

Effects of Experimental Clearcut Logging on Gray Treefrog (*Hyla versicolor*) Tadpole Performance

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ABSTRACT.—Clearcutting detrimentally affects the populations of many amphibian species. However, Gray Treefrogs (*Hyla versicolor*) have shown a preference for breeding sites located in clearcuts near forested habitat. To test the implications of this preference, we examined Gray Treefrog tadpole performance in cattle tanks along a gradient from clearcut to forest habitat. We replicated this design at three experimental clearcut sites. Tadpole performance was measured as length of the larval period, size at metamorphosis, and survival. We also examined the influence of temperature, periphyton productivity, and invertebrate predator abundances on tadpole performance. Time to metamorphosis was shorter in the clearcuts, but metamorphs tended to be smaller than metamorphs in the forest tanks. Survival was also greater in the clearcuts than in the forest treatments. Higher temperatures in the clearcuts primarily contributed to tadpole performance whereas invertebrate predators did not appear to influence performance. Although clearcuts benefited tadpoles through higher survival and shorter larval periods, there are potential fitness consequences for small metamorphs emerging in clearcuts.

Habitat loss and alteration are among the greatest threats to biodiversity and are a major cause of amphibian declines (Wilcove et al., 1986; Semlitsch, 2003; Lannoo, 2005). With rapidly increasing human populations, the need for natural resources such as timber is also on the rise. Desire for profits from high-demand timber products stimulates logging practices that often result in reduced amphibian diversity and abundance (reviewed in deMaynadier and Hunter, 1995; Cushman, 2006). However, the mechanisms responsible for such declines remain poorly understood (Cushman, 2006). Most studies investigating the effects of forest management on amphibian demography have focused on woodland salamanders and the terrestrial stage of pond-breeding species (Ash, 1995; Chazal and Niewiarowski, 1998; Karracker and Welsh, 2006; Todd and Rothermel, 2006). Few have investigated the potential impacts on the aquatic larval stage of amphibians (but see Wahbe and Bunnell, 2001). However, both the terrestrial and aquatic life stages of pond-breeding amphibians may be influenced by timber harvest and are important in population dynamics.

The larvae of pond-breeding amphibians are confined to ponds until metamorphosis, which subjects them to changing aquatic conditions. The larval stage is dedicated to growth and exploits transient aquatic resources (Wilbur and

Collins, 1973; Wilbur, 1980). Species differ in the duration of their larval stage depending on the predictability and quality of the aquatic resources, particularly the hydroperiod (Alford and Harris, 1988; Alford, 1999; Ryan and Winne, 2001; Skelly 2001). The duration of the larval period and the size at metamorphosis depend on both biotic and abiotic conditions in the pond. The time and size at metamorphosis are directly related to fitness in some pond-breeding amphibians. For some nonpaedomorphic species, individuals that metamorphose earlier and at a larger size reach maturity sooner and have larger clutch sizes (Smith, 1987; Semlitsch et al., 1988; Berven, 1990), although this has not been directly tested with Gray Treefrogs.

Clearcutting around ephemeral ponds opens the forest canopy, which can alter resource availability for amphibian larvae. Tadpoles of some species grow faster and have greater survival in open canopy ponds compared with closed canopy ponds (Werner and Glennemeier, 1999; Skelly et al., 2002). Additionally, higher temperatures and food quality in open canopy ponds can positively affect tadpole performance (Schiesari, 2006). Therefore, clearcutting around ponds may be expected to improve the habitat quality for the aquatic larval stage of some anuran species.

However, the open canopy created by clearcutting can also alter predator communities in ponds. Anisopteran (Odonata) larvae are known to prey upon tadpoles (Semlitsch, 1990; Skelly and Werner, 1990; Petranka and Hayes, 1998). Many anisopteran species prefer to breed in open canopy ponds resulting in higher

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predator densities than closed canopy ponds (Corbet, 2004; McCauley, 2005). Predators can have direct effects on tadpole survival but can also have indirect impacts, including costly behavioral and morphological responses (Skelly and Werner, 1990; Skelly, 1992; Relyea, 2002a; Relyea and Hoverman, 2003). Behaviorally, tadpoles may reduce foraging activity in response to these predators. These behavioral changes can result in reduced growth and subsequent size-specific mortality by predation (Lawler, 1989; Semlitsch, 1990). Morphological responses to predators include deeper, more muscular tails with increased coloration. These morphological antipredator responses have fitness costs that can persist after metamorphosis (McCollum and Van Buskirk, 1996; McCollum and Leimberger, 1997; Relyea, 2003). However, the tadpoles that avoid predation can potentially benefit from reduced competition (Fauth, 1990; Alford, 1999; Relyea, 2002b).

