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Effects of timber harvesting on terrestrial survival of pond-breeding amphibians

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ABSTRACT

Successful forest management for multiple uses requires balancing extractive practices with maintaining biodiversity, among other important goals. Amphibians comprise an important and abundant part of the biodiversity of many forests. Previous studies have documented declines in the abundance and diversity of amphibians in harvested forests. However, only recently have studies begun to elucidate the mechanisms that underlie such declines. Here, we studied the effects of timber harvesting on survival of geographically widespread ambystomatid salamanders in three forest regions of North America. We used terrestrial enclosures in the Northeast, Midwest, and Southeast to compare amphibian survival in unharvested controls, partially harvested stands (∼25% canopy reduction), and clearcuts with coarse woody debris either retained or removed. In all regions, patterns of amphibian survival were similar, with both juvenile and adult salamanders generally having significantly lower survival in clearcuts compared with unharvested controls. Survival of juvenile salamanders in partially harvested stands was also low, but adult salamanders survived as well or better in partially harvested stands as in controls. Larger body size in juveniles was significantly correlated with recapture, irrespective of treatment, in both the Northeast and Southeast, but not in the Midwest or for adults in any region. Relatively heavier adults were more likely to be captured again in the Southeast, but relative mass was not correlated with recapture in any other regions or for juveniles. Our results suggest that increased amphibian mortality may contribute to declines of amphibian abundance and richness after forest clearcutting for the regions evaluated here. Although our results indicate that partial harvesting is compatible with survival of adult salamanders, retention of intact forest around breeding ponds would benefit all terrestrial stages of pond-breeding salamanders and represents a best management practice for the maintenance of amphibian biodiversity.

1. Introduction

Alteration of terrestrial habitat from deforestation or harvesting is a leading cause of global species declines and population extinctions (Mace et al., 2005). Although harvesting of primary forest remains a major concern (Gardner et al., 2007), industrial silviculture and logging of second-growth forests are more prevalent in developed countries and continue to have ecological consequences to biodiversity and ecosystem processes (Coates and Burton, 1997). For example, 6.1 million ha of a total 734 million ha forest area is estimated to be affected by harvest each year in North America, with an additional 1 million ha converted to other land uses (Masek et al., 2011). Because of the large scale of forestry and its global reach, there has long been interest in understanding the effects of harvesting practices such as clearcutting on plant and animal populations, particularly where such knowledge can inform management and reduce negative effects. In some cases, this has led to improvements in land management that benefit threatened species (e.g., uneven-aged stand management for Red-cockaded woodpeckers, *Picoides borealis*; Hedrick et al., 1998) or that restore ecosystem integrity (e.g., retention of riparian buffer zones; Lowrance et al., 1997), demonstrating a valuable role for solution-based research on forestry impacts.

Applied ecological research on amphibians has lagged behind that of other vertebrates (Clark and May, 2002), but growing appreciation for the current plight of amphibians has generated greater interest in mechanisms of amphibian decline (Wake and Vredenburg, 2008). As with many fauna, habitat loss is a major factor in global amphibian declines (Alford and Richards, 1999; Stuart et al., 2004). However, unlike nearly all other vertebrates, many amphibians have complex life histories that require them to live

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in both aquatic and terrestrial habitats at different stages in their lives. This aspect of their ecology makes them especially sensitive to habitat loss or alteration and may contribute to their high level of imperilment among vertebrates (Stuart et al., 2004; Bielby et al., 2008; Murray et al., 2011). Over 80% of amphibians are forest-dependent (Stuart et al., 2004), and in some studies, amphibians have been found to comprise more forest biomass than all other vertebrate groups combined (Burton and Likens, 1975; Peterman et al., 2008), playing an important role in ecosystem dynamics (e.g., Wyman, 1998). Thus, there is an urgent need to understand the degree to which structural changes in forests after harvesting affect amphibian biodiversity.

Past studies of forestry effects on amphibians have focused on evaluating changes in amphibian abundance and diversity after clearcutting (Kroll, 2009). Generally, these studies have found reduced amphibian abundance and richness in clearcuts (reviewed in deMaynadier and Hunter, 1995; Tilghman et al., 2012). Such studies identify declines in abundance and richness that can result from forest harvesting but provide little insight into the processes that underlie such declines. Moreover, due to high inter-annual variation in amphibian abundance (Pechmann et al., 1991), it is often difficult to anticipate long-term consequences of forest harvesting on amphibian populations based solely on changes in abundance. Consequently, there is an increasing need to understand demographic responses of amphibians to forest harvesting. Population models have also found that post-metamorphic, terrestrial stages of amphibians typically have the greatest impact on population persistence compared with aquatic stages (Biek et al., 2002; Vonesh and De la Cruz, 2002). It is therefore important to determine how forest harvesting and other activities affect demographic processes such as survival or growth (i.e., vital rates; Todd and Rothermel, 2006). Understanding such demographic responses is an important step in improving forest management for amphibians and will also inform future modeling efforts aimed at understanding the long-term demographic consequences of forest alteration. There are currently few studies that provide estimates of vital rates in amphibians, especially in response to factors expected to alter survival or reproduction. Moreover, studies of forestry impacts on amphibians have typically focused on woodland salamanders (i.e., plethodontids), excluding a broad range of pond-breeding amphibians whose primary terrestrial habitat is forest.

