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Effects of timber harvest on breeding-site selection by gray treefrogs (*Hyla versicolor*)

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ABSTRACT

Despite numerous studies showing reduced amphibian abundance and diversity following habitat modification, little is known about the mechanisms causing these observed patterns. We examined the effects of four experimental forest management treatments on breeding-site selection by gray treefrogs (*Hyla versicolor*) in Missouri. Our study of four management treatments included a clearcut with high amounts of coarse woody debris (CWD), a clearcut with lower amounts of CWD, a partial timber cut, and an uncut control. We placed five plastic wading pools in each treatment replicated at three sites and found that gray treefrogs laid significantly more eggs in the clearcuts (low-CWD 77,185 eggs; high-CWD 51,990 eggs) than in either the partial (13,553 eggs) or the control (14,068 eggs) treatments. We further examined the importance of distance between breeding sites and mature forest habitat by placing cattle tanks 50 m into clearcuts, 10 m into clearcuts, 10 m into forests, and 50 m into forests. Gray treefrogs oviposited eggs more frequently in the clearcut-edge tanks (17 occasions) than in the clearcut (7), forest (8), or forest-edge (3) tanks, but eggs were not counted. Despite the preference for open canopy breeding sites, oviposition was less in sites located farther from forest edges. Male captures at the tanks indicated that males also preferred clearcut treatments but were not inhibited by the 50 m distance from the forest edge. Although reduced canopy cover over breeding ponds may benefit tadpoles, logging operations should avoid excessively isolating aquatic habitat from forested uplands.

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1. Introduction

Habitat alteration and destruction remain the greatest threat to amphibians (Lannoo, 2005; Semlitsch, 2003). Therefore, it is essential to understand the multiple habitat needs of species to ensure population persistence in an increasingly fragmented landscape. Due to their biphasic life cycle, pond-breeding amphibians require terrestrial habitat for juvenile and adult growth and maturation, in addition to aquatic habitat for larval growth and development. Some species require additional habitat types for over-wintering (Johnson, 2005; Lamoureux and Madison, 1999), and foraging (Johnson, 2005;

Lamoureux et al., 2002). Further, amphibians require these complementary habitats in spatial configurations that allow for movements between them. Landscape complementation refers to both the amount of different habitat types in a given area and the spatial relationships among them (Dunning et al., 1992). Consideration of landscape complementation is essential for amphibian conservation because many human-altered habitats create significant resistance to amphibian migration and dispersal, effectively dissociating aquatic and terrestrial habitats (Chan-McLeod, 2003; Gibbs, 1998; Rittenhouse and Semlitsch, 2006; Rothermel, 2004; Rothermel and Semlitsch, 2002). Even if forests offer sufficient quantities of

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required habitats, the spatial configuration among them could render some habitats unavailable.

Forestry practices can create patchy, fragmented forests, separated by an inhospitable habitat matrix for some species. In particular, clearcutting generally reduces the abundance and diversity of amphibians (e.g. Ash, 1997; deMaynadier and Hunter, 1995; Herbeck and Larsen, 1999). Although timber harvest is a temporary alteration, the effects on amphibians can persist for decades (e.g. Ash, 1997; Herbeck and Larsen, 1999; Karracker and Welsh, 2006; Semlitsch et al., 2006). Individuals residing in recently clearcut terrestrial habitats face greater risks of mortality due to desiccation (Rittenhouse unpublished data; Rothermel and Luhring, 2005). In clearcuts, individuals may also have stunted post-metamorphic growth rates (Todd and Rothermel, 2006) which can reduce total lifetime reproduction (Berven, 1990; Semlitsch et al., 1988; Smith, 1987).

Clearcutting can also affect the terrestrial stage of pond-breeding amphibians by creating inhospitable habitat that impedes the movement of migrating individuals. Altered habitats have greater resistance for adults migrating to or from a breeding pond (Chan-McLeod, 2003; Mazerolle and Desrochers, 2005; Rittenhouse and Semlitsch, 2006). Additionally, non-forested habitat creates significant resistance for emigrating juveniles following metamorphosis. Clearcut habitats may restrict juvenile dispersal events, thereby altering meta-population dynamics and restricting any rescue effects (Brown and Kodric-Brown, 1977; Gill, 1978; Pope et al., 2000; Rothermel, 2004).