Tadpole performance in aquatic habitats can significantly affect adult fitness in some pond-breeding amphibians (e.g., Smith, 1987; Semlitsch et al., 1988; Scott et al., 2007) and must be considered when evaluating the complete effects of clearcutting terrestrial habitats. Gray Treefrogs (*Hyla versicolor*) often use small ephemeral ponds for breeding, and logging may occur around these ponds with little or no legal protection (Semlitsch and Bodie, 1998). In a previous study, we found that Gray Treefrogs preferred breeding in ponds in recent clearcuts near forest habitat rather than in closed canopy ponds in a forest (Hocking and Semlitsch, 2007). Here, we evaluate the implications of this oviposition selection by examining Gray Treefrog tadpole performance along a clearcut-forest gradient. Additionally, we examine how biotic and abiotic factors influence tadpole performance. We expect that higher temperatures and periphyton productivity in clearcuts will benefit tadpoles whereas invertebrate predator abundance will reduce tadpole survival. Although logging around ponds can also increase hydroperiod caused by reduced evapotranspiration (Brooks, 2004), we do not examine the effects of hydroperiod in this study.

MATERIALS AND METHODS

Study Design.—We conducted our study in the Daniel Boone Conservation Area (DBCA; 1,425 ha) in Warren County, Missouri. Replicate 2.3-ha clearcuts were established in 2004 (Hocking and Semlitsch, 2007). We set up cattle tanks in clearcuts and control forests at three replicate sites. We placed three replicate cattle tanks in four positions: clearcuts at 50 m and 10 m from

the nearest forest-edge; and in the forest 10 m and 50 m from the same edge. Tanks at these locations represent four habitat treatments commonly associated with forests subjected to logging: clearcut, clearcut-edge, forest-edge, and forest treatments. Three tanks were used as subsamples in each treatment at each replicate site (36 total tanks).

Tanks were each filled with 570 liters of tap water in February 2006. After allowing one week to dechlorinate, we added 1 kg of dry deciduous leaf litter to each tank. We added zooplankton inoculum and 1 liter of pond water strained through a 100- μ m net the first week of April and again the first week of May. Tank covers made of fiberglass window screen prevented unwanted oviposition by treefrogs. We removed the covers from the tanks during the day to allow invertebrate colonization and natural solar radiation a minimum of three days per week.

On 29 May, we collected 15 pairs of Gray Treefrogs from five ponds in the DBCA surrounded (> 100 m radius) by forested habitat similar to our control plots. We do not expect significant genetic structure among the Gray Treefrogs at these five ponds less than 2 km apart (Johnson, 2005). Each pair was placed in a plastic container (75 \times 45 \times 15 cm) with water and allowed to oviposit overnight. We removed the pairs the following morning and checked the eggs daily, removing any dead eggs. On 7 June, we pooled all clutches and haphazardly selected tadpoles (Gosner stage 25) and added 100 of them to each of 36 plastic containers. These 36 plastic containers were then randomly assigned to tanks and the tadpoles from the containers were added to the cattle tanks.

Data Collection.—Tadpoles were observed daily for forelimb emergence, at which point they were removed and kept in plastic containers until the completion of metamorphosis (tail stub < 2 mm). Upon metamorphosis, we weighed tadpoles to the nearest 0.001 g using an electronic balance. We monitored each tank for 60 days following the addition of tadpoles. Afterwards, we removed all leaf litter from the tanks and recorded the number of surviving tadpoles and number of anisoptera larvae. Our measures of tadpole performance were the length of larval period, size at metamorphosis, and survival.

