

# Love It or Leaf It: Site Selection of Breeding Treefrogs Based on Leaf Litter Subsidies

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**Breeding organisms rely on numerous environmental cues to determine optimal sites for oviposition. Site selection is often associated with factors that increase fitness, and the identification of these factors can help conservation efforts. For amphibians that breed in wetlands, the quality of terrestrial subsidies (e.g., leaf litter) can strongly influence larval survival and development by altering water chemistry and available nutrients. In this study, we examined the preference of breeding Gray Treefrogs (*Hyla versicolor*) for wetlands containing litter species of varying chemical quality. Based on previous studies of larval survival, we hypothesized that treefrogs would oviposit more eggs into wetland mesocosms containing litter with high nutrient concentrations and low phenolic concentrations. To test our hypothesis, we counted the number of eggs oviposited by treefrogs in artificial wetland mesocosms containing either Red Maple (*Acer rubrum*), Black Oak (*Quercus velutina*), or Eastern Hemlock (*Tsuga canadensis*) litter. We conducted this study over two breeding seasons. Counter to our hypothesis, we found that treefrogs preferred to oviposit in mesocosms containing maple litter, which contains high levels of both nutrients and phenolic acids. We discuss possible explanations for this result, including the possible anti-parasitic effects of phenolic acids. This is the first study demonstrating that breeding amphibians can differentiate between wetlands containing leaf litter species of differing chemistry. Given global declines in amphibian species concurrent with widespread changes in forest composition, our results emphasize the importance of considering leaf litter quality in wetland management and conservation efforts.**

THE choice of breeding habitat often plays an important role in the reproductive success of an individual (Jaenike, 1978). Although natal philopatry (i.e., return to the site of birth or hatching) might provide a low-risk solution given the demonstrated survival of the parents, competition and changing environments frequently force organisms to find new breeding habitats (Semlitsch, 2008). To discern among optimal and suboptimal habitats within the restricted timeframe of breeding periods, organisms must employ environmental cues such as chemical (e.g., volatile chemicals), physical (e.g., coloration), and acoustic (e.g., sounds of conspecifics) signals (Bentley and Day, 1989; Williams et al., 2007; Li et al., 2009; Buxton et al., 2015). The manipulation and management of these signals can greatly aid conservation of species, particularly for species of conservation concern (Werner et al., 2007).

One-third of all amphibian species are currently threatened with extinction, and research predicts that their loss can have dramatic consequences for ecological function (Collins et al., 2009; Hoffman et al., 2010; although see Rubbo et al., 2012). One suggested reason for amphibian declines is their heightened sensitivity to environmental conditions (Collins et al., 2009), which they use to discern optimal breeding locations. Because many amphibians have a biphasic life cycle where larvae develop in water but spend their adult life on land, breeding individuals must be particularly sensitive to environmental conditions in and around aquatic environments. For example, several species of amphibians are more likely to breed in open-canopy systems because elevated light levels increase periphyton resources (Binckley and Resetarits, 2007; Werner et al., 2007; Mokany et al., 2008). Newly filled wetlands might also be preferable for oviposition because they generally have greater oxygen levels

and productivity than older wetlands (Pintar and Resetarits, 2017). Some species of amphibians also oviposit fewer eggs in wetlands with less per-capita resources or greater risk of larval predation (Resetarits and Wilbur, 1989). In addition, amphibians generally prefer to breed in systems without contaminants such as pesticides (Takahashi, 2007; Vonesh and Buck, 2007; Vonesh and Kraus, 2009) and road deicing salt (Karraker et al., 2008). As humans continue to impact the chemical and physical properties of aquatic systems, the abundance of optimal breeding habitats for amphibians might also change.

Terrestrial subsidies into wetlands might provide an additional environmental cue for optimal breeding site selection. In temperate systems, leaf litter is a particularly massive subsidy that leaches nutrients and other compounds into freshwater systems (reviewed in Stoler and Relyea, 2020). Litter inputs to wetlands generally consist of tree species mixtures, but inputs to small wetlands can be dominated by only one or two tree species (Holgerson et al., 2016; Stoler and Relyea, unpubl.). Variation in the chemistry of litter species and subsequent variation in the properties that they generate might serve as indicators of habitat quality for individuals seeking breeding habitat. Although we know little about whether subsidies might provide a cue for breeding amphibians, research on aquatic-breeding insects indicates that several species do prefer darker-colored habitats typically associated with litter inputs (Li et al., 2009). One reason for this might be the nutritional benefits of leaf litter for larvae (Bentley and Day, 1989). Plant litter inputs that are rich in nutrients can promote growth of periphyton resources, which can lead to increased larval growth and development (Stoler and Relyea, 2020). However, litter subsidies that contain toxic chemicals (e.g., phenolic

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Submitted: 7 June 2020. Accepted: 24 March 2021. Associate Editor: M. J. Lannoo.

