SALAMANDER RESPONSE TO WOODY BIOMASS HARVESTS IN CLEARCUT ASPEN STANDS IN MICHIGAN.

By

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ABSTRACT

SALAMANDER RESPONSE TO WOODY BIOMASS HARVESTS IN CLEARCUT ASPEN STANDS IN MICHIGAN.

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Interest in woody biomass as a source of renewable energy is increasing. In response, managers have developed retention guidelines that are intended to mitigate the negative effects of biomass harvests on forest floor-dwelling wildlife, particularly species that depend on downed wood like terrestrial salamanders. The theme of my thesis is how woody biomass harvest may affect a prevalent terrestrial salamander species in Michigan. The primary objective of my thesis is to assess the woody biomass retention guidelines created by the Michigan Department of Natural Resources (MDNR). In Chapter 1, I discuss *Plethodon cinereus* use of downed wood retained following clearcut timber harvest. I used experimental enclosures and mark-recapture methods coupled with linear and logistic regression modeling to determine the association of population-level and individual *P. cinereus* response to downed wood. In Chapter 2, I assessed the effects of MDNR guidelines for woody biomass harvest retention on *P. cinereus*. I used wood removals based on MDNR guidelines coupled with single-season occupancy models and N-mixture models to quantify occupancy probability and estimate salamander abundance based on downed wood characteristics. This study is one of the first to quantify terrestrial salamander habitat selection at varying levels of biological organization and to quantitatively assess the effects of woody biomass harvest guidelines on terrestrial salamanders. This study has relevance to the experimental design of future amphibian-forest management studies and provides guidance on how downed wood can be managed to potentially improve conservation of forest floor-dwelling wildlife like *P. cinereus* in recent clearcuts.

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INTRODUCTION

Human population growth is projected to be almost 9 billion by 2050 (United Nations, 2004). Population growth is explicitly linked to increased demands for natural resources and energy that result in additional and exacerbated stressors on wildlife populations. Increasing energy needs and concurrent interests in diversified sources have caused some to consider woody biomass as a source of renewable energy (often referred to as bioenergy). Although logging residue resulting from timber harvests is often viewed as waste, research has demonstrated that several wildlife species depend on logging residue for habitat (reviewed by Riffell et al., 2011). While interest in harvesting logging residue is increasing in response to demands for bioenergy, natural resource managers and academia are just beginning to understand the potential effects of woody biomass extraction on existing ecosystems and wildlife populations.

Woody biomass is a potential alternative energy source that, in one form, results in the harvest of logging debris such as snags, tree tops, and limbs that result from timber harvest (Becker et al., 2009; Janowiak and Webster, 2010; MDNR&E, 2010). Some forest floor-dwelling wildlife are known to negatively respond to timber harvest, thus additional wood removal through harvesting biomass may exacerbate the negative effects these populations are experiencing (Petranka et al., 1993; Ash, 1997; Butts and McComb, 2000; Semlitsch et al., 2008; Moorman et al., 2011; Riffell et al., 2011; Otto et al., 2013). Retention of woody biomass provides coarse woody debris as refugia and has been suggested as an approach for mitigating the negative consequences of timber harvesting on some wildlife populations (Franklin et al., 1997; Butts and McComb, 2000; Moorman et al., 2011; reviewed by Riffell et al., 2011; Otto et al., 2013). Several states, including Michigan, have created woody biomass harvesting and retention guidelines as a means to promote sustainable forestry practices and conservation of species (MDNR&E, 2010). However, quantitative evidence on the effectiveness of these guidelines for conserving wildlife is lacking. Michigan has almost 20 million acres of forest land (MDNR&E, 2010) which "contribute[s] over $12 billion" to the economy annually (MDNR, 2013). As managers consider multi-purpose land uses they must seek a balance between economic and ecological sustainability.

Salamanders can be crucial elements of terrestrial ecosystems (Burton and Likens, 1975) and can function as gauges of ecosystem health (Welsh and Droege, 2001). Furthermore, terrestrial salamanders have been used as model organisms in past timber harvest studies and their sensitivity to clearcutting has been documented (*e.g.*, Petranka et al., 1993; Ash, 1997), although causal mechanisms related to salamander declines following timber harvests are not well understood (*e.g.*, Petranka et al., 1993; Ash, 1997; Semlitsch et al., 2008; Homyack and Hass, 2009). Retained downed wood potentially benefits salamanders by providing sites for forage, shelter, and micro-climate stability that can limit desiccation (Heatwole, 1962; Patrick et al., 2006; Bunnell and Houde, 2010). Understanding the mechanisms related to salamander population declines and assessing how management actions influence habitat use can better inform managers and policymakers in their efforts to incorporate wildlife conservation into a viable wood products industry.