To examine the influence of invertebrate predators, we swept each tank with a dipnet (3-mm mesh) immediately prior to adding the tadpoles. The total number of dytiscid beetle larvae and adults were quantified; however, we found no anisoptera dragonfly larvae. Additionally, we measured temperature, DO, and pH in each tank the week tadpoles were added,

after three weeks to correspond with the start of metamorphosis and at the end of the experiment. Measurements were taken 10 cm below the surface of the water. We also sampled periphyton productivity simultaneously with the other water quality measurements. Three weeks prior to the start of the experiment, we hung glass slides (25 × 75 mm) 10 cm below the surface of the water. Three slides were hung on the south-facing wall of each tank. To sample the periphyton, we randomly selected one slide from each tank and scraped any periphyton off with a razor blade and cotton swab. We placed the cotton swab in buffered acetone and kept the samples in a refrigerator for 24 h. Samples were allowed to come to room temperature prior to chlorophyll analysis. We determined chlorophyll *a* concentration following EPA Method 445.0 (Arar and Collins, 1997) using a Turner Designs Model 10-AU digital fluorometer. We expect the chlorophyll *a* concentration from surface attached periphyton to be a good measure of available high quality food for Gray Treefrog tadpoles based on their mouth parts and observed feeding behavior. While diatoms may make up much of the attached periphyton and contain additional chlorophyll pigments, it is likely that much of the diatom biomass is being passed through the tadpole undigested due to the silicate structure of diatoms. Tadpoles may also be obtaining planktonic material from the water column, but primary productivity in the water column is likely to follow similar trends to the attached periphyton.

Analyses.—We used tadpole survival, mean number of days to metamorphosis and mean size at metamorphosis of tadpoles in each tank as our dependent variables for measuring tadpole performance. Percent survival for each tank was calculated by adding the number of remaining tadpoles plus the number of metamorphs from each tank, dividing by the initial number of tadpoles (100) and multiplying by 100. Metamorphs were confined to the tanks until checked in the morning by the mesh lids

secured with elastic cords. We analyzed our data as a split block design where distance and habitat treatment formed strip plots of the whole plot (site). The combination of treatment and distance was our experimental unit, which was replicated at three sites for a total of 12 experimental units. Individual cattle tanks and tadpoles within tanks were considered subsamples of the experimental unit for statistical purposes. We tested the effect of treatment and distance on our dependent variables using mixed models in SAS v9.1 (Proc Mixed; Littell et al., 2006). We used $\alpha \geq 0.10$ to accept the null hypothesis of no difference among treatments and $\alpha \leq 0.05$ to reject the null. Because of the low level of true replication ($N = 3$), we evaluate results between 0.05–0.10 based on biological relevance.

We developed nine a priori mixed effects models with continuous covariates to determine the relative importance of variables predicted to impact tadpole growth, development, and survival (Table 1). We used the mean temperature, DO, and pH from the three sampling periods for analysis. Initial periphyton productivity was used in our models rather than mean productivity because tadpoles consumed the majority of periphyton in the first three weeks in all treatments. As such, differences in initial periphyton should have the greatest influence on the tadpoles. Additionally, the final periphyton levels would be dependent upon the timing of metamorphosis and tadpole survival as well as the proportion of edible periphyton. We also used dytiscid abundance at the start of the experiment in our models because predators present early in tadpole development should have a greater impact on tadpole performance (Fauth, 1990; Relyea, 2002b, 2003). Anisopteran abundance at the end of the study was used for analysis because we found no anisopteran larvae initially. We compared the nine models using Akaike's Information Criterion for small sample sizes (AIC_c). We used model averaging to improve our estimates of parameter effects

TABLE 1. Abbreviations and descriptions of the fixed effect variables and nine a priori models used to analyze tadpole performance.

Model variables	Description
1. Temperature (Temp)	Mean temperature (°C)
2. Anisoptera	Abundance of anisoptera larvae and exuviae
3. Dytiscid	Abundance of dytiscid larvae and adults
4. Chlorophyll (Chloro)	Initial chlorophyll <i>a</i> ($\mu\text{g}/\text{m}^2$)
5. Temp Chloro	Temperature and high quality food level
6. Temp DO pH	Water quality: temp, dissolved oxygen, pH
7. Temp Chloro Anisoptera Dytiscid	Temperature, food, and predation
8. Anisoptera Dytiscid	Invertebrate predator abundances
9. Temp DO pH Anisoptera Dytiscid Chloro	Global model

TABLE 2. Mixed model tests for differences among forest treatments and distance (10 m or 50 m from the clearcut-forest edge) for time to metamorphosis, mass at metamorphosis, and percent survival.