© 2021 by the American Society of Ichthyologists and Herpetologists DOI: 10.1643/h2020090 Published online: 15 September 2021

**Table 1.** Major chemical constituents of the three litter species used in this study. We present all values as percentages of total litter mass. Details of chemical analyses are provided in Stoler and Relyea (2016).

Leaf	C	N	P	Ca	K	Mg	Lignin	Tannin	Phenolics	Soluble carbon
Red Maple	42.454	0.009	0.001	0.001	0.004	0.002	8.218	2.068	6.594	42.454
Black Oak	33.212	0.009	0.001	0.001	0.004	0.002	17.987	1.645	8.287	33.212
Eastern Hemlock	47.459	1.309	0.109	1.846	0.052	0.047	1.309	1.840	4.722	26.716

acids) can also reduce tadpole survival and slow development (Maerz et al., 2005).

In this study, we hypothesized that amphibians would preferentially oviposit eggs in wetlands containing leaf litter that is rich in primary compounds (e.g., nutrients such as N and P) and deficient in soluble secondary compounds (e.g., phenolic acids and other humic compounds). To test this hypothesis, we provided naturally breeding Gray Treefrogs (*Hyla versicolor*) with a choice of wetlands containing one of three different tree litter species that varied in primary and secondary compound content. Species included Red Maple (*Acer rubrum*), Black Oak (*Quercus velutina*), and Eastern Hemlock (*Tsuga canadensis*). We predicted that treefrogs would oviposit more eggs in wetlands with Eastern Hemlock, which has comparatively high concentrations of nutrients, low concentrations of lignin that would prevent accessibility to those nutrients, and low concentrations of soluble secondary compounds.

## MATERIALS AND METHODS

We conducted our experiment during the treefrog breeding seasons of 2009 and 2010 (i.e., early May to late July). The experiment consisted of a randomized blocked design with a single replicate of all treatments within each spatial block. There were three leaf-litter treatments: Eastern Hemlock litter, Red Maple litter, and Black Oak litter. We chose these three species because they were chemically dissimilar and because they are common to the study area. All species are mid-to-late successional species; growth of both maple and hemlock respond positively to disturbances that eliminate competing tree species (Burns and Honkala, 1990). In the area of study, forests are generally dominated by either maple species (*A. rubrum* or *A. saccharum*) or oak species (*Q. alba*, *Q. velutina*, or *Q. rubra*; Wilson et al., 2013). Eastern Hemlock (*Tsuga canadensis*) is less dominant but can be found in high densities on rocky outcrops and mesic hillsides. At the scale of a single wetland, litter inputs are generally dominated by a single species, although complete monocultures are rare (A. Stoler, unpubl.). Whereas Red Maple is rapidly increasing in dominance, hemlock and oak are declining in abundance due to deer overbrowsing and invasive pests (Orwig et al., 2002; Abrams, 2003). We provide the results of chemical analysis for each of these three litter species in Table 1, according to methodology described in Stoler et al. (2016a). Overall, Red Maple and Black Oak litter have similarly high levels of phenolic acids, yet the high quantity of lignin in oak prevents these acids from leaching into the water. In contrast, maple rapidly stains the water due to leaching. Hemlock is relatively nutrient-rich and contains relatively low levels of lignin.

We replicated each of the three litter treatments ten times in 2009 and 14 times in 2010, for a total of 30 and 42 experimental units in each respective year. The experimental units were 100 L blue-colored polyethylene wading pools

filled with well water and leaf litter. In each block, we arranged the three pools in a row, spaced 0.5 m between pools. We established blocks throughout a 28,000 m<sup>2</sup> area at the Pymatuning Laboratory of Ecology in northwest Pennsylvania (41.569720°N, -80.455789°W). In 2009, we placed blocks mostly along a forest edge and a few near human-made structures in an open field (e.g., sheds, cattle tanks). During this season, we determined that treefrogs prefer to breed near structures. Consequently, we placed most of the blocks near these structures in the 2010 breeding season. During both years, we placed blocks at least 25 m apart from any other block.

