
INFLUENCE OF FOREST COVER ON TADPOLE VITAL RATES IN TWO TROPICAL TREEFROGS

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Abstract.—The vital rates of anuran tadpoles inhabiting ephemeral pools may be influenced by the amount of forest cover. To better understand this topic in a tropical system, I compared the vital rates of tadpoles of the treefrogs *Agalychnis callidryas* and *Dendropsophus ebraccata* in pools with different extents of forest cover in the Osa Peninsula, Costa Rica. I used a randomized block design, with artificial pools in pasture, edge, and forest, to measure the growth, development, and survival of tadpoles within each habitat. I assessed abiotic conditions in each forest-cover treatment by quantifying the light environment, water temperature, and dissolved oxygen content. Pasture-light environments were open with few obstructions, whereas edge- and forest-light environments were closed, with a complex vegetation structure obstructing solar radiation. Water temperature was strongly correlated with the amount of light contacting the ground in each forest-cover treatment. Tadpoles of both species grew larger in pasture than in forest. Survival of *A. callidryas* was lower in pasture (42%) than in edge and forest (> 90%), whereas survival of *D. ebraccata* was high in all forest-cover treatments (> 87%). These results suggest that the use of pasture pools for breeding represents a trade-off for some species, such that tadpoles have reduced survival but gain fitness benefits of faster growth compared to tadpoles in edge and forest pools. Water temperature may be the primary factor responsible for interspecific and intraspecific variation in tadpole performance across tropical forest-cover gradients.

Key Words.—abiotic conditions; *Agalychnis callidryas*; amphibian; conservation; *Dendropsophus ebraccata*; forest cover; tropical pasture

INTRODUCTION

Whether species avoid, tolerate, or exploit matrix habitats influences the distribution of species within fragmented landscapes (Gascon et al. 1999); however, we have a poor understanding of the mechanisms involved. Abiotic conditions in matrix and forest habitats may influence species' distributions by affecting the vital rates of different life stages. For instance, some adult frogs may tolerate abiotic conditions in matrix habitats (Gascon 1993), but the habitat may function as an ecological trap if offspring survival is reduced (Gates and Gysel 1978; Schlaepfer et al. 2002).

Forest cover influences many abiotic and biotic characteristics of ponds and these traits can influence the vital rates of tadpoles. Ponds with an open canopy typically have higher average temperatures (Werner and Glennemeier 1999; Skelly et al. 2002) than closed canopy ponds. Rates of tadpole growth and development are generally faster at warmer water temperatures (Ultsch et al. 1999; Skelly et al. 2002). However, these benefits are diminished as temperatures exceed 35° C for most species; in fact, at extreme temperatures, tadpole survival is decreased and catastrophic mortality of entire cohorts may occur (Ultsch et al. 1999). Dissolved oxygen concentrations are lower in closed- than in open-canopy ponds as a result of both increased demand for oxygen by decaying

leaf litter in closed-canopy ponds and increased primary productivity in open-canopy ponds (Werner and Glennemeier 1999; Skelly et al. 2002). Low dissolved oxygen can negatively affect tadpoles by reducing their growth and survival rates (Schiesari 2006). Finally, food resources in open-canopy ponds are of a higher nutritional quality for some anuran tadpoles (Schiesari 2006). For example, periphyton, a common source of food for tadpoles (Holomuzki 1998), is more diverse and abundant in open- compared to closed-canopy ponds (Skelly et al. 2002). When abiotic and biotic conditions confer performance benefits in the larval stage, metamorph size is often larger and larval duration commonly shortens. This leads to further fitness benefits, such as reaching reproductive maturity at an earlier age than slow-growing individuals (Smith 1987; Pechenik et al. 1998).