The theme of my thesis is how woody biomass harvest may affect a prevalent terrestrial salamander species in Michigan. In Chapter 1, I assessed Red-Backed Salamander (*Plethodon cinereus*) use of downed wood retained following clearcut timber harvest. I used mark-recapture methods coupled with linear and logistic regression modeling to determine the association of population-level and individual *P. cinereus* response to downed wood covariates such as amount and size. In Chapter 2, I assessed the effects of Michigan Department of Natural Resources (MDNR) guidelines for woody biomass harvest retention on *P. cinereus*. I used single-season occupancy models and N-mixture models to quantify occupancy probability and estimate salamander abundance with the inclusion of treatment type and wood characteristics as covariates. This study is one of the first to quantify terrestrial salamander habitat selection at varying levels of biological organization and to quantitatively assess the effects of woody biomass harvest guidelines on terrestrial salamanders. This study has relevance to the experimental design of future amphibian-forest management studies. Additionally, I provide guidance on how downed wood can be managed to potentially improve conservation of forest floor-dwelling wildlife like *P. cinereus* in recent clearcuts.

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CHAPTER 1

RED-BACKED SALAMANDER (*Plethodon cinereus*) RESPONSES TO DOWNED WOOD IN ASPEN (*Populus* spp.) CLEARCUTS, MICHIGAN, USA

Abstract

Retention of downed wood is often used to mitigate the negative consequences of timber harvesting on some wildlife populations. Quantitative evidence showing wildlife response to retained downed wood is lacking. Red-backed salamanders (*Plethodon cinereus*) are viewed as an indicator species sensitive to forest management activities; their absence following timber harvest is often viewed as evidence of localized extinction. The goal of this project was to describe *P. cinereus* use of sites with varying amounts and sizes of downed wood that was retained following clearcutting of aspen (*Populus* spp.) in Michigan. I individually marked 450 red-backed salamanders and released 10 each into 21 and 24 enclosures (9 m^2) during the springs of 2010 and 2011, respectively. I recorded the release locations of each salamander and 1-month after release I recorded and mapped recaptures. I measured downed wood (>2.5 cm diameter) counts, sizes, and decay classes within each enclosure. I also measured soil temperature and moisture on the peripheries of the enclosures. I used mark-recapture to quantify capture probabilities and linear and logistic regression modeling to portray habitat selection. The results indicate that wood count most influenced whether salamanders were available for capture on the forest floor; at low wood counts (i.e., <20 pieces/enclosure) <40% of the marked salamander population was available for capture. As wood counts increased (i.e., >80 pieces/enclosure), >70% of the marked population was available for capture. I documented both subterranean retreat and mortality as mechanisms that influenced results of salamander surveys

at the population level. At the micro-site level (i.e., 1 m^2), I found that the likelihood of capturing an individual *P. cinereus* was positively associated with size of downed wood, with the probability of recapturing a marked salamander >80% if wood >20 cm diameter occurred. For those terrestrial salamanders that survive site disturbance events like timber harvest, my results indicate that the amount and size of residual downed wood can be used to alleviate adverse surface conditions. For monitoring the effects of timber harvest on *P. cinereus*, wood counts and diameter must be explicitly accounted for as these variables influence the likelihood of salamanders being available for capture on the forest floor.

1.1. Introduction

Retention of downed wood may be used to mitigate the negative consequences of timber harvesting on some wildlife populations (Franklin et al., 1997; Butts and McComb, 2000; Moorman et al., 2011; Otto et al., 2013). Potential benefits of retaining downed wood include increasing habitat heterogeneity and reducing microclimate extremes resulting from clearcutting (Franklin et al., 1997; Rothermel and Semiltsch, 2002). An increased interest for renewable energy sources has focused forest management on harvest of woody biomass (MDNR&E, 2010). For example, prior to the development of woody biomass markets in Michigan logging slash in aspen (*Populus* spp.) harvest units was typically spread throughout the harvest area resulting in an abundance of dispersed downed wood. More recently, logging contractors have expressed interest in piling and chipping logging debris as an additional forest product, prompting the Michigan Department of Natural Resources (MDNR) to develop biomass retention guidelines (MDNR&E, 2010). Quantitative evidence for evaluating the effectiveness of biomass retention guidelines for conserving wildlife is lacking (Otto et al., 2013).

Salamanders can be key components of terrestrial ecosystems (Burton and Likens, 1975) and can serve as indicators of ecosystem health (Welsh and Droege, 2001). Furthermore, terrestrial salamanders have been used as model organisms in past timber harvest studies and their negative response to clearcutting has been documented (*e.g.*, Petranka et al., 1993; Ash, 1997). These studies showed that salamander numbers decline rapidly after clearcutting however the causes of these declines are not fully understood. Understanding the causal mechanisms associated with population declines are critical for developing effective conservation strategies.