Despite the detrimental impacts of logging on the terrestrial stage of pond breeding amphibians, opening the canopy over a pond through logging can be beneficial for the aquatic larvae of some amphibian species. Open canopy ponds have greater primary productivity, which increases high quality food resources for herbivorous tadpoles. Additionally, the increased solar radiation warms the water, resulting in increased developmental rates beneficial to aquatic larvae (Halverson et al., 2003; Schiesari, 2006; Skelly et al., 2002; Werner and Glennemeier, 1999). However, open canopy ponds have greater abundances of dragonflies, increasing the risk of predation on amphibian larvae (Gunzburger and Travis, 2004; McCollum and Leimberger, 1997; Semlitsch, 1990). In the absence of parental care, adults must choose breeding habitats that balance the benefits and risks to offspring with the risks to themselves.

The gray treefrog is an ideal study species because individuals require both terrestrial and aquatic habitats, and they readily breed in artificial ponds that can be experimentally manipulated (Johnson and Semlitsch, 2003; Resetarits and Wilbur, 1989). Gray treefrogs live and forage in trees but make annual migrations to small ponds to mate and lay eggs (Johnson, 2005). They often oviposit in small isolated ponds that receive little or no legal protection from logging near the pond. Additionally, gray treefrogs are selective in their use of oviposition habitats by preferring breeding habitats devoid of competitors and predators (Resetarits and Wilbur, 1989). These past studies reveal that gray treefrogs have evolved mechanisms to select oviposition habitats that maximize their fitness through increased offspring survival. However, in a fragmented landscape, adult anurans must balance the opti-

mal conditions for their offspring with their own risks in an altered forest environment.

Understanding the mechanisms causing the patterns observed in forest landscape studies is critical to the mitigation of detrimental effects on amphibians (Cushman, 2006; Rittenhouse and Semlitsch, 2006). Our study addresses adult use of habitat for oviposition in an altered forest environment. Specifically, we examine gray treefrog (*Hyla versicolor*) breeding site selection in response to four different forestry treatments and determine how pond distance from a forest patch affects breeding-site use in recently clearcut habitats. This information will help elucidate how forest alteration impacts the connectivity between terrestrial and aquatic habitats essential for amphibian persistence.

2. Methods

2.1. Study site and experimental forest manipulations

Our research was conducted as part of an experiment examining the impacts of different forest management practices on pond-breeding amphibians. The Land-use Effects on Amphibian Populations (LEAP) project compares amphibian responses to four forest management treatments surrounding ephemeral ponds. All sites used in our study are located within the Daniel Boone Conservation Area (1424.5 hectares) in Warren County, Missouri. The sites are situated in secondary growth oak-hickory forest (80–100 years old) in the upper Ozark Plateau. The pond at the center of each of three sites were selected from approximately 40 ponds in the conservation area to be greater than 1000 m apart and similar in size (high water area 160–330 m²). These ponds were originally built for wildlife and are 27–47 years old.

The four treatments at each site consist of a clearcut with high levels of coarse woody debris (High-CWD), a clearcut with less CWD (Low-CWD), a partial canopy removal, and an unmanipulated control forest (Fig. 1). Coarse woody debris consists of logs on the ground greater than 10 cm diameter. In the clearcuts, all marketable timber greater than 25 m diameter at breast height (DBH) was removed for sale. The clearcuts with high CWD had the remaining trees (<25 cm DBH) felled and left on the ground. In the clearcuts with low CWD, the remaining trees (<25 cm DBH) were left standing to reduce the CWD on the ground, but were killed by girdling. The partial cut treatment was thinned to a basal area of 13.8 m² per hectare, which is approximately 60% stocking level. This was achieved by girdling or felling poor quality trees and undesirable species (such as *Acer saccharum*). This type of partial cut treatment is a common form of timber stand improvement in central Missouri. The two clearcut treatments were designed to test the potential for retaining more CWD to mitigate negative effects of clearcutting on amphibians. Coarse woody debris is predicted to benefit amphibians by providing moisture retaining refugia (deMaynadier and Hunter, 1998).