Neotropical tree frogs of the family Hylidae occur in a variety of habitats, including primary closed-canopy forest and disturbed open-canopy areas (Duellman 2001). This makes them ideal subjects for investigation of how forest canopy cover influences tadpole vital rates. I quantified the growth, development, and survival of *Agalychnis callidryas* and *Dendropsophus ebraccata* in artificial pools in forest, edge, and pasture. Specifically I asked whether abiotic conditions in pasture, edge, and forest pools differ and whether such variation leads to differences in tadpole survival, growth, and development

across pools. I predicted that warmer temperatures in pasture pools would result in faster tadpole development and indirectly result in larger tadpole size via the effect of temperature on food quality. However, I expected survival of both species to be lower in pasture pools than in forest or edge pools because of warmer temperature extremes.

MATERIALS AND METHODS

I conducted this study in the Osa Peninsula, Puntarenas Province, Costa Rica (Fig. 1). Mean annual precipitation is 5500 mm per year, with the rainy season occurring May to November (Sanchez-Azofeifa et al. 2002). The habitats of the study area consist of lowland wet forest (Hartshorn 1983) and pasture (40 years old) with distinct edges separating the habitats.

Study species.—I studied *A. callidryas* and *D. ebraccata* because of their abundance in the study area, ease of manipulation, and similar life histories. Both species occupy forest and disturbed habitats in the study region (Savage 2002; Hawley 2008). In the rainy season, *A. callidryas* congregate in ponds and females lay clutches (11–104 eggs/clutch) on leaf surfaces over water (Savage 2002). Tadpoles complete development in < 55 days (Vonesh and Warkentin 2006). *Dendropsophus ebraccata* frequents temporary ponds and deposits egg clutches (15–296 eggs/clutch) on leaves close to the water surface (Savage 2002).

Metamorphosis occurs within 28–42 days (Savage 2002).

Experimental design.—I used a randomized block design, with three blocks, each composed of three sub blocks, in forest, pasture, and at the forest-pasture edge (Fig. 2). The block design controlled for variation from environmental sources. I placed each block at a different cardinal angle with respect to forest and pasture and blocks were located 200–400 m from one another. Pasture sub blocks occurred 65 m from the pasture-forest edge and forest sub blocks were 80 m from the edge. The experimental unit was an artificial plastic pool (10 L; 19 cm depth; 31 cm diameter) and I randomly assigned each pool to a sub block and a position within each sub block. Pools were located 50–100 cm from one another in each sub block. There were two pool replicates per species in each sub block, for a total of 18 pools/species.

I filled each pool with water from a nearby stream (6 L) and with damp leaf litter (150 g). I collected zooplankton and phytoplankton as whole water samples from two nearby ponds, filtered the samples using a 1 mm nylon-mesh cloth, and then added 1 L to each pool. The remaining volume of the 10 L pools filled with rain water within a week. The pools had a nylon-mesh cover, preventing introductions of non-target insect or frog larvae, and had drainage holes along the rim to prevent flooding. I prepared all pools within a block simultaneously and left the pools for 14 days at the