Source	Num df	Den df	F	P
Time to metamorphosis				
Forest treatment	1	2	23.19	0.0405
Distance	1	2	0.96	0.4298
Treatment \times distance	1	2	0.10	0.7807
Mass at metamorphosis				
Forest treatment	1	2	4.69	0.1628
Distance	1	2	0.16	0.3394
Treatment \times distance	1	2	4.45	0.1693
Survival				
Forest treatment	1	2	12.77	0.0702
Distance	1	2	0.39	0.5955
Treatment \times distance	1	2	5.72	0.1393

when no single model had overwhelming support (i.e., $w < 0.9$ Burnham and Anderson, 2002; Johnson and Omland, 2004). We performed all statistical tests using SAS v9.1 (SAS Institute, Cary, NC).

RESULTS

Two tanks did not hold water for the first weeks because of cracks, apparently created during setup, and were not used for analysis. All additional tanks maintained greater than 90% their initial water volume throughout the study through a balance of precipitation and evaporation. During the study, adult treefrogs or eggs were found under the net covers in three additional tanks, which were also excluded from the study. One tank in a clearcut and one tank in a clearcut-edge treatment developed thick unknown algae that covered the leaf litter and walls of the tanks. These two tanks had 5% and 40% survival, respectively, whereas the rest of the tanks had a mean percent survival of 78.2 (1.7 SE) and, therefore, were excluded from all statistical analyses. Excluding these tanks did not alter the total replication, because at least one tank remained in each replicate treatment (29 total tanks). Upon exclusion, the mean percent survival, mass at metamorphosis, and time to metamorphosis were all normally distributed and exhibited homogeneity of variance. This allowed use of linear mixed models without transformation of the data or the use of nonlinear link functions.

In the 29 remaining tanks, mean time to metamorphosis ranged from 26.3–43.3 days. Mean mass at metamorphosis ranged from 0.301–0.642 g, whereas percent survival ranged from 61–93%. Time to metamorphosis was significantly shorter in the clearcut and clearcut-edge treatments than in the forest-edge and forest treatments (Table 2; Fig. 1A). The lack of significant treatment by distance effect revealed

no difference between the clearcut and clearcut-edge treatments or between the forest and forest-edge treatments. There was no significant difference in size at metamorphosis among treatments (Table 2), although metamorphosis tended to be larger in the forest treatments than in the clearcut treatments (Fig. 1). Although there was not a statistically significant difference ($P = 0.0702$) in survival among the treatments, we believe that these results are biologically significant (Table 2).

The mean (\pm SE) number of dytiscid beetles per tank was 8.4 (2.5), 16.9 (14.0), 0.2 (0.2), and 0 (0.0) for the clearcut, clearcut-edge, forest-edge, and forest treatments, respectively. Although zero dragonfly larvae were present at the start of the experiment, means (\pm SE) of 47.2 (28.9), 84.8 (51.1), 0.2 (0.2), and 0 (0.0) were found in the clearcut, clearcut-edge, forest-edge, and forest treatments, respectively, at the end of the study. Mixed model analysis of anisoptera and dytiscid abundances at the end of the experiment failed to converge assuming either Poisson or negative binomial distributions.

Despite far greater predator abundances in the two clearcut treatments than in the two forest treatments, there was little apparent influence on tadpole performance. Mixed-model analysis using AIC_c revealed the best models predicting time to metamorphosis were Temperature and Temperature-Chlorophyll (Table 3). The other models did not perform as well and were unlikely to be better models of time to metamorphosis. There was no clear support for a best model of size at metamorphosis (Table 3). Temperature was the only predictor in any model of size at metamorphosis with 90% confidence intervals that did not overlap with zero. The model averaged temperature effects estimate was $-0.0091 \text{ g } ^\circ\text{C}^{-1}$ with confidence intervals that did not overlap zero (Table 4), indicating a potential small