To delineate the treatments, the circular area with a radius of 164 m from a pond was divided into four equal quadrants. A radius of 164 m was used because this distance represents the core habitat for pond breeding salamanders (Semlitsch, 1998). The control treatment was randomly assigned to one

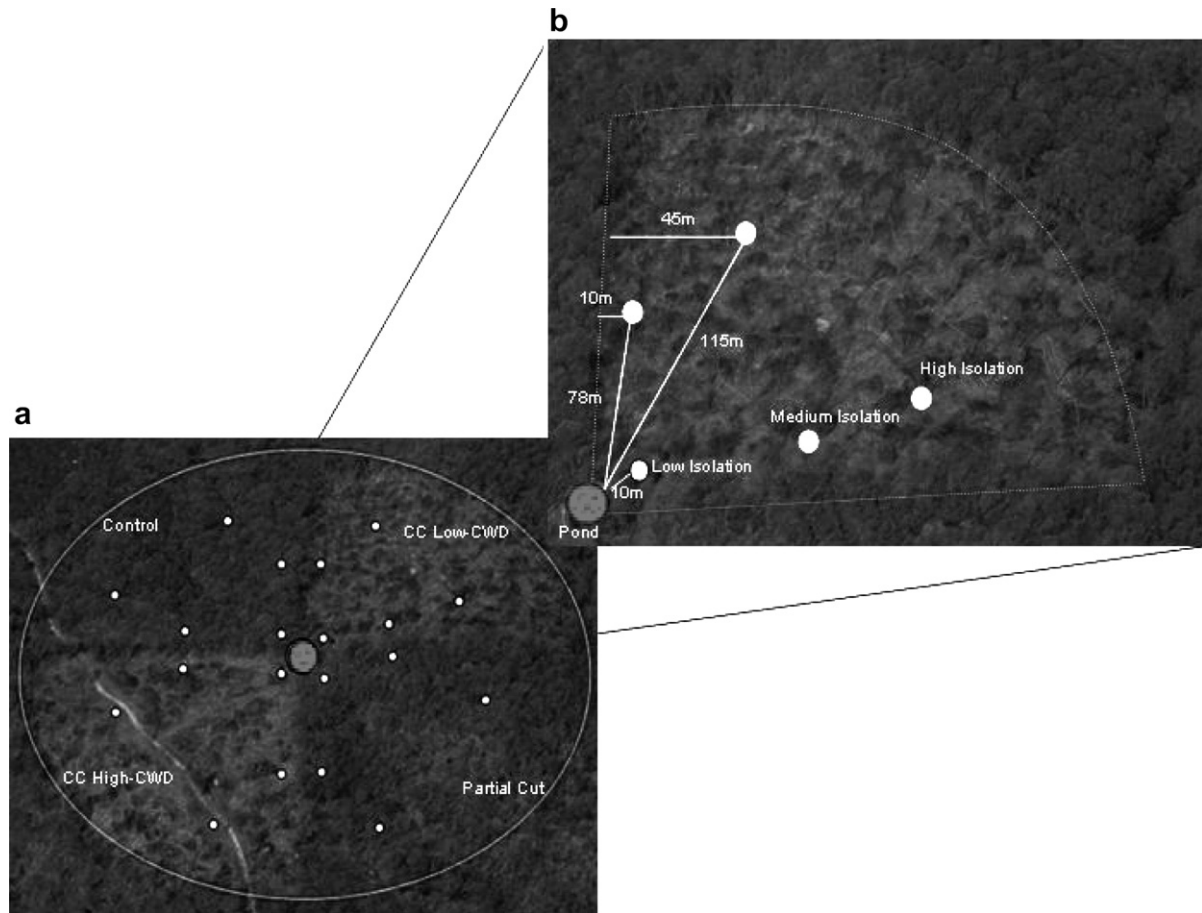


Fig. 1 – (a) The aerial photograph of one study site in the Daniel Boone Conservation Area, Warren County, MO shows the four forest management treatments with a pond at the center. The smaller circles show the placement of the artificial pools in each habitat. **(b)** The expanded view diagrams the arrangement and distances of the low, medium, and high isolation pools within a forest treatment.