In both years, we set up pools in early May and allowed oviposition to occur until the end of July. After filling pools with well water, we added 100 g of dried leaf litter. The resulting concentration of leaf litter (1 g L<sup>-1</sup>) is within observed values (Rubbo et al., 2008). We collected freshly abscised litter in autumn 2008 and autumn 2009 for the 2009 and 2010 breeding seasons, respectively, and air-dried litter over the winter. Although this litter is less decayed than what treefrogs are naturally exposed to in the spring, prior experiments indicate that fall- and spring-collected leaf litter generate similar chemical properties in wetlands (Stoler and Relyea, 2011, 2016). At the same time as litter addition, we also added equal aliquots of pond water and zooplankton collected from natural wetlands. We collected water and zooplankton from ponds that were surrounded by either maple, hemlock, or oak, and we mixed all collected water before distributing to our pools. To accelerate the growth of periphyton, phytoplankton, and zooplankton, we added 5 g of rabbit chow for an initial pulse of labile, organic nutrients. Immediately after adding the rabbit chow, we covered the pools with a 60% shade cloth lid to allow the microbial communities to develop without the addition of natural colonists. After two weeks, we uncovered the pools and allowed free colonization by all organisms.

We checked the pools for treefrog eggs every 2–3 d. When we found eggs, we collected them with a siphon and counted them in the laboratory. Because Gray Treefrogs scatter their eggs across the surface of a water body, we gently disturbed leaf litter around the edges to ensure that we collected all eggs. After counting eggs, we released them into a nearby wetland to allow for natural development. By removing the eggs from the pools, we avoided the possibility that treefrogs might avoid ovipositing eggs in wetlands with conspecific competitors (Rieger et al., 2004), although egg removal does not necessarily remove all conspecific cues. We checked pools from 27 May–22 July and from 26 May–14 July in 2009 and 2011, respectively. Within those time periods, we recorded oviposition from 18 June–22 July and from 26 May–21 June in 2009 and 2010, respectively.

**Statistical analysis.**—We removed any blocks from the analysis that did not receive treefrog eggs in any of the three

treatments. Lack of any oviposition reflects poor placement of blocks, not an effect of treatment. Consequently, we removed six of the ten blocks in 2009 and four of the 14 blocks in 2010, leaving a total of 14 blocks across both years (i.e., 42 total mesocosms).

To test the effect of leaf litter on Gray Treefrog oviposition, we employed generalized linear modeling. We first verified the lack of a treatment-by-year interaction by conducting a generalized linear model (GLM) that included both leaf litter treatment and year as fixed effects. We then conducted a generalized linear mixed-effect (GLMER) model with leaf litter treatment as a fixed factor and both year and block as random factors. Because we replicated treatments only once within a block, we did not include a block-by-treatment interaction in our design. We used a Poisson distribution without data transformation. To obtain test statistics for a categorical design, we conducted type III sums of squares analysis of variance (ANOVA) on the model. To assess treatment differences, we conducted *post hoc* Tukey's tests.

We verified that data fit a Poisson distribution by examining the distribution of data points in a Q-Q plot. We conducted all analyses in R (Version 4.0.0, R Core Team, 2020) using the *stats*, *lme4*, *car*, and *multcomp* packages for GLM, GLMER, ANOVA, and Tukey's tests, respectively.

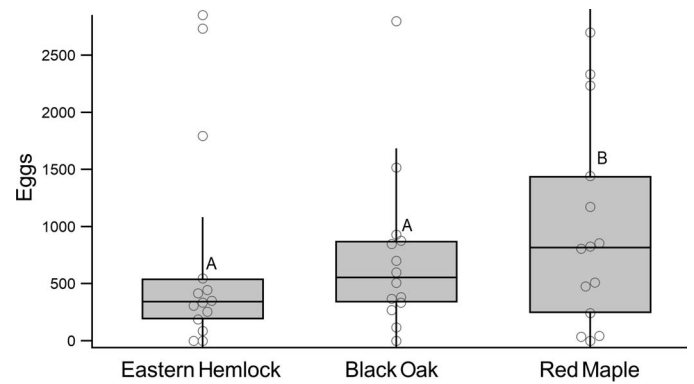
## RESULTS

We counted 5,641 eggs in 2009 and 28,623 eggs in 2010. We verified the lack of a treatment-by-year interaction ( $F_{2,36} = 0.504$ ,  $P = 0.608$ ). We found an effect of leaf litter treatment on the number of eggs oviposited in pools ( $\chi^2 = 669.89$ ,  $P < 0.001$ ). Treatment comparisons revealed that treefrogs oviposited more eggs in pools containing maple litter relative to pools containing hemlock or oak litter ( $P < 0.001$ ; Fig. 1). We did not find any difference in egg numbers between hemlock and oak treatments ( $P = 0.911$ ). On average, we found 241 and 245 more eggs in pools with maple litter than in pools with hemlock or oak litter, respectively, which represents a 33% higher oviposition in Red Maple pools compared to hemlock and oak pools.