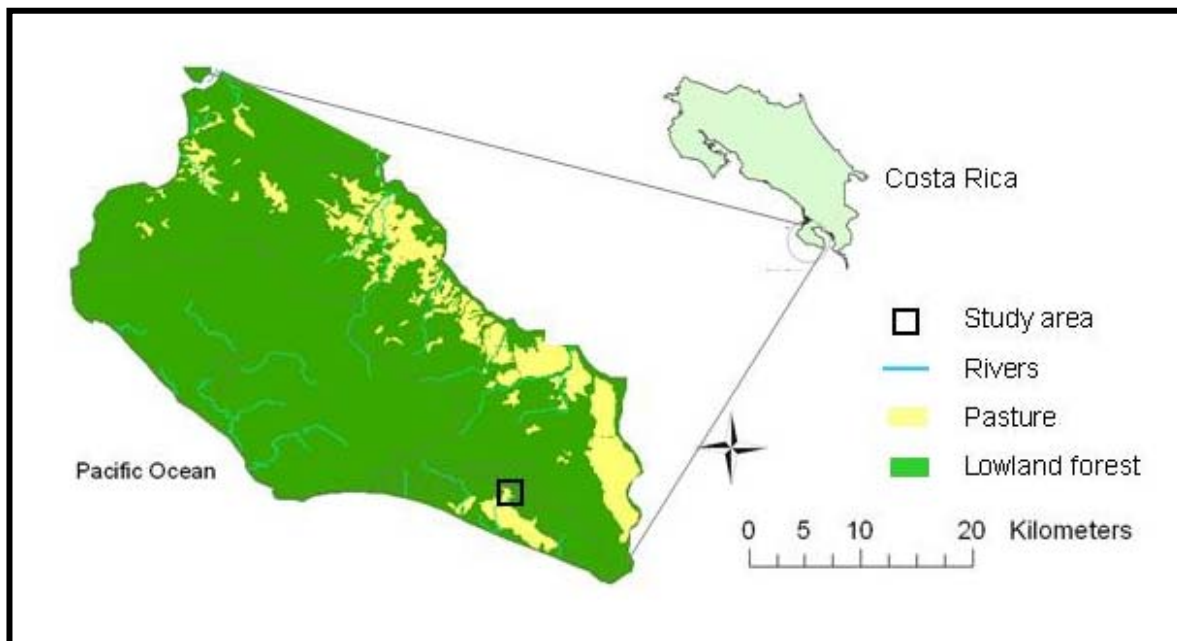


FIGURE 1. Map showing the location of the study area (8°26' N, 83°22' W) in the Osa Peninsula, Costa Rica. The study area consists of lowland tropical forest and pasture habitats.

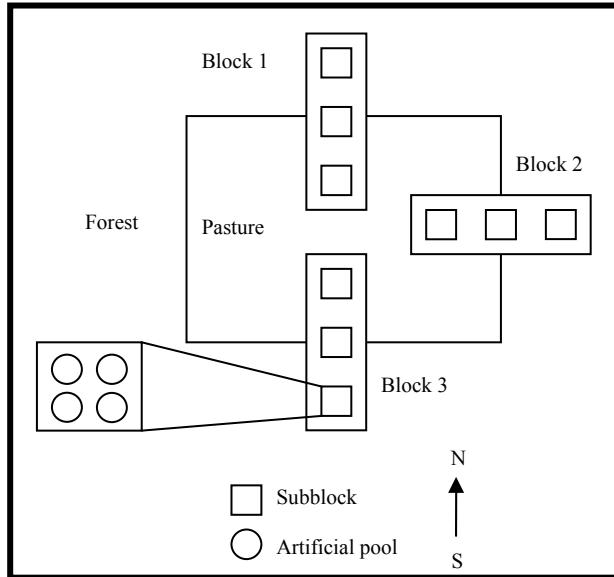


FIGURE 2. Randomized complete block design used for the tadpole performance experiment. Each block was composed of three sub blocks, representing three forest-cover treatments (forest, pasture, and forest-pasture edge). Each treatment had two pool replicates within each sub block for each species, for a total of six pools per species in each block and a total of 18 pools/species.

pasture-forest edge sub block until the experiment started. On the first day of the experiment, I transported the pools to their appropriate position within each sub block and buried them in the ground, leaving approximately 4 cm of the pool rim exposed above the soil surface.

I added tadpoles to pools in a consecutive manner: block 1 on 27 June, block 2 on 3 July, and block 3 on 10 July 2006. For each block, I collected three to five clutches of eggs from each species. I reared the clutches in individual 10 L containers until hatching. From these clutches, I randomly selected tadpoles (2–4 days old; stage 23 to 25 [Gosner 1960]) for each pool. Although there was variation in age and stage across blocks, within each block, tadpoles of each species were the same age and developmental stage when added to pools. I stocked *A. callidryas* at six tadpoles/pool and *D. ebraccata* at eight tadpoles/pool. The difference in stocking density was because newly hatched *A. callidryas* were approximately 56% larger (mean total length) than *D. ebraccata*. I digitally photographed tadpoles from each pool over a reference grid (0.5 cm²; Fig. 3) and determined the initial mean total length/pool using Image J, version 1.34s (Rasband, W.S. 2008. The ImageJ User’s Guide. Available from: <http://rsb.info.nih.gov/ij/> [Accessed 12 January 2008]).