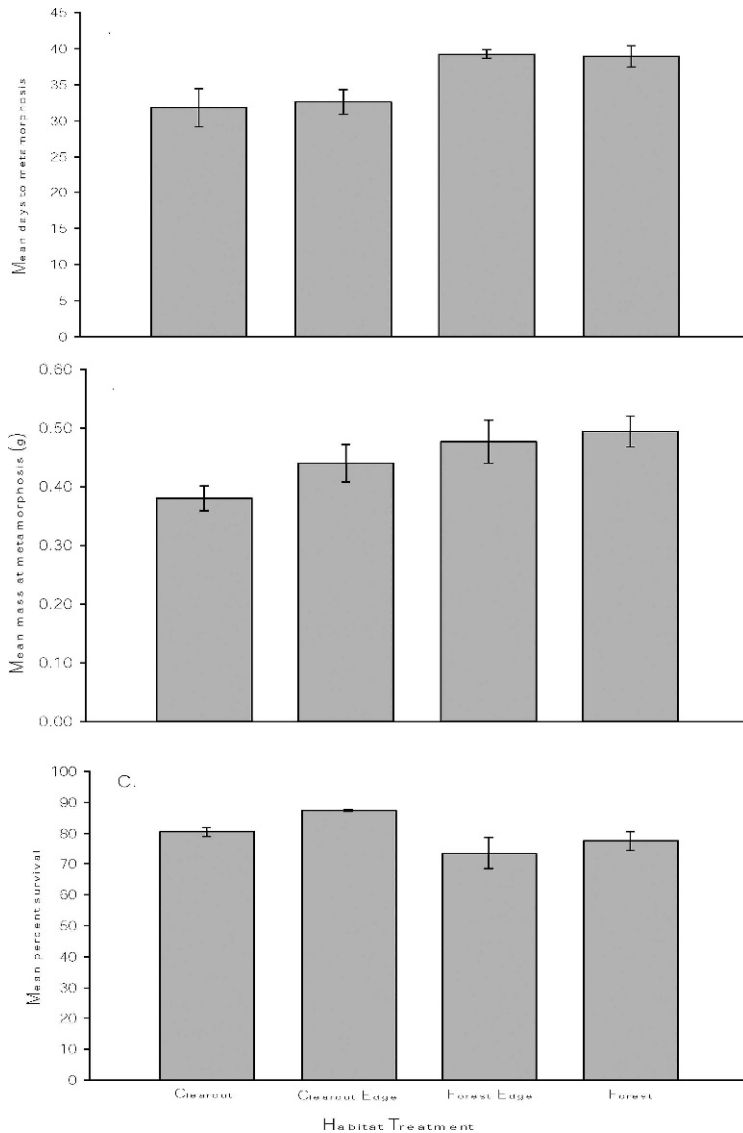


FIG. 1. Tadpole performance in the four treatments based on (A) mean time to metamorphosis (days), (B) mean mass at metamorphosis, and (C) mean percent survival. Bars represent means with standard error bars.

decrease in size at metamorphosis with increasing temperature. The addition of time to metamorphosis as a post hoc covariate did not improve the fit of the model. Models predicting size that included beetle and dragonfly predators had low to moderate support as indicated by ΔAIC_c and Akaike's weight (Table 3). However, the conditional 90% intervals for each predator predictor overlapped zero in all models. Similarly to time to metamorphosis, survival was best fit by Temperature-Chlorophyll and the Temperature alone models. Model averaging revealed temperature had the largest effect on all three tadpole performance metrics,

whereas periphyton productivity had little effect (Table 4). The mean (\pm SE) temperature was 30.8 (0.6), 29.5 (0.7), 24.3 (0.5), and 23.7 (0.4) °C, for tanks in the clearcut, clearcut-edge, forest-edge, and forest treatments, respectively.

DISCUSSION

Tadpoles in the two clearcut treatments metamorphosed in an average of 6.9 fewer days than those in the two forest treatments. Even small differences in time to metamorphosis can result in large differences in recruitment, especially in rapidly drying ephemeral ponds

TABLE 3. Mixed effects models for time and size at metamorphosis and survival. We used Akaike's Information Criterion for small sample sizes (AIC_c) and Akaike's Weight (w) to evaluate our a priori models based on model fit and the number of parameters in each model.