## DISCUSSION

This is the first study demonstrating that variation in the species of leaf litter inputs can alter breeding patterns of amphibians. Counter to our prediction, Gray Treefrogs oviposited more eggs in wetlands containing Red Maple litter, which contains high concentrations of both nutrients and phenolic acids. In contrast, they laid fewer eggs in wetlands with oak litter, which has nutrients and toxic compounds that are bound in lignin and do not easily leach into the water. Treefrogs also laid fewer eggs in wetlands with hemlock litter, which has high levels of nutrients but very little phenolic acids. This finding is important because it suggests that amphibians might distinguish among ponds containing different species of leaf litter when deciding where to oviposit their eggs. Moreover, our finding suggests that changes in forest composition that influence the composition of litter inputs to wetland might also result in altered amphibian breeding patterns.

The attraction of breeding treefrogs to wetlands with maple litter might be maladaptive. In a mesocosm study that exposed Gray Treefrogs to 12 different species of tree litter, Stoler and Relyea (2011) found slightly reduced



**Fig. 1.** Box and whisker plot of egg numbers counted in litter treatments across the 2009 and 2010 treefrog breeding seasons. Boxes represent the median and interquartile range; whiskers extend to inner quartiles. Individual data points are shown in gray. Letters above interquartile ranges denote significant differences. We analyzed data assuming a Poisson distribution; graphed data are untransformed.

metamorph mass in treatments with either Black Oak litter or Red Maple litter relative to hemlock litter. This might occur for several reasons. Red Maple and oak litter are associated with fewer periphyton resources than hemlock litter (Stoler and Relyea, 2011), which might increase larval competition. Red Maple also decomposes faster relative to oak and hemlock, which can lower dissolved oxygen to suboptimal concentrations for tadpoles (i.e., through aerobic decomposition; Stoler and Relyea, 2016). In addition, Red Maple litter leaches substantial amounts of phenolic acids, which can reduce tadpole survival and biomass (Martin and Blossy, 2013; Stoler and Relyea, 2016; Dodd and Buchholz, 2018). This occurs because phenolic acids can disable gill function and because humic compounds can stain the water, attenuate light levels, and further reduce the growth of algal resources. Nevertheless, Dodd and Buchholz (2018) and our current study found that breeding treefrogs exhibit an affinity for wetlands containing such compounds.

Our results are not without precedent. Dodd and Buchholz (2018) found that amphibians preferred to oviposit in artificial wetlands amended with tannic acids (i.e., a type of phenolic acid), and some species of mosquitoes prefer to breed in aquatic systems containing larvicidal compounds (Afify and Galizia, 2015). There are several hypotheses for such behavior. One possibility is that treefrogs prefer to oviposit in wetlands with Red Maple litter because these inputs deter the oviposition of tadpole predators. Although we did not measure the number of ovipositing or emergent predators (e.g., dragonflies) during our study, this possibility is unlikely. Many tadpole predators (e.g., dragonflies) prefer ovipositing eggs into dark-colored waters due to their high reflectance (Wildermuth, 1998; Kriska et al., 2006), and Red Maple litter rapidly stains the water a dark color by leaching soluble carbon. Nevertheless, Smith and Harmon (2019) demonstrated that treefrogs do avoid ovipositing in wetlands with free-ranging fish predators, and future work should explore record the number of predators that oviposit in wetlands alongside amphibians.

A second hypothesis is that maple leaf litter might inhibit the effectiveness of visual predators by providing physical refugia from predators or by staining the water, and the resulting reduction in predation risk might encourage



oviposition. Tadpoles frequently use leaf litter as a source of shelter (Hoverman and Relyea, 2008), yet we observed less oviposition in mesocosms with oak litter which provides similar or more surface area for refuge relative to Red Maple litter. Laboratory assays do indicate that stained water and reduced light availability deters visual predation (Martin et al., 1974); however, an experimental increase of Red Maple leachate concentrations in outdoor mesocosms actually resulted in greater predation risk of Wood Frog (*Rana sylvatica*) tadpoles by Eastern Newts (*Notophthalmus viridescens*) relative to no-leachate controls (Stoler and Relyea, 2013). This result likely occurred because Red Maple leachate slowed tadpole growth and prevented tadpoles from reaching a size refuge against the newts.