Potential benefits of retaining downed wood include forage and shelter sites for salamanders (Heatwole, 1962; Patrick et al., 2006; Bunnell and Houde, 2010). Additionally, downed wood in clearcuts provides more stable micro-climates that can protect terrestrial salamanders from the hotter and drier conditions that result from clearcutting (Heatwole, 1962; Patrick et al., 2006; Bunnell and Houde, 2010). The function of downed wood as terrestrial salamander habitat in timber harvest units varies geographically. For example, salamander abundance was not correlated to downed wood in southern pine stands (Owens et al., 2008; Davis et al., 2010). These researchers posited that downed wood is less important in ecosystems that historically experienced frequent understory fire (Owens et al., 2008; Davis et al., 2010). In contrast, higher abundance of salamanders was found in unharvested or partially harvested areas in Maine that contained more downed wood when compared to clearcuts (Patrick et al., 2006). In Michigan, Otto (2012) found that occupancy of red-backed salamanders (*Plethodon cinereus)* was not related to downed wood amounts, but apparent survival was positively correlated. Otto et al. (2013) conducted a literature review on studies of amphibian responses to downed wood and found that terrestrial salamander abundances were positively associated with downed wood quantity in general, but that quality of downed wood (size and level of decay) may be the primary determinant of small-scale habitat use.

The goal of this project was to describe *P. cinereus* use of sites with varying amounts and types of downed wood in recent aspen clearcuts. Insight into *P. cinereus* use of downed wood can further our understanding of the mechanism(s) associated with terrestrial salamander population dynamics following timber harvest (*e.g.*, Petranka et al., 1993; Ash, 1997), help refine monitoring programs and studies, and ultimately inform management of logging residuals. The objectives of this project were to 1) observe the population-level response of *P. cinereus* to downed wood at the plot level (9 m^2) and 2) observe the individual response of *P. cinereus* to downed wood at the micro-site level (1 m^2).

1.2. Methods

1.2.1. *Study Area*

This study was conducted from May to July 2010 and 2011, on state-owned forest lands currently managed for aspen production in Missaukee and Wexford Counties, northwestern Lower Peninsula, Michigan. The study areas have well-drained, sandy soils characteristic of glacial outwash plains and moraines (Barnes and Wagner, 2004). Elevation ranges from 274-457 m with minimum and maximum temperatures averaging approximately 1 to 12°C, respectively, and average precipitation of 88 cm annually (NOAA, 2011). The dominant regenerating tree species in the sampled areas was aspen, with varied overstory retention that included mixed oak (*Quercus* spp.), maple (*Acer* spp.), beech, (*Fagus* spp.), cherry (*Prunus* spp.), and white pine (*Pinus strobus*).

1.2.2. *Study Design*

I selected 3 stands in Missaukee County (2010) and 3 stands in Wexford County (2011) that were 1-5 years post-harvest. Here, a stand refers to an area of relatively homogenous overstory vegetation that was harvested at approximately the same time. Selected stands ranged in size from 8-12 hectares. Within a stand, sample sites (30 x 30 m) were stratified by retained canopy coverage to help ensure that a range of woody debris amounts and sizes would be included in the sample. Unless logging residue is removed from the site or piled and burned (practices not used in the stands sampled), the amount of timber removed positively relates to the amount of woody debris in the form of tree tops and limbs (Patrick et al., 2006; Visser and Sherman, 2007). Canopy cover of retained trees (i.e., those purposefully retained during timber harvest) was digitized from 1-m resolution 2009 and 2010 NAIP (National Aerial Imagery Program) aerial photos (Otto, 2012). Each stand was divided into 30 x 30 m grid cells in a Geographic Information System (GIS; ArcGIS, Environmental Systems Research Institute, Redlands, CA) and the proportion of canopy cover estimated within each grid cell (Otto, 2012). Each grid cell was then assigned to 1 of 3 categories based on the amount of retained green-tree canopy cover: 1-10%, 10-25%, and >25% (Bielecki et al., 2006).

For each category of canopy cover in the timber harvest stands (6 stands in total), I randomly selected 6-30 x 30 m sites per stand, resulting in 18 sites in each 2010 and 2011. Additionally, I selected a mature aspen stand (40+ years-old) in each county to represent sites with 100% canopy retention. Within each mature aspen stand, I selected 3-30 x 30 m sites and 6-30 x 30 m sites in 2010 and 2011, respectively. Hence, a total of 21 and 24 sites were sampled in 2010 and 2011, respectively. All sampled sites were ≥50 m from other sample sites, forest edges, roads and wetlands. I used spatial separation between sampling sites (i.e. ≥ 50 m) to meet the assumption of independence. I recognize this limitation but based on species biology (i.e.

home range averages are 13-24 m^2; Petranka 1998) and the variability in the vegetation sampled I felt the independent assumption was met.

I installed an enclosure (9 m^2) at the center of each 30 x 30 m site during the first week of May for both sampling years. Enclosures measured 3 x 3 m and were constructed of aluminum flashing 50 cm high (Figure 1.1.1.). The top 7.5 cm was bent inward at a 90° angle to prevent emigration over enclosure walls (Figure 1.1.1.). Edges of adjacent flashing walls overlapped by 2 cm at the corners and were attached with staples to wooden stakes, which doubled as inner wall supports. To prevent salamander emigration at seam edges, all stake-to-flashing corners were sealed with silicone caulk.