Model	AIC_c	ΔAIC_c	w
Time to metamorphosis			
Temp	161.20	0.00	0.68
Temp Chloro	164.10	2.90	0.16
Temp Chloro Anisoptera Dytiscid	165.40	4.20	0.08
Temp DO pH	165.90	4.70	0.06
Anisoptera	169.70	8.50	0.01
Chloro	171.60	10.40	0.00
Anisoptera Dytiscid	172.00	10.80	0.00
Dytiscid	172.20	11.00	0.00
Temp DO pH Anisoptera Dytiscid Chloro	176.20	15.00	0.00
Size at metamorphosis			
Temp	-69.30	0.00	0.41
Dytiscid	-67.40	1.90	0.16
Anisoptera	-67.10	2.20	0.14
Chloro	-66.80	2.50	0.12
Temp Chloro	-66.60	2.70	0.11
Anisoptera Dytiscid	-65.00	4.30	0.05
Temp DO pH	-63.70	5.60	0.02
Temp Chloro Anisoptera Dytiscid	-60.30	9.00	0.00
Temp DO pH Anisoptera Dytiscid Chloro	-52.90	16.40	0.00
Survival			
Temp Chloro	206.60	0.00	0.66
Temp	208.60	2.00	0.24
Chloro	212.10	5.50	0.04
Temp Chloro Anisoptera Dytiscid	212.70	6.10	0.03
Temp DO pH	214.10	7.50	0.02
Temp DO pH Anisoptera Dytiscid Chloro	218.80	12.20	0.00
Anisoptera	220.10	13.50	0.00
Dytiscid	220.50	13.90	0.00
Anisoptera Dytiscid	223.10	16.50	0.00

(Pechmann et al., 1989; Ryan and Winne, 2001). Gray Treefrog tadpoles are moderately weak competitors (Morin, 1987; Wilbur, 1987) and are also susceptible to predators that invade ponds with long hydroperiods (Morin, 1983; Semlitsch, 1990; Relyea, 2003), making the use of ephemeral ponds advantageous for this species. With an extended summer breeding season (late April to July), Gray Treefrog tadpoles are subjected to ponds drying in the heat of the summer. The ability to metamorphose quickly from ephemeral ponds located in clearcuts may increase survival.

Despite emerging earlier, tadpoles in clearcuts tended to be smaller in size at metamorphosis than those in forest treatments. Although not statistically significant, the metamorphs from the clearcut treatments were 15.5% smaller than metamorphs from the forested treatments. Smaller size at metamorphosis can reduce fitness through lower energy stores, delayed reproductive maturity, reduced fecundity of females, and lower survival (Smith, 1987; Semlitsch et al., 1988; Scott et al., 2007). Additionally, smaller body size increases the

surface area to volume ratio and may make small individuals more susceptible to desiccation. Smaller size at metamorphosis significantly reduces postmetamorphic survival and dispersal success in Northern Red-Legged Frogs (*Rana aurora aurora*; Chelgren et al., 2006). Smaller size could be especially problematic in clearcut habitats where higher temperatures and winds increase the likelihood of desiccation during dispersal (Keenan and Kimmins, 1993; Chan-McLeod, 2003; Wahbe et al., 2004). Dispersal success may also be lower for metamorphs leaving ponds farther from forested edges (Rothermel and Semlitsch, 2002; Rothermel, 2004). Future research should examine the effects of timber harvest on size at metamorphosis and the resultant postmetamorphic effects for various pond-breeding amphibians.

Although postmetamorphic survival is known to be lower in old fields (Rothermel, 2004), survival of tadpoles to metamorphosis was 8.5% greater in ponds in clearcut treatments than in forest treatments. Thus, higher larval survival and shorter time to metamorphosis may offset any potential consequences of

TABLE 4. The model averaged estimates of temperature ($^{\circ}\text{C}$) and periphyton (chlorophyll *a* $\mu\text{g}/\text{m}^2$) effects on tadpole performance.

Parameter	Model averaged estimate	Unconditional SE	90% CI	
			Lower	Upper
Time to metamorphosis				
Intercept	35.6892	22.0554	-0.5897	71.9680
Temperature	-0.7015	0.3292	-1.2431	-0.1599
Periphyton	-0.00022	0.00009	-0.00037	-0.00006
Size at metamorphosis				
Intercept	0.5984	0.1882	0.2888	0.9080
Temperature	-0.0091	0.0027	-0.01344	-0.00471
Periphyton	0.000002	0.000050	-0.00008	0.00008
Survival				
Intercept	37.3944	16.7401	9.8586	64.9302
Temperature	1.4752	0.4268	0.7731	2.1772
Periphyton	0.0059	0.0017	0.0031	0.0087

small size at metamorphosis. However, in a previous study, we found that Gray Treefrogs preferred to oviposit in tanks along a clearcut-edge but also oviposited in forest, forest-edge, and clearcut tanks, albeit at a reduced level (Hocking and Semlitsch, 2007).