A third hypothesis is that maple litter inhibits chemosensory activity between predators and prey such that breeding treefrogs could not detect the presence of predators. Possible inhibition of chemosensory activity is difficult to refute because most chemosensory signals among predators and prey are unknown, but there is evidence that variation in pH generally reduces the effectiveness of chemical signals (Turner and Chislock, 2010). However, the concentration of maple litter used in this study does not alter the pH by an amount large enough to alter predator-prey interactions (Stoler and Relyea, 2011, 2013). Alternatively, the humic acids that leach from maple litter might interfere with environmental cues. Humic acids are demonstrated to provide an attractive signal to some invertebrates (Steinberg et al., 2006). Further research is warranted to determine if maple leachates provide such signals.

A fourth hypothesis is that the dark coloration generated by soluble humic substances (including phenolic acids) might also allow larvae to camouflage themselves against terrestrial predators that visit wetlands. Williams et al. (2007) demonstrated that pond-breeding invertebrates in a boreal forest are attracted to artificial ponds with a brown background or containing darkly colored leaf litter. This behavior likely occurs because ponds with dark colors reflect highly polarized light that is easier to see by airborne organisms (Williams et al., 2007). This explanation is not necessarily applicable to amphibians; many larvae in wetlands are darkly colored and probably camouflaged from terrestrial predators by the dark colors. In addition, some tadpoles are capable of darkening skin colors in response to their environment (King and King, 1991). This possibility certainly warrants further investigation, particularly because it could alter aquatic-terrestrial linkages.

A fifth hypothesis is that maple litter can reduce the risk of parasitism. Leachates of Red Maple litter and other species that contain high amounts of phenolic acids can sharply reduce population densities of the widespread fungal pathogen *Batrachochytrium dendrobatidis* (Stoler et al., 2016b), leading to lower rates of infection (Davidson et al., 2012). Indeed, concentrations of phenolic acids that are sublethal for tadpoles might be quite lethal for their microscopic parasites. Hence, the antimicrobial effects of maple litter might be sufficient to counter the negative effects on tadpole growth and development. Given that amphibians are particularly sensitive to ecto- and endoparasites due to their relatively permeable skin, this possibility might provide insight into the heterogeneity of disease prevalence among amphibian populations across regional scales (Raffel et al., 2010).

Overall, our study adds to a growing body of literature exploring the effects of leaf litter inputs on wetlands (reviewed in Stoler and Relyea, 2020), as well as the more general importance of subsidy quality as an environmental gradient (Marcarelli et al., 2011). The interspecific variation in litter chemistry among plant species provides a multi-dimensional environmental gradient that can filter wetland species composition. The influence of single litter species provides a basis for understanding the potential influence of litter species mixtures, which can exert both additive and non-additive effects of wetland chemistry (Stoler and Relyea, 2020). In addition, the effect of leaf litter inputs should be considered in conjunction with other important gradients (e.g., canopy cover, predator presence, temperature, species composition). For example, canopy cover provides a complementary, but only partially overlapping, predictor of wetland community composition (Binckley and Reseratis, 2007; Werner et al., 2007). Similarly, elevated temperature induces faster rates of leaching, periphyton growth, and nutrient cycling (Aerts, 1997). Under a warming scenario, chemical differences among litter species might become less important as an environmental cue. By using a mesocosm approach, our study isolated the independent effects of litter chemistry on wetlands, yet further studies are necessary to understand how litter chemistry interacts with other environmental gradients. Moreover, our study provides further evidence for the importance of considering subsidy quality when attempting to conserve and manage wildlife (Marcarelli et al., 2011). This is particularly important in the context of ongoing and predicted widespread changes to forest composition (Hansen et al., 2001).

#### DATA ACCESSIBILITY

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#### ACKNOWLEDGMENTS

We thank Brianna Bailey, Jenise Brown, Will Brogan, Rickey Cothran, Catherine Giancola, Kate Henderson, Chris Hensley, Jessica Hua, John Hammond, Dean Matthews, Caitlin Newcamp, Dave Schmidenberg, Andy Stiff, and Lindsay Skovira for assisting with the experiment. This project was funded by an Arthur and Barbara Pape Award to A. B. Stoler, a McKinley Research award to A. B. Stoler, and NSF funding to A. B. Stoler and R. A. Relyea. This is a PLE research paper. We conducted all work according to permits from the University of Pittsburgh Institute for Animal Care and Use Committee.

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