quadrant, the clearcut treatments were randomly assigned to the two quadrants adjacent to the control, and the partial treatment was fixed in the quadrant opposite the control (Fig. 1). All forest treatment manipulations were performed between March 2004 and February 2005.

2.2. Experiment 1

To test how different forest management treatments affect oviposition habitat selection by gray treefrogs, we used artificial pools located in each of the forest management treatments. Five plastic wading pools (1.5 m diameter, 30 cm high) were placed above ground in each treatment at three levels of isolation within the treatments in February 2005. Pools filled with rainwater (>5 cm) by 1 April, prior to gray treefrogs emerging from over-wintering. Because we expected more adult treefrogs to be concentrated near the pond and in the forested treatments, we defined degree of isolation with respect to both distance from the pond and from treatment edges. At low isolation, the pools were 10 m from the pond and 10–12 m from each treatment edge. The pools at medium isolation were 64 m from the pond edge and 10–12 m from the treatment edge. The pools at high isolation were placed 115 m

from the pond edge and 45 m from the treatment edge. There was one pool in each treatment at low isolation, and two pools in each treatment at each of the medium and high isolation levels (Fig. 1). We replicated this design at three study sites each separated by greater than 800 m.

Pools were checked for treefrog eggs for 47 days following the first oviposition event on 7 May 2005, with no greater than 48 h between monitoring periods. *H. versicolor* is the only treefrog (genus: *Hyla*) that occurs in the Daniel Boone Conservation Area, and females lay their eggs in distinctive floating packets of 20–90 eggs, allowing for reliable identification. Using artificial wading pools prevented the use of pools by other amphibians, with one exception. Two American toads (*Bufo americanus*) were found with eggs in one pool on 10 June. The individuals and their eggs were removed, and no additional eggs from other species were found in any pool.

Treefrog eggs were counted, removed from the pools, and transferred to the pond at the center of each site. Any tadpoles that hatched from missed eggs were removed and assigned to a previous oviposition event based on tadpole development. All leaves and debris were consistently removed from the pools to ensure all the eggs in a pool could be located and counted.

To test for differences in oviposition habitat selection among forest treatments and isolation levels, we used an analysis of variance (ANOVA). Our experiment was set up as a balanced split-block design with the main plots (forest treatments) arranged in complete blocks (sites). The subplots (isolation) were in the same location within each forest treatment, therefore separate error terms were used for the forest treatment, isolation, and forest treatment by isolation interaction effects. The number of eggs was square-root transformed to meet the assumptions of normality and homogeneity of variances. For comparison with the second experiment, the number of eggs divided by the number of times eggs were found in a pool (oviposition events) was compared among treatments using a split-block ANOVA.

2.3. Experiment 2

We designed a second experiment to examine breeding site selection in relation to a forest-clearcut edge with distance from existing breeding ponds held constant. In this experiment, cattle tanks (2 m diameter) were placed in clearcut, clearcut edge, forest edge, and forest habitats in February 2006. Tanks in the clearcut treatment were 50 m from the nearest forest edge. Clearcut edge treatments had tanks 10 m from the forest edge, forest edge tanks were in a forest 10 m from a clearcut, and forest treatments were 50 m from the nearest clearcut. All tanks were located an equal distance (65 m) from the nearest pond. This design was replicated using three forest-clearcut edges separated by more than 800 m. All clearcuts were 12–18 months old at the start of the experiment. Each tank was filled with 570 l of tap water and allowed to dechlorinate for greater than 48 h before the addition of 1 kg of dry deciduous leaf litter. Additionally, one liter of pond water was added to each tank as phytoplankton and zooplankton inoculum.