I assessed tadpole survival on day 3 by removing tadpoles from each pool and thoroughly searching the leaf litter. Thereafter, I assessed survival in the same manner every five days. On days 13, 23, 33, and 43, I

digitally photographed tadpoles from each pool and determined total length in the same manner as described previously. I ended the experiment on day 43 and quantified the dependent variables survival, tadpole total length, and developmental stage (Gosner 1960). The most developmentally advanced tadpole was in Gosner stage 36–40, with clear differentiation of hindlimb digits. Therefore, I estimated the developmental stage of each tadpole from photographs using two categories, 0 = no or barely visible hindlimb



FIGURE 3. Images of tadpoles of *Dendropsophus ebraccata* (top) and *Agalychnis callidryas* (bottom) on July 16 from pasture pools. Tadpoles are in a petri dish with a measuring grid (squares 0.5 cm on a side). (Photographed by Tanya Hawley)

development (stages 25–27) or 1 = visible hindlimb development (stages 28+).

I transformed survival (i.e., fraction surviving; square root arcsin) to meet parametric assumptions of normality and homogeneity of variance. I compared survival among forest-cover treatments using analysis of variance (ANOVA), excluding the block factor because it was not significant. I used repeated-measures ANOVA to test for differences in mean tadpole length by forest-cover treatment (i.e., forest, edge, pasture; fixed) and block (random) factors. Tadpole length met parametric assumptions of normality and homogeneity of variance and did not require a transformation. The block factor was not significant so I reanalyzed the data with only the forest-cover factor. For both analyses, I used Tukey's Honestly Significant Differences (HSD) multiple comparisons test to compare differences among treatments when ANOVA yielded a significant result. I assessed variation in tadpole development among forest-cover treatments by comparing the number of pools in each treatment containing at least one tadpole with hindlimb development with a Fisher exact test for each species. All statistical tests were conducted using SPSS 12.0 (SPSS Inc., Chicago, Illinois, USA) with an alpha value of 0.05.

To compare water temperature in experimental pools to those found in natural pools, I monitored temperature every hour in five shallow ephemeral pools (8–18 cm deep) in pasture for 1–11 days in November 2006 using I-button loggers (Maxim Integrated Products, Sunnyvale, California, USA) placed in plastic bags 18 cm below the surface of a randomly chosen pool in each sub block over 30 days (10 July–8 August 2006). Tadpoles were present in all of these natural pools during this time period. From those data I found the maximum and minimum water temperature and calculated a mean daily maximum and minimum over the 30 days in each sub block. I measured dissolved oxygen (DO) content with a hand-held YSI DO200 (YSI Environmental, Inc., Yellow

Springs, Ohio, USA) in three randomly chosen pools in each sub block on 19–20 July 2006 between 1400 and 1700. I examined heterogeneity in mean maximum and minimum daily water temperature among forest-cover treatments using ANOVA. I examined variation in GSF and dissolved oxygen content by forest cover (fixed) and block (random) factors using ANOVA. Then I examined relationships between mean GSF and mean maximum and minimum daily water temperatures in each sub block ($n = 30$ days in each) by calculating Pearson product-moment correlation coefficients. Before performing statistical tests, I confirmed that the data met the assumptions of normality (Shapiro-Wilks test) and homogeneity of variance (Levene's test) for parametric tests.

RESULTS

Abiotic environments.—Maximum daily water temperature was 7.0–9.0 °C significantly warmer in pasture pools (33.67 ± 0.46 °C; average \pm SE) than in forest pools (24.64 ± 0.19 °C) and edge pools (26.13 ± 0.35 °C; $F_{2,8} = 192.12$, $P < 0.001$). However, maximum temperature did not differ significantly between edge and forest pools ($P = 0.053$). Minimum daily water temperature was significantly warmer in pasture pools (25.16 ± 0.06 °C) than in either edge (24.18 ± 0.15 °C) or forest pools (23.75 ± 0.19 °C; $F_{2,8} = 25.20$, $P = 0.001$), but temperatures in edge and forest pools did not differ significantly ($P = 0.165$). Afternoon DO content was significantly higher in pasture pools (6.08 ± 0.26 mg/L) than in either edge (3.16 ± 0.24 mg/L) or forest pools (2.87 ± 0.33 mg/L; $F_{2,26} = 133.73$, $P < 0.001$), but it did not differ significantly between edge and forest pools. Global site factor (GSF) was significantly higher in pasture (0.90 ± 0.01 ; mean \pm SE) than in edge (0.12 ± 0.01) and forest (0.13 ± 0.01 ; $F_{2,35} = 5764.85$, $P < 0.001$), but there was no significant difference between edge and forest ($P = 0.307$). There was a significant