The primary goal of our study was to examine the effects of forest harvesting on patterns of survival of ambystomatid salamanders in multiple regions of North America. We focused on the Northeast, Midwest, and Southeast, three economically important timber-producing regions with closely related amphibian species, but with widespread variation in other factors such as climate, topography, and land ownership, among others. By examining amphibian responses across multiple regions, our results should offer broad management applicability. We examined salamander survival using replicated field enclosures in forest habitats harvested at varying intensities, including unharvested controls, partially harvested forests ($\sim$25% canopy reduction), and clearcuts with coarse woody debris either retained or removed. Previous studies have shown at least short-term decreases in the abundance of many amphibians following forest harvesting, often simultaneously with increases in temperature and a loss of refuge that may be associated with lower survival of these species (deMaynadier and Hunter, 1995; Rothermel and Luhring, 2005; Tilghman et al., 2012). Thus, we predicted that salamanders would exhibit decreasing rates of survival as the degree of forest harvesting increased and conditions presumably became less favorable for many amphibians. Also, because body size in amphibians is often correlated with survival (Semlitsch et al., 1988), we predicted that larger animals would be more likely to survive and be recaptured irrespective of treatment.

2. Methods

2.1. Study sites

We conducted our study in three regions of the United States, the Northeast, the Midwest, and the Southeast (Table 1), as part of the LEAP study (Semlitsch et al., 2009). Our study site in the Northeast was located in the University of Maine Demeritt and Penobscot Experimental Forests, Penobscot County, Maine. The forests were predominately mixed coniferous-deciduous forests with dominant tree species of balsam fir (*Abies balsamea*), eastern white pine (*Pinus strobus*), northern white cedar (*Thuja occidentalis*), red maple (*Acer rubrum*), eastern hemlock (*Tsuga canadensis*), red oak (*Quercus rubra*), and paper birch (*Betula papyrifera*). Understory included American beech (*Fagus grandifolia*), bigtooth aspen (*Populus grandidentata*), quaking aspen (*P. tremuloides*), and balsam poplar (*P. balsamifera*) (see also Patrick et al., 2006).

Our study site in the Midwest was located in the Daniel Boone Conservation Area, Warren County, Missouri. The Daniel Boone Conservation Area is a 1424 ha oak-hickory forest managed by the Missouri Department of Conservation. The canopy is dominated by second-growth oak (*Quercus spp.*) and hickory (*Carya spp.*) and the understory was predominantly sugar maple (*Acer saccharum*) (see also Semlitsch et al., 2008).

Our study site in the Southeast was located on the Department of Energy's Savannah River Site (SRS) in Barnwell County, South Carolina. The Savannah River Site is a 770 km^2 restricted-access site with forests managed by the US Forest Service – Savannah River. The areas used in this study were composed of second-growth planted loblolly pine (*Pinus taeda*) with a few interspersed, naturally-occurring hardwoods (oaks [*Quercus* spp.], red maple [*Acer rubrum*], hickories [*Carya* spp.], dogwood [*Cornus florida*], and sweetgum [*Liquidambar styraciflua*]). Understory consisted of sweetgum (*Liquidambar styraciflua*), wax myrtle (*Morella cerifera*), and holly (*Ilex opaca*) (see also Rothermel and Luhring, 2005; Todd and Rothermel, 2006).

2.2. Experimental arrays

In each of the three regions, we centered replicated circular experimental arrays on four separate, isolated seasonal wetlands (Northeast and Southeast) or 40+ year old wildlife ponds (Midwest) that serve as reproduction sites for local amphibians. The experimental arrays extended 165 m from the wetland edges. We divided each circular array into four quadrants via two perpendicular transects that intersected at the center of each wetland (e.g., Todd et al., 2009). Each quadrant was randomized to receive one of four of the following treatments with the stipulation that clearcut plots were always opposite from each other. The four treatments included: an unharvested control (>30 years old, hereafter 'control'); a partially harvested stand in which the canopy was thinned by approximately 25% (hereafter 'partial'); a clearcut with coarse woody debris retained (hereafter 'CC-retained'); and a clearcut with coarse woody debris removed (hereafter 'CC-removed'). Not all coarse woody debris (CWD) could be removed in the Northeast, but enough was removed to make CWD comparatively lower in the CC-removed than in CC-retained (13.8 m^3 per ha versus 55.2 m^3 per ha; Table 2). Logging was completed in 2004 in all regions. We did not perform any subsequent site manipulation such as replanting, harrowing, burning, or biocide application after harvesting.

Our treatments were chosen and applied in close consultation with site foresters and the applicable forest stewards. The treatments were designed to encompass a range of practices represented by forest harvesting methods in North America, which