (b) surface water temperature (T_{surf}) at clearcut (blue square) and forest (green triangle) breeding ponds.