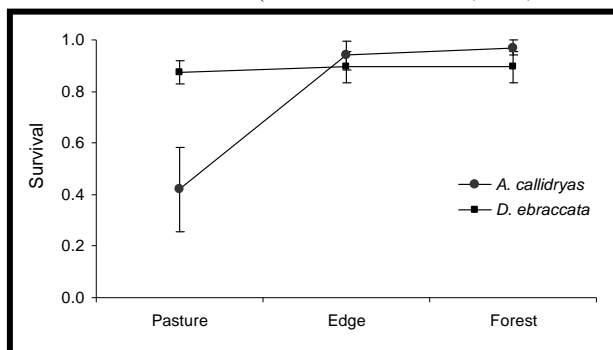


FIGURE 4. Tadpole survival (mean proportion \pm SE; $n = 6$ pools in each habitat) of *Agalychnis callidryas* and *Dendropsophus ebraccata* in pasture, edge, and forest at the end of the experiment (43 d).

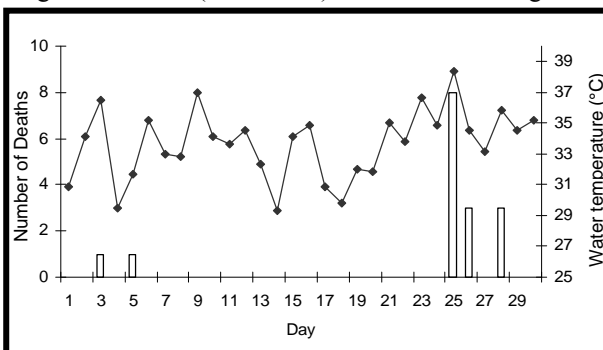


FIGURE 5. The number of deaths of *Agalychnis callidryas* (vertical bars) in relation to maximum daily water temperatures (points; mean of three pasture sub blocks) during a 30 day period, 10 July–8 August.

strong positive correlation between GSF and both maximum ($r = 0.982$, $P < 0.001$) and minimum ($r = 0.911$, $P = 0.001$) water temperatures across the sub blocks ($n = 9$).

Tadpole performance.—At least one tadpole of *A. callidryas* survived in all pools until the end of the experiment, except a pasture pool where mortality was 100%. Average survival in pasture (42%) was less than half of survival in edge and forest (> 90%) and the difference was significant ($F_{2,17} = 9.02$, $P = 0.003$; Fig. 4). Survival in pasture was significantly less than that in edge ($P = 0.007$) and forest ($P = 0.005$) but survival in edge and forest ($P = 0.988$) did not differ significantly. Mortalities during the 30-day index period always occurred on the same day or within two days after high maximum water temperatures (> 37 °C) were recorded (Fig. 5). Eight deaths occurred on the day water temperature reached the highest values recorded during the experiment (38.3 ± 0.7 °C; mean \pm SE; $n = 3$ pasture sub blocks). In natural pools in pasture, the single highest daily maximum temperature ranged from 36–39.5 °C (mean \pm SD = 37.6 ± 1.39 °C, $n = 5$).