Flashing walls were buried 10 cm into the ground. To retain habitat elements within the enclosure disturbance during construction was minimized (Todd and Rothermel, 2006). Pre-existing woody debris and leaf-litter were not manipulated within enclosure sites. Pieces of downed wood extending outside of an enclosure were cut at the enclosure edge to accommodate the fence. Overhead photographs (2011) and sketches (2010, 2011) of downed wood, leaf litter, grass, or bare patches were completed at each enclosure site. Photographs were taken by attaching a camera to a telescoping pole adjusted to 5 m above the center point of the enclosure and were used to verify the accuracy of sketches. Photographs and sketches were used to accurately map salamander release and recapture locations within each 1 m^2 enclosure cell (Figure 1.1.2.).

I tested the ability of enclosures to hold salamanders by constructing a miniature replica (30.5 x 30.5 cm) with a complete bottom, placing the replica in a plastic container with lid, and releasing 12 *P. cinereus* into the replica. The bottom of the replica was lined with moist paper towels to prevent desiccation. I monitored salamander locations for 3 consecutive days in the replica.

1.2.3. *Data Collection*

I collected 210 and 240 *P. cinereus* from unharvested forests <2 km from the study sites in 2010 and 2011, respectively. Basic morphometric data were collected: snout to vent length (SVL), total length, gravidity, and color phase. Salamanders with >30 mm SVL were individually injected with elastomer (Davis and Ovaska, 2001; Grant, 2008). One of 10 individual identifying marks was assigned to each salamander using a combination of green and orange fluorescent elastomer injected into 2 of 4 ventral body locations (NMT, 2008). Visual Implant Elastomer (VIE) (Northwest Marine Technology, Shaw Island, Washington) is a pliable compound that is injected under the skin of amphibians and can be detected with ultra-violet light (Phillips and Fries, 2009).   The use of fluorescent elastomer as a marking tool for mark/recapture of plethodontid salamanders is a less invasive and more enduring method than toe-clipping (Davis and Ovaska, 2001). All animal handling was done in compliance with Michigan State University's Institutional Animal Care and Use Committee (IACUC) procedures and guidelines (IACUC #07/08-118-00). All applicable state permits were obtained.

One salamander from each of the 10 uniquely marked groups was randomly assigned to each of the enclosures. The second week of May, each enclosure received the assigned 10 salamanders; a density that reflects natural population density of *P. cinereus* in mature forest stands in northern Michigan (Petranka, 1998). Enclosures were gridded into 9-1 x 1 m cells by attaching flagging to the lip of enclosures walls (Figure 1.1.2.). A single salamander was placed into each cell, with two salamanders being placed into the center cell. Cell release locations for each individual were recorded. After salamander releases the flagging tape was removed.

At each enclosure micro-climate information was collected from early May to mid-June during both sampling years. Soil temperature and soil moisture were collected using an Aquaterr Temp-300 soil moisture probe (Aquaterr Instruments & Automation, Costa Mesa, CA) twice per week at 16 locations 1 m outside the perimeter of each enclosure (4 readings per enclosure side). Measurements were collected by penetrating the ground approximately 18 cm with the probe.

During the second week of June enclosures were again gridded into the same 9-1 x 1 m cells. A single observer systematically searched each 1 x 1 m area and captured salamanders. Debris was methodically searched and placed into separate holding containers and held until all 9 cells were searched. Container debris was subsequently searched a second time to account for salamanders potentially missed during the initial search. I defined downed wood as any woody debris >2.5 cm in diameter. Downed wood that intersected multiple 1 m^2 cells within an enclosure was simultaneously rolled by multiple observers. These logs were assigned to the single 1 m^2 cell with the largest proportion of the log making contact with the ground. Downed wood piece count, piece size (length and diameter), and decay class were collected per 1 x 1 m area. Decay class was based on the 5 part classification described by Maser et al. (1979).

Individual salamanders were identified by viewing elastomer markings under an ultra-violet light. Sketches and photographs were used to map individually marked salamander release and recapture points. After each enclosure cell was searched and all captures processed the debris from the separate holding containers was returned to the cell of origin. All captured salamanders were then released back into the enclosure at the point of capture. All enclosures were searched twice more during successive days (1-6 day gap), each 1 x 1 m cell by a different observer. All sampling was completed over a 9 day period in 2010 and 7 day period in 2011. At the conclusion of the experiment the salamanders were released at enclosures sites and enclosures were removed.

1.2.4. *Statistical Analysis*

I used mean soil temperature and moisture measurements collected during the 11 days preceding salamander recapture to evaluate micro-climate conditions among sites. Each measurement at a site (n=16) was considered a sub-sample within a day and we constructed box plots of site averages to evaluate central tendencies and help identify outliers.

Capture probabilities and apparent survival were estimated by Otto (2012) using Huggins parameterization of the robust design population model (Pollock, 1982; Bailey et al., 2004). Covariates used in modeling at the enclosure level included wood count, largest diameter, length, downed wood decay class, soil moisture, soil temperature, and overstory (i.e., retained mature trees) canopy cover (Table 1.1.). I used Pearson correlation coefficients and corresponding probability values to examine correlations between covariates.