Tanks were checked for eggs following rain events and at a minimum of once per week from 17 April until 13 July 2006. The census was conducted more frequently during the peak of the breeding season and following rain events when oviposition is most common (Ritke et al., 1990). Each tank was classified as used or unused during each census based on the presence or absence of newly deposited eggs. Each day eggs were found in a tank was considered one oviposition event. Litter in the bottom of each tank and the large size of the tank increased breeding site realism but prevented enumeration of eggs. Although eggs could not be counted, the presence of new eggs was always apparent as egg development and hatching is rapid (<1 week) and no cohorts of tadpoles were observed that did not correspond to a particular oviposition event. Therefore, we used the number of oviposition events as the response variable for analysis. Eggs were not counted and were left in the tanks to account for the influence of conspecific attraction or density dependent avoidance on breeding site selection (i.e. Marsh and Borrell, 2001; Resetarits and Wilbur, 1989; Spieler and Linsenmair, 1997).

Additionally, we visited each tank on 38 nights between 17 April and 29 June. Calling males were hand captured and given a unique toe-clip. All woody branches (>1 cm diameter) within a 3 m radius of the tank and below 3 m from the ground were searched using a headlamp. We compared the

number of nights males were captured and mean number of males captured per night to examine if males and females respond to the treatments in the same way. If males respond as females do, then it is possible that females are simply relying on calling males for habitat choice rather than making habitat choices themselves based on oviposition preference. Single factor analysis of variance was used to test for differences in response variables among treatments. We used Tukey's honestly significant difference (HSD) tests for pairwise comparisons between treatments when the overall ANOVA was significant. All statistical procedures for both experiments were performed using Statistical Analysis Software (SAS) version 9.1 and tested at a significance level of $\alpha = 0.05$.

Gray treefrog males tend to be more difficult to detect and capture in scrubby secondary growth than in mature forest (personal observation). Therefore, we expect our analysis of the mean numbers of males per pool in each treatment to be potentially biased with lower detection in the clearcut and clearcut-edge treatments. To account for this potential bias, we used the male capture histories in an open population model to generate population estimates for the four treatments. We used the POPAN formulation in program Mark (v.4.3, <http://www.warnercnr.colostate.edu/~gwhite/mark/mark.htm>) because it provides the same abundance estimates as Jolly-Seber, but the Jolly-Seber model in the program is not numerically stable (G.C. White, personal communication).

3. Results

3.1. Results of experiment 1

We counted a total of 156,796 eggs laid in the artificial pools across all treatments. The mean number of eggs laid differed significantly among the forest treatments ($P = 0.0141$, Table 1) and among isolation levels ($P = 0.0194$, Table 1). Treefrogs preferred ovipositing in the clearcuts (low CWD 77,185 eggs; high CWD 51,990 eggs) compared with the partial (13,553 eggs) or the control (14,068 eggs) treatments. The two clearcut treatments did not differ significantly, nor was there a significant difference between the partial cut and the control treatments (Fig. 2). The number of eggs tended to decrease with increasing isolation (Fig. 2), a trend driven by the isolation effect

Table 1 – Analysis of variance (ANOVA) of the number of eggs oviposited per pool in a split-block design

Source	d.f.	MS	F-value	P-value ^a
Site	2	315.15	0.8100	0.4673
Forest treatment	3	6135.48	8.4700	0.0141
Site × treatment (treatment error)	6	724.80	1.8700	0.1686
Isolation	2	466.90	12.3500	0.0194
Site × isolation (isolation error)	4	37.81	0.1000	0.9813
Treatment × isolation	6	1078.75	2.7800	0.0624
Error	12	388.54		

The main plots (forest treatment) and subplots (isolation) are arranged in strips and therefore each has their own error term for the F-test. Treatments are also arranged in three blocks (site).
a Significant results $P < 0.05$.