Total length of *A. callidryas* more than doubled in pasture and edge and nearly doubled in forest in the first 13 days (Fig. 6). In general, the length of *A. callidryas* increased over the experiment (Wilks lambda = 0.015, $F_{4,11} = 185.38$, $P < 0.001$), but at different rates among the treatments, creating an interaction between time and

forest cover (Wilks lambda = 0.106, $F_{8,22} = 5.72$, $P < 0.001$). In forest, growth slowed after 13 days until tadpoles began to lose length in the final 10 days of the experiment (Fig. 6). Overall, the length of *A. callidryas* was larger in pasture than in forest ($P < 0.001$), larger in edge than in forest ($P = 0.012$), but did not differ between pasture and edge ($P = 0.100$; Table 1). Tadpoles of *Agalychnis callidryas* had visible hindlimb development in four of five pools in pasture, one of six pools at the edge, and in zero of six pools in forest; development was not statistically different among treatments (Fisher's exact value = 6.164, $P = 0.065$).

Survival of *D. ebraccata* was high (> 87%) in all habitats and differences were not significant ($F_{2,17} = 0.653$, $P = 0.535$; Fig. 4). Tadpoles of *D. ebraccata* nearly doubled in length in edge and forest and more than doubled in length in pasture during the first 13 days (Fig. 6). Length of *D. ebraccata* increased with time (Wilks lambda = 0.017, $F_{4,12} = 169.16$, $P < 0.001$) and the rate of increase differed significantly among forest-cover treatments, creating an interaction between time and forest cover (Wilks lambda = 0.084, $F_{8,24} = 17.32$, $P < 0.001$). After 13 days, length continued to increase in pasture and edge but growth slowed in forest. During the first 23 days, *D. ebraccata* in edge and forest were similar in length, but after 23 days tadpoles in edge were more similar in length to tadpoles in pasture than those in forest. Overall, *D. ebraccata* were significantly larger in pasture than in edge ($P = 0.019$) and forest ($P < 0.001$) and tadpoles were significantly larger in edge than in forest ($P = 0.050$; Table 1). At the end of the experiment, tadpoles of *D. ebraccata* had visible hindlimb development in three of six pasture pools, one of six edge pools, and zero of six forest pools; development was not significantly different among treatments (Fisher's exact value = 3.827, $P = 0.250$).

DISCUSSION

Species had differential survival across the forest-cover gradient, with lower survival of *A. callidryas* in pasture than in edge or forest and equally high survival of *D. ebraccata* in all forest-cover treatments. The tadpoles of both species grew larger in pasture than in forest pools, in agreement with my expectations. Contrary to my expectations, I did not find support for faster development in pasture compared to edge or forest pools for either species. All abiotic variables showed clear differences in pasture compared to edge and forest habitats and likely contributed to differences in tadpole vital rates within and between species.

The light environments in pasture, edge, and forest were quantitatively different, with solar radiation unobstructed by vegetation in pasture but highly obstructed by complex vegetation structure in edge and forest. The global site factor was strongly correlated

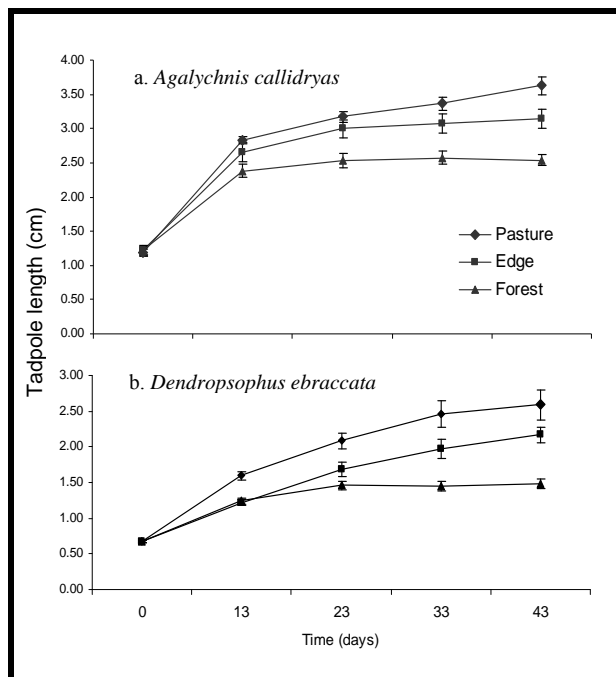


FIGURE 6. Tadpole length (mean \pm SE, $n = 6$ pools for each time period in each habitat) of a) *Agalychnis callidryas* and b) *Dendropsophus ebraccata* in pasture, edge, and forest, from the start (0 days) to the end (43 days) of the experiment.