To analyze a population (n=10 marked salamanders) response at the enclosure level I used generalized linear models to relate the proportion of marked individuals that was recaptured to the measured environmental attributes. Technically, the marked salamanders in my study represent a statistical population. I believe that these groups mimicked a natural population because I stocked enclosures with salamander densities similar to natural densities for this species (i.e. 0.89 salamanders per m^2 in Michigan; Heatwole, 1962). Prior to regression modeling, I evaluated scatterplots of each environmental covariate against the proportion of salamanders recaptured. If a linear or non-linear pattern was observed in the scatterplot I included the covariate in the candidate model set. I initially generated 18 candidate models (Table 1.2.). Length was excluded from the candidate model set because of no apparent relationship based on the scatterplot. I used Akaike Information Criterion, adjusted for small sample sizes (AIC_c), to rank and weight the models (Burnham and Anderson, 2002). I also calculated adjusted r-squared values for the top-ranking model(s) (i.e., <2 ΔAIC) to assess model fit, and evaluated the significance of model parameters based on whether the 95% confidence intervals overlapped 0.

I analyzed individual salamander response at the 1 m^2 cell-level using logistic regression. For each 1 m^2 cell in the study (n=405), I recorded occupancy status by a marked salamander during the recapture period. Cell occupancy status was then regressed on cell-level downed wood attributes (wood count, largest diameter, presence of advanced decay {4+ category; Maser et al. 1979}). To account for similarities in 1 m^2 cells (n=9) within enclosures, I included a random intercept term for each enclosure to help account for the independence assumption. I again used AIC_c to rank candidate models (Burnham and Anderson, 2002) and evaluated the significance of model parameters based on whether the 95% confidence intervals overlapped 0. A likelihood ratio test was used to assess model fit (Burnham and Anderson, 2002). All modeling was conducted using program R version 2.15.3 (RDCT, 2008).

1.3. Results

At the enclosure level, canopy cover ranged from 0-100%, soil moisture from 20-98%, and soil temperature from 13-21°C (Table 1.1.). Downed wood piece count per enclosure ranged from 1-112, lengths ranged from 8-288 cm, and diameters ranged from 2.7-43.0 cm (Table 1.1.). Soil moisture measurements for the week prior to salamander sampling indicated that wetter sites were surveyed in 2010 compared to 2011 (Figure 1.2.1.). No differences in soil temperature were detected between years (Figure 1.2.2.).

I found that the enclosure replicas successfully prevented horizontal emigration. Although salamanders were observed climbing the internal walls of the replica, no salamanders were found outside the enclosure walls. In the field enclosures, capture probabilities ranged from ~0.58 (first survey) to ~0.28 (third survey); with the likelihood of capturing an individually marked salamander at least once during the 3 surveys being 0.78 (Otto 2012). Of 197 recaptured individuals, 11% were only found within the soil profile (up to 20 cm deep). These individuals were located by pulling up roots, digging along root channels, or in soft areas that could be excavated by hand. Additionally, the carcasses of 3 marked salamanders were found.

The number of marked salamanders available for recapture on the forest floor depended on wood count and decay (97% weight of evidence; Table 1.2). Correlated variables ($r \geq 0.37$, $P \leq 0.05$) were not included in the same candidate model (Table 1.3.). Parameter estimates for wood count consistently differed from 0 for the 3 top-ranking models (0.16 < 95% CI < 1.34), however parameter estimates for decay did not differ from 0 (-20.87 < 95% CI < 24.37). Strong support existed for a wood count effect on the population-level response of marked salamanders, although adjusted r-squared values (0.18-0.19) indicated low predictive power. I found that the majority (>50%) of the marked salamander population was available for surface sampling when wood counts exceeded 50 pieces per 9 m^2 enclosure (Figure 1.3.).

I further evaluated wood count as an explanatory variable for influencing the surface availability of marked salamanders by including other environmental variables into the wood count model (Table 1.4.). Weight of evidence suggested support for a variety of models (Table 1.4.) but again only wood count was a significant parameter in any of the new models. Adjusted r-squared values (0.15-0.19) again showed low predictive power for the new models, suggesting poor model fit.

For the 1 m^2-level analysis, I removed cells with log diameters >35 cm from the analysis to reduce the impacts of these outliers (n=2) on model estimates. At the 1 m^2 level, I found that log diameter and decay most influenced the likelihood of capturing marked salamanders (Table 1.5.). Parameter estimates for log diameter consistently differed from 0 for all models with $AIC_w>0$ ($z \geq 4.148$, $P \leq 0.001$), whereas parameter estimates for decay did not differ from 0 ($P \geq 0.253$). My data indicate substantial support for a log diameter effect on micro-site level salamander occurrence. The model indicated that the probability of capturing a marked salamander was approximately 0.25 at micro-sites with small diameter wood but increased to >0.80 as log sizes exceeded 20 cm (Figure 1.4.).