In the second part of our study, we examined the biotic and abiotic factors that contributed to tadpole performance in the different treatments. Although we did not explicitly test the effects of these factors independently of the treatments, we suggest that higher temperatures in clearcuts had the greatest contribution to tadpole performance. A 1°C increase in temperature reduces the length of the larval period by nearly one day, while having little effect on size at metamorphosis and increasing the percent survival (Table 4). This lends strong support to previous research indicating that temperature and food quality are the most important factors for tadpoles along a gradient of canopy cover (Werner and Glennemeier, 1999; Skelly et al., 2002; Schiesari, 2006). Although we did not directly compare the temperatures in our tanks to natural ponds, we suggest that the range of temperatures we observed ($19.7\text{--}34.3^{\circ}\text{C}$) were well within the range in which ponds that Gray Treefrogs are known to breed, which includes small, shallow pools with open canopy to deep close canopy ponds (DJH, pers. obs.). In a separate study, temperatures in 11 open canopy ponds in Missouri ranged from $20.0\text{--}38.5^{\circ}\text{C}$ during the period of Gray Treefrog larval development (C. D. Shulse and R. D. Semlitsch, unpubl. data).

In contrast to our expectations, predatory invertebrates had no detectable influence on any aspect of tadpole performance we measured. Moreover, earlier completion of metamorphosis by tadpoles in clearcut tanks was not a result of the greater predator abundance in

clearcut tanks compared to forest tanks, as evidenced by the general lack of support for models including predator abundance as a factor affecting time to metamorphosis. Dytiscid beetle larvae and adults prey upon Gray Treefrog tadpoles, as do anisoptera dragonfly larvae. In cattle tanks, anisopteran larvae can reduce tadpole survival by up to 50% (Relyea, 2002b). McCollum and van Buskirk (1996) found that anisopteran larvae in the genus *Anax* (family: Aeshnidae) reduced tadpole survival more than *Pantala* (family: Libellulidae). *Anax* oviposit into aquatic macrophytes and, therefore, were not present in our tanks. Instead, only anisopteran larvae of the family Libellulidae were present. Gray Treefrogs have been shown to exhibit behavioral and morphological anti-predator defenses in response to anisoptera (Relyea, 2003; Relyea and Hoverman, 2003). These defenses may be sufficient to prevent predation by some species of dytiscids and anisoptera. More research is needed to determine the impact of different anisoptera species on tadpoles and the generality of antipredator responses in Gray Treefrogs. Additionally, our inference is limited to the linear effects of these invertebrate predators resulting from model construction and from ponds that do not support overwintering invertebrate predators but hold water through most of the summer.

In addition to tadpole behavioral and morphological defenses, breeding site selection and breeding phenology may reduce exposure to many predators. Breeding in ephemeral ponds prevents exposure to predators that accumulate in more permanent ponds, including species of anisoptera dragonflies like Aeshnidae that overwinter as larvae and require long hydroperiods. Additionally, breeding during the late spring to early summer allows Gray Treefrog tadpoles to avoid the highest densities of late

instar anisoptera larvae. Many anisoptera metamorphose in the early summer and adults breed synchronously or slightly after Gray Treefrogs (McCollum and van Buskirk, 1996; DJH, unpubl. data). Therefore, tadpoles may be able to complete their larval period before dragonfly larvae become large enough to inflict significant mortality. Gray Treefrogs are known to avoid ovipositing in cattle tanks containing fish and predatory newts but show no avoidance of anisoptera larvae (Resetarits and Wilbur, 1989). The lack of avoidance coupled with our data showing little or no effect suggests that dytiscids and anisoptera larvae may not strongly impact tadpole performance in more ephemeral breeding habitats.

Gray Treefrog tadpoles appear to benefit from breeding ponds with open canopy created by small-scale clearcutting or potentially other disturbances. However, this benefit may be limited to ephemeral ponds where predators are unable to accumulate and will not apply to all amphibian species. The advantages may also be offset by reduced juvenile survival if ponds are isolated a long distance from forest habitat, but this remains to be tested. It is essential to consider the impacts of logging not only on aquatic amphibian larvae but also terrestrial juvenile stages, as the latter is predicted to have the greatest influence on population regulation (Biek et al., 2002; Vonesh and De la Cruz, 2002). Future studies should also examine competitive and predatory interactions among amphibians, in addition to predatory invertebrates, that might be altered through clearcutting. Finally, it will be important to examine tadpole performance during forest succession to better understand deterministic change on species persistence and its relationship to restoration efforts.

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