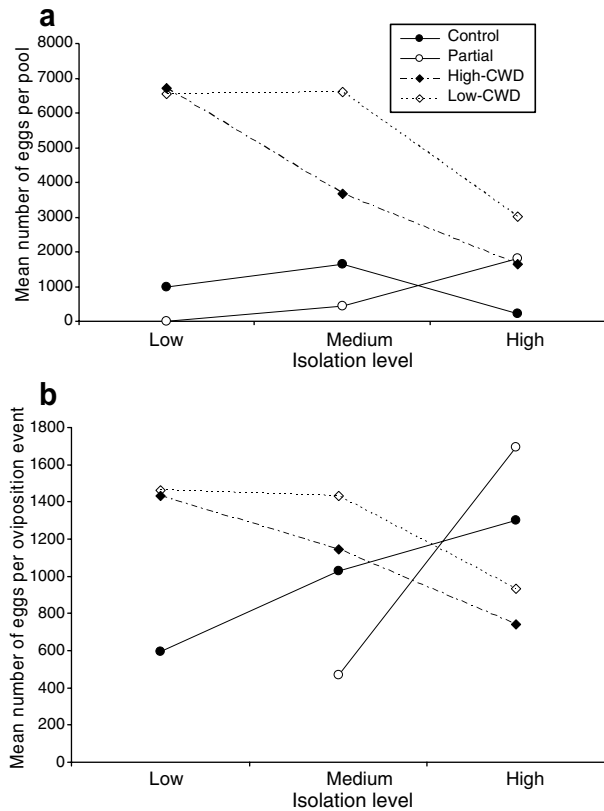


Fig. 2 – Interaction diagrams of the (a) mean number of eggs laid per pool in each forest and isolation treatment combination and (b) mean number of eggs per oviposition event in each treatment combination (forest treatment \times isolation level).

in the clearcuts. The forest treatment by isolation level interaction effect was marginally significant ($P = 0.0624$, Table 1). In the two clearcut treatments oviposition decreased with increasing isolation (Fig. 2). The partial cut and control treatments both had few eggs and an isolation effect was not found in either the partial or control treatments.

The number of eggs laid per oviposition event differed among the forest treatments depending on the level of isolation (d.f. = 5, $F = 11.18$, $P = 0.0053$, Fig. 2b). The number of eggs per oviposition event increased with isolation within the control and partial cut treatments. The opposite was true for the clearcut treatments where the number of eggs per event decreased with increasing isolation.

3.2. Results of experiment 2

We recorded 35 oviposition events on 18 occasions. Eggs were laid in all tanks except one tank in a forest-edge treatment. There was a marginally significant difference among the four treatments (d.f. = 3, $F = 3.33$, $P = 0.0773$). Comparison using Tukey's HSD reveals more oviposition events in the clearcut-edge treatment than in any of the other treatments (Fig. 3a). Although these results are only marginally significant, we believe that they are biologically meaningful. Due to the scale of this project, we only used three replicates which resulted in