1.4. Conclusion

My results showed that factors influencing *P. cinereus* surface activity differed at the population versus individual level. Over the range of field measurements I sampled, wood count was positively correlated with the proportion of my marked salamander population that was recaptured at the enclosure level. Hence, availability of wood on the forest floor appears to directly affect the proportion of the salamander population available for sampling during monitoring programs. Additionally, others have shown that apparent survival estimates for *P. cinereus* positively relate to wood count (Otto, 2012). At the 1 m^2 level, log diameter was positively associated with the likelihood of capturing a marked salamander. Thus, if enough wood is present to encourage the majority of the terrestrial salamander population to remain surface active, my findings indicate that individuals will select micro-sites with larger wood. Collectively, these results demonstrate the importance of explicitly (through either design- or model-based approaches; Otto, 2012) accounting for downed wood characteristics in studies that use *P. cinereus* as indicators of habitat changes resulting from forest management.

Peterman et al. (2011) summarized the main hypotheses concerning salamander population declines following timber harvest as mortality, retreat, and evacuation. When controlling for horizontal evacuation, I found that the amount and size of downed wood retained at a site following clearcutting affected the likelihood of finding terrestrial salamanders. In my study, this likelihood was influenced by both mortality and subterranean retreat. Mooreman et al. (2011) posited that mortality was most likely the reason for reduction of plethodontid salamander abundances (such as red-backed salamanders) following timber harvest due to decreased leaf litter, which provides habitats used for surface feeding. However, Otto (2012) estimated that apparent survival of *P. cinereus* in our study system approximated 1.00 for recent clearcuts that contained high levels of overstory canopy cover or downed wood. Although neither my study nor Otto (2012) can fully address the mortality hypotheses, my results indicate that downed wood micro-sites and retreat to the subterranean environment are used by salamanders to ameliorate the negative effects of clearcutting.

Wood count, size and decay status are known to affect salamander response to timber harvest (Moorman et al., 2011), however most of the literature has emphasized population-level responses and not individual choice (Burton and Likens, 1975; Petranka et al., 1993, 1994; Ash, 1997; Harpole and Hass, 1999; Patrick et al., 2006). This study is one of the first to quantify habitat selection processes at different levels of biological organization for terrestrial salamanders. Population-level dynamics, such as survival, reproduction, and movement, depend on resource availability and selection, or how individuals perceive habitat quality within a population (McDonald et al., 2005). Amphibians generally exhibit a patchy spatial distribution due to various life history requirements (i.e., foraging, reproduction, dispersal, etc.) that are linked to microhabitat (Heyer et al., 1994). Thus, the determinants of habitat selection by amphibians likely differ depending on scale (McDonald et al., 2005). My results confirm that the factors related to habitat selection for *P. cinereus* are multi-scalar, varying between the population and individual levels. This finding has relevance to the experimental design of future amphibian-forest management studies. For studies based on species occupancy (i.e., the confirmation of a single individual at a site), size of downed wood should be factored in to the experimental design or analyses. For studies based on a population-level parameter like abundance the amount of downed wood should be accounted for.

Future monitoring and research of terrestrial salamanders conducted at stand- or landscape- scales should control for downed wood characteristics among treatment types (e.g., clearcut, mature forest) to: 1) help standardize likelihoods of capture, and 2) avoid confounding the effects of treatment type with downed wood characteristics (at both the population and individual levels) on occupancy, abundance, or habitat selection. Past studies reporting negative effects of clearcutting on terrestrial salamanders have produced mixed results (*e.g.*, Petranka et al., 1993; Ash, 1997; Homyack and Hass, 2009); potentially related to how downed wood was accounted for in the experimental design. For example, Petranka et al. (1993) explicitly noted that downed wood diameter increased with stand age and that salamander abundance increased with increasing availability of downed wood volumes (>10 cm, decay class 3-5). Petranka et al. (1993) thus concluded that older stands provided better salamander habitat. Ash (1997) and Homyack and Hass (2009) found that relative abundance of salamanders was lower following timber harvest, but neither study accounted for downed wood characteristics. In my study, I rarely (3 out of 45) accounted for 100% of the marked individuals during surface surveys in my enclosures; I found additional marked salamanders in the soil profile. Hence, surface surveys (e.g., visual encounter surveys, drift fences) for *P. cinereus* likely produce results that confound survival and movements (vertical and horizontal) away from the disturbed surface.