Hawley.—Tadpole vital rates and forest cover.

TABLE 1. Results of repeated measures ANOVA for effects of time and forest cover (i.e., forest, edge, pasture) on tadpole growth (total length) of *Agalychnis callidryas* and *Dendropsophus ebraccata*. Degrees of freedom for within-subjects effects are Greenhouse-Geisser corrected because the assumption of sphericity was violated.

	Sum of squares	df	F	P
<i>Agalychnis callidryas</i>				
Between-treatment effects				
Forest Cover	5.294	2	15.211	< 0.001
Error	2.436	14		
Within-treatment effects				
Time	41.635	1.673	339.285	< 0.001
Time x Forest Cover	2.080	3.347	8.477	< 0.001
Error	1.718	23.427		
<i>Dendropsophus ebraccata</i>				
Between-treatment effects				
Forest Cover	5.741	2	16.175	< 0.001
Error	2.662	15		
Within-treatment effects				
Time	23.346	1.314	185.853	< 0.001
Time x Forest Cover	2.809	2.628	11.181	< 0.001
Error	1.884	19.709		

with average maximum and minimum water temperatures in pools across the forest-cover treatments, and temperatures were warmer in the pasture. These abiotic conditions apparently allowed tadpoles in pasture pools to attain a larger size over the 43-day experiment in comparison to those in forest pools. These findings are consistent with results of field studies conducted in temperate locations. For instance, Spring Peepers, (*Pseudacris crucifer*) were larger in size and more developed in wetlands with high GSF values (Halverson et al. 2003). In addition, several studies demonstrate positive correlations between open canopies, temperature, and tadpole growth and development, with interspecific variation in the strength of the responses (Werner and Glennemeier 1999; Skelly et al. 2002; Schiesari 2006). A positive correlation between temperature and tadpole growth and development is well established from laboratory studies (e.g., Smith-Gill and Berven 1979; Alvarez and Nicieza 2002). Therefore, while I did not find statistical support for faster developmental rates in pasture pools, those past studies suggest that this pattern may be supported in future research. Higher dissolved oxygen concentrations may also contribute to faster tadpole growth in pasture pools. One laboratory experiment found the influence of DO on tadpole growth depends on the species; high DO had no effect on Leopard Frog growth and only slightly increased Wood Frog (*Lithobates sylvaticus*) growth (Schiesari 2006).

Faster tadpole growth in pastures may be attributable to improved food quality in addition to, or instead of, the direct effects of abiotic factors. The quality of food resources available to tadpoles in open- and closed-canopy habitats may be the primary factor responsible

for intraspecific and interspecific variation in vital rates (Schiesari 2006; Williams et al. 2008). Tadpoles of *D. ebraccata* are macrophagous, eating particles that are large in size compared to their body size, whereas those of *A. callidryas* are suspension rasps, feeding in the water column and on detritus (Savage 2002). Positive relationships have been demonstrated between light, temperature, and composition and abundance of periphyton (DeNicola 1996) and zooplankton (Covich and Thorp 1991). Enhanced food quality or quantity can offset the low growth and development rates that occur at low temperatures, but the strength of this response varies among species (Newman 1998; Werner and Glennemeier 1999; Skelly et al. 2002; Schiesari 2006). In my study, tadpole growth curves reached an asymptote after 23 days in forest, suggesting that the food remaining was sufficient to maintain tadpoles but insufficient to support continued growth. It would be helpful to assess food quality quantitatively in future studies to separate the effects of temperature and food quality on tadpole vital rates.