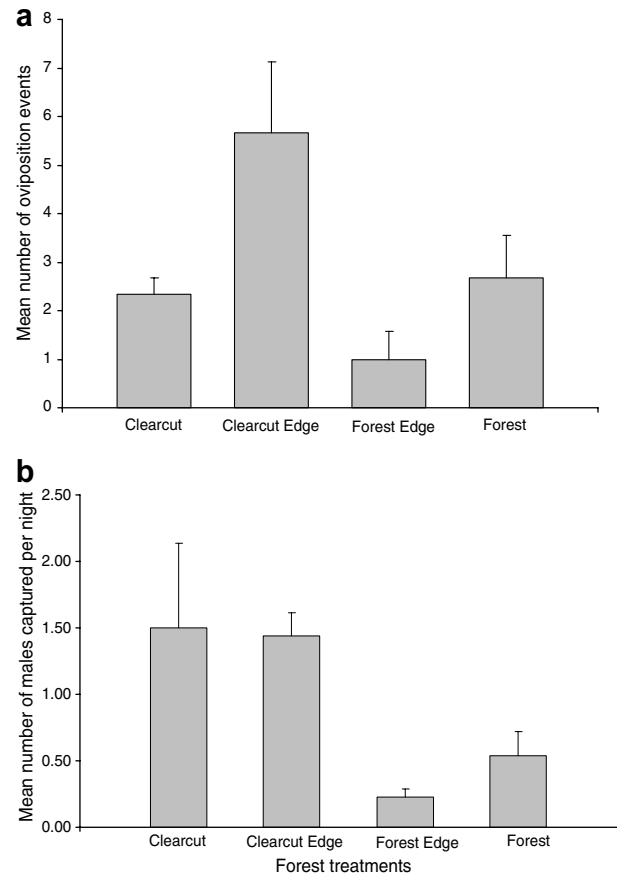


Fig. 3 – Mean number of (a) oviposition events and (b) male captures per survey night in each of the four forest treatments. Bars represent means + SE.

low power to detect a significant difference (power = 0.676). Additionally, we used oviposition events as our response variable rather than number of eggs, which is not as precise a measure of reproductive output.

There was a marginally significant effect of treatment on the mean number of males captured per night (d.f. = 3, $F = 3.46$, $P = 0.0711$). Contrast comparisons between the clearcut treatments and the forest treatments indicate that the forest and forest-edge treatments had fewer males captured on average compared with the clearcut and clearcut-edge treatments (d.f. = 1, $F = 9.98$, $P = 0.0134$, Fig. 3b). Unlike the female response, there was no difference between the clearcut and clearcut-edge treatments using Tukey's HSD. There was no difference among the treatments in the number of nights males were captured at the tanks ($P = 0.2476$). Analysis of the mark-recapture data produced similar results. The total number of males estimated to use the tanks during a season was greatest in the clearcut-edge (975 ± 87 SE) and clearcut (892 ± 83 SE) followed by the forest (449 ± 76 SE) and the forest-edge (172 ± 37 SE) treatments.

4. Discussion

Gray treefrogs strongly selected pools for oviposition that were located in clearcuts compared with pools in partial cut

treatments or control forests. The preference for breeding sites that were located in clearcut treatments is likely a response to open canopy. Open canopy ponds are beneficial for many anuran larvae because higher quality food resources and higher temperatures result in increased growth and developmental rates (Schiesari, 2006; Skelly et al., 2002; Werner and Glennemeier, 1999). Increased growth and development benefits the larvae by reducing the time they are vulnerable to gape-limited predators (Semlitsch and Gibbons, 1988; Skelly, 1996) and decreasing the risk of mortality due to pond drying (Babbitt et al., 2003; Skelly, 1996). Additionally, larger size and shorter time to metamorphosis allows individuals to reach maturity sooner, possibly increasing lifetime fitness (Semlitsch et al., 1988; Smith, 1987).

Although, breeding adults favored open canopy ponds, females oviposited fewer eggs in high isolation ponds in the clearcut treatments, but this same pattern did not occur in the partial cut or control treatments. This interaction effect suggests that female treefrogs were less willing to oviposit in pools farther into clearcuts. Additionally, fewer eggs were found per oviposition event in high isolation clearcut pools in experiment one. Differences in the number of eggs per oviposition event can be explained by multiple females ovipositing in preferred pools on a favorable breeding night (i.e. high humidity, wet leaf litter, warm air temperatures) or may be due to individual females laying more eggs per clutch in preferred pools. Distance from the existing wildlife pond and distance from the treatment edge were confounded in experiment one. However, the distance from the pond is unlikely to have caused the decrease in the number of eggs per oviposition event found in the clearcuts because the same trend was not observed in the control or partial cut treatments. Results of experiment one suggested that the distance of breeding sites from mature forest habitat could be important for gray treefrogs and this was confirmed by the second experiment.