My results showed that downed wood counts and size of the wood affect the likelihood of finding salamanders on the forest floor. Downed wood in recent timber harvest areas likely mitigates the loss of leaf litter in some forest types (*e.g.*, Ash, 1997), thereby providing habitats that allow a larger proportion of the salamander population to be surface active. Downed wood in this study was abundant, averaging almost 29,000 pieces per ha, although pieces were generally small (length averaged about 1 m and diameter averaged 8 cm). I suggest that this type of downed wood is typical of that following roundwood timber harvest in aspen, where logging slash is re-distributed throughout the harvest unit and the majority of treetops are retained on site. However, logging residue is generally patchy at small scales; counts in our study ranged from 1-112 pieces at 9 m^2. This small-scale patchy distribution aligns with *P. cinereus* space use. *P. cinereus* are territorial and dispersal distances are relatively short (adults range from 0.37-1.85 m; juveniles from 0.52-8.45 m; Ousterhout and Liebgold, 2010). Territories for both juveniles and adults average 0.25 m^2 while home ranges for females and juveniles range between 13-24 m^2 (Petranka, 1998). By extrapolating my results for 9 m^2 to a scale more relevant to logging operations, I suggest that denser patches of dispersed downed wood (not slash piles), i.e., ~3,000-4,000 pieces per 25 m^2 areas, will allow the majority (i.e., >75%) of *P. cinereus* to remain surface active following clearcutting (Figure 1.3.). Individual territory sites can also be improved by providing some pieces that are >20 cm diameter. I found 2-3 pieces of >20 cm diameter wood per 1,000 pieces of logging residue, thus I suggest leaving 6-12 pieces of this larger diameter wood per 25 m^2. These guidelines can be used by managers to improve use of recent clearcuts by *P. cinereus*.

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APPENDIX

APPENDIX

Response Modeling

Table 1.1.

Enclosure-level (9 m^2) covariates used in candidate models for evaluating the response of *P. cinereus* to timber harvest in the northern Lower Peninsula of Michigan, 2010-2011.

Variable	Mean	Standard Error	Range
Wood Count	26	3.92	1-112
Largest Diameter (cm)	8.3	0.26	2.7-43.0
Largest Length (cm)	105	3.77	8-288
Soil Moisture (%)	58	2.59	20-98
Soil Temperature (Celsius)	17	0.26	13-21
Canopy Cover (%)	42	5.94	0-100

Table 1.2.

Ranking of candidate models for predicting population-level response of *P. cinereus* to enclosure-level (9 m^2) covariates, northern Lower Peninsula of Michigan, 2010-2011.

Candidate Models	-2l[a]	k	AIC_C	ΔAIC	AICw
Wood Count	395.2	2	274.6	0.00	0.60
Wood Count + Decay	394.7	3	276.5	1.84	0.24
Wood Count * Decay	393.5	4	277.6	3.01	0.13
Largest Diameter	403.8	2	283.2	8.57	0.01
Soil Moisture	405.4	2	284.8	10.17	0.00
Largest Length	405.7	2	285.2	10.54	0.00
Canopy Cover	405.8	2	285.2	10.61	0.00
Soil Temperature	405.9	2	285.4	10.73	0.00
Largest Diameter + Decay	403.7	3	285.4	10.80	0.00
Canopy Cover * Decay	401.6	4	285.8	11.16	0.00
Soil Moisture + Decay	405.3	3	287.1	12.44	0.00
Soil Temperature * Decay	403.0	4	287.1	12.50	0.00
Largest Length + Decay	405.7	3	287.4	12.78	0.00
Canopy Cover + Decay	405.7	3	287.4	12.81	0.00
Soil Temperature + Decay	405.9	3	287.6	12.99	0.00
Largest Diameter * Decay	403.7	4	287.8	13.22	0.00
Soil Moisture * Decay	405.3	4	289.5	14.83	0.00
Largest Length * Decay	405.5	4	289.7	15.03	0.00

Table 1.2. (cont'd)

[a]-2l = 2 times the negative log likelihood, k= number of parameters, AICc= takes sample size into account, ΔAIC= difference from best model, AICw= weight of evidence in support of model.

Table 1.3.

Pearson correlation coefficients among environmental variable combinations that were used to model *P. cinereus* response to timber harvest in the northern Lower Peninsula of Michigan, 2010-2011.

	Wood Count	Length	Diameter	Canopy	Soil Temperature	Soil Moisture
Wood Count	1	0.0578	0.4821[a]	-0.4158[a]	0.1650	-0.0244
Length		1	0.0284	-0.0303	0.1734	-0.1927
Diameter			1	-0.4359[a]	0.0966	0.1941
Canopy				1	-0.3741[b]	-0.4680[a]
Soil Temperature					1	-0.2907
Soil Moisture						1

[a] Highly significant (p<0.01).

[b]Significant (p<0.05).

Table 1.4.

Ranking of candidate models based on varying combinations of wood count for predicting population-level response of *P. cinereus* to enclosure level (9 m^2) covariates, northern Lower Peninsula of Michigan, 2010-2011.