Water temperature was likely largely responsible for differential survival of tadpoles of *A. callidryas* among forest-cover treatments. Deaths of *A. callidryas* occurred on a day with extreme maximum daily water temperatures (≥ 37 °C) or on the following days. Extreme water temperatures (maximum = 38.5 °C) recorded in my artificial pools were comparable to temperatures experienced by tadpoles in natural ephemeral pools in pasture in my study area (36–39.5 °C). Although these measurements were taken at a different time of year than the experimental treatments, these data suggest that tadpoles in natural pools experience conditions similar to those in my experiment. Survival of *A. callidryas* in pasture would likely have been even lower if the experiment had been continued through metamorphosis, because tadpoles become more sensitive to temperature extremes in later developmental stages (Noland and Ultsch 1981). Thus, temperature may limit the occurrence of *A. callidryas* in pastures. In contrast, *D. ebraccata* survival was high in all treatment groups, suggesting that it has a higher tolerance to warm temperatures than *A. callidryas*.

Tadpoles behaviorally thermoregulate in order to maximize rates of development and growth (Brattstrom 1962, 1979; Smith-Gill and Berven 1979) and minimize exposure to extreme temperatures (Ultsch et al. 1999). In natural pasture pools in my study area, tadpoles may move to areas with higher temperature for growth benefits and escape to areas with more vegetation cover if the temperature begins to exceed their tolerance limits. Yet, at times, behavioral thermoregulation may be insufficient to allow escape from lethal conditions.

Water temperature variability may differ in temperate versus tropical systems and thus we would expect temperature to have a stronger impact on tadpole vital

rates than other factors in some locations. Several studies conducted in temperate locations (e.g., Werner and Glennemeier 1999; Skelly et al. 2002; Halverson et al. 2003; Williams et al. 2008) report less variability in water temperature on a daily basis within treatments as well as between treatments (2.5–5.0 °C maximum difference between open- and closed-canopy treatments) in comparison to my study (up to 9.0 °C difference between treatments). In those studies there was stronger support for food quality and quantity as the primary factors causing differential performance among species in forest-cover treatments rather than temperature. Although differences in temperature variability may largely be an artifact of geographic location, more study is needed to determine whether temperature plays an equivalent or even larger role than food quality in determining anuran tadpole performance in tropical compared to temperate ponds.

It is likely that eggs of *D. ebraccata* and *A. callidryas* suffer greater desiccation mortality in pastures than in locations with more forest cover. Both species attach their egg clutches to vegetation above the surface of water. Desiccation is the main source of egg mortality for *D. ebraccata* at La Selva, Costa Rica (Roberts 1994) and is known to cause mortality of egg clutches of *A. callidryas* (Warkentin 2000) as well. Pasture pools with emergent vegetation vary in the amount of cover available for egg clutches and adult frogs must select oviposition sites to reduce the risk of mortality caused by clutch desiccation. *Phyllomedusa tarsius*, a hylid frog that breeds in pasture, secondary forest, and primary forest in Brazil, has the lowest hatchling success in pastures because of desiccation and flooding (Neckel-Oliviera 2004).

Site selection by adult anurans breeding across a forest-cover gradient in tropical systems likely represents a trade-off, such that adults selecting forest pools risk reduced fitness from depressed tadpole growth and developmental rates, whereas adults selecting pasture pools risk reduced fitness from egg desiccation and reduced tadpole survival. For some species, such as *A. callidryas*, pasture pools may represent an ecological trap, where habitat cues that formally correlated with improved fitness become maladaptive due to anthropogenic change (Gates and Gysel 1978). For other species, selecting tropical pastures can offer tadpoles growth advantages that may improve the fitness of later life stages. A compromise for some species may be the selection of edge pools, where tadpoles may attain a larger size than those in forest pools as well as have high survival (e.g., *D. ebraccata*). My findings support the view that matrix habitats should be recognized as important to maintaining diversity in fragmented landscapes (Vandermeer and Perfecto 2007). Yet my findings emphasize the importance of studying how forest-cover impacts each species individually, as even

species with similar life-history traits may respond differently. A better understanding of the mechanisms underlying frog distributions such as those elucidated in my study will allow land managers to prepare more effective management plans to respond to land-use change.

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