The preference for breeding sites in clearcuts close to forested habitat suggests that females from forested treatments likely moved into the clearcuts to breed. Given that we did not record individual treefrog movements, it is possible that the greater use of clearcut edge sites may be due to more treefrogs residing in the clearcuts. However, this explanation is unlikely, because a greater number of eggs in the clearcuts were oviposited near forest edges than in pools further into the clearcuts. Johnson (2005) found that gray treefrogs use large trees for foraging and tree cavities for diurnal refuges and are known to make single-night breeding migrations greater than 100 m in forested habitat (Johnson, 2005). Females are capable of moving from a refuge in a forested treatment to pools in the clearcuts, and although we observed some frogs in clearcuts, we believe it is unlikely they can subsist for prolonged periods in clearcut habitats due to risk of desiccation (Johnson, 2005; Perison et al., 1997; Todd and Rothermel, 2006).

As with female gray treefrogs, males appear to prefer the open canopy breeding sites of the clearcut and clearcut-edge treatments. However, neither the number of males nor the frequency of male captures differed between the clearcut and clearcut-edge treatments. This indicates that males are likely not limited by the 50 m isolation distance, even though the

risk of desiccation for adult amphibians is significantly greater in clearcuts than in mature forests (Rittenhouse unpublished data; Rothermel and Luhring, 2005). Males may be more willing to risk desiccation to use the 50 m breeding sites in the clearcuts to reduce competition for mating opportunities compared to the clearcut-edge sites (Fellers, 1979; Wells, 1977). Females likely had comparable opportunities for mating at both clearcut and clearcut-edge sites, suggesting that females were primarily responsible for selecting the breeding sites closer to the forest edge instead of those 50 m into the clearcut. Future studies should examine if there are differences in the size or acoustic attractiveness of males using breeding sites located different distances into open canopy habitats. The difference in male and female breeding site selection has implications for anuran surveys, which often focus on calling males at the breeding site because they are more conspicuous (e.g. Heyer et al., 1994; Royle, 2004; Stevens et al., 2002). Researchers should use caution when drawing conclusions about habitat use from observations based solely on one sex.

Ultimately, we found that clearcutting can disrupt the connectivity between breeding and non-breeding habitats for gray treefrogs. Breeding was reduced at sites only 50 m from the nearest forest, indicating that even relatively small clearcuts can create resistance to migrating females. Altered habitat that separates required habitats reduces landscape complementation and could be potentially detrimental to populations where alternative breeding sites are not available. Although clearcuts are only a temporary form of habitat alteration, most species of anurans have a maximum longevity of much less than 15 years (Lannoo, 2005). Specifically, the gray treefrog is not known to live more than four years in natural populations (Roble, 1985). If breeding ponds are located in clearcuts greater than 50 m from a forest, it is possible that the local population would substantially decline due to reduced recruitment over five years. Therefore, future studies should examine this isolation effect for other species with short population turnover times.

Although timber harvest that creates open canopy over ponds may be beneficial for some species, it is essential to maintain mature forest nearby for forest-dependent species (Johnson, 2005). Not all species benefit from open canopy ponds, and some ponds should also be maintained within closed-canopy forests for species such as woodfrogs (Skelly et al., 2002). Additionally, although the lack of difference in breeding site use between the two clearcut treatments in experiment one indicates that CWD does not influence breeding site use, CWD could still affect the vital rates (i.e. survival, growth, fecundity) of individuals via desiccation or altered foraging, especially for males that spend multiple nights calling around breeding sites in clearcuts.

In addition to examining the effects of CWD on adult vital rates, future studies should examine the performance of eggs and larvae in recent clearcuts and mature forest ponds. Information on egg and larval responses will help determine the mechanisms controlling population level responses to clearcutting and adult breeding site selection in a fragmented landscape. Testing the fate of emigrating juveniles from ponds in clearcuts at different distances from mature forests will help toward understanding the total effects of clearcutting on landscape complementation. Finally, while some amphibian

populations can be affected by forest alteration for decades (e.g. Ash, 1997; Karracker and Welsh, 2006), others may respond more quickly to forest regeneration (Marsh et al., 2004). It will be important to determine how long the clearcuts function as barriers to female breeding-site use and how selection and habitat resistance are affected by succession.

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