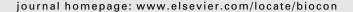


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Effects of timber harvest on breeding-site selection by gray treefrogs (Hyla versicolor)

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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, pondbreeding 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 humanaltered 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 metapopulation 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

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