Candidate Model	-2l[a]	k	AICc	ΔAIC	AICw
Wood Count	395.2	2	274.6	0.00	0.25
Wood Count + Soil M	394.6	3	276.3	1.67	0.11
Wood Count + Decay	394.7	3	276.5	1.84	0.10
Wood Count + Length	395.1	3	276.8	2.18	0.08
Wood Count + Soil T	395.1	3	276.8	2.19	0.08
Wood Count * Soil M	393.2	4	277.4	2.77	0.06
Wood Count * Decay	393.5	4	277.6	3.01	0.06
Wood Count + Soil M + Decay	394.2	4	278.4	3.75	0.04
Wood Count + Soil T + Decay	394.4	4	278.5	3.91	0.04
Wood Count * Length	394.5	4	278.6	4.01	0.03
Wood Count + Length + Soil M	394.5	4	278.7	4.06	0.03
Wood Count + Length + Decay	394.6	4	278.8	4.17	0.03
Wood Count + Soil T	394.7	4	278.9	4.28	0.03
Wood Count + Length + Soil T	394.9	4	279.1	4.45	0.03
Wood Count + Length + Soil T + Soil M	394.1	5	280.8	6.22	0.01
Wood Count + Length + Soil M + Decay	394.2	5	280.9	6.27	0.01
Wood Count + Length + Soil T + Decay	394.2	5	280.9	6.29	0.01

Table 1.4. (cont'd)

[a]-2l = 2 times the negative log likelihood, k= number of parameters, AICc= takes sample size into account, ΔAIC= difference from best model, AICw= weight of evidence in support of model, Soil T=soil temperature, Soil M=soil moisture.

Table 1.5.

Ranking of candidate models for predicting the likelihood of micro-site (1 m^2) occupancy by a marked *P. cinereus* in the northern Lower Peninsula of Michigan, 2010-2011.

Candidate Model	-2l[a]	k	AIC	ΔAIC	AICw
Diameter	508.73	3	514.73	0.00	0.60
Diameter + Decay Class	508.66	4	516.67	1.94	0.23
Diameter * Decay Class	507.31	5	517.32	2.59	0.17
Wood Count	527.52	3	533.53	18.80	0.00
Wood Count + Decay Class	527.12	4	535.12	20.39	0.00
Wood Count * Decay Class	526.99	5	537.00	22.27	0.00

[a]-2l = 2 times the negative log likelihood, k= number of parameters, lowest AIC value = top ranked model, ΔAIC= difference from best model, AICw= weight of evidence in support of model.

Figure 1.1.

Salamander enclosures used to study the factors affecting salamander surface activity in the northern Lower Peninsula of Michigan, 2010-2011, before (1.) and after (2.) 9-1 m^2 gridding.

"<u>For interpretation of the references to color in this and all other figures, the reader is referred to the electronic version of this thesis.</u>"

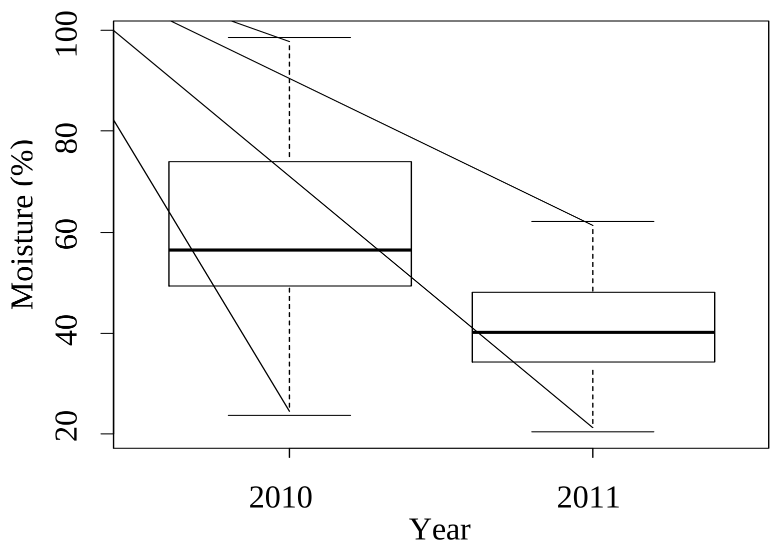
1.

2.

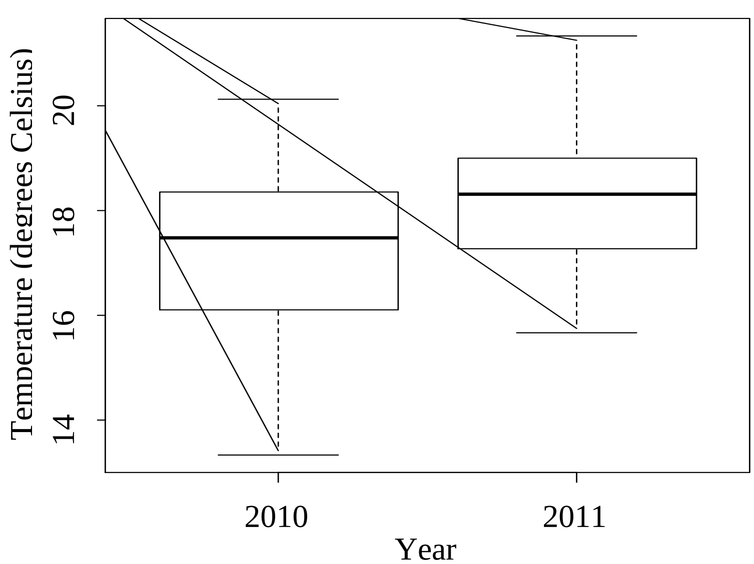
Figure 1.2.

Enclosure-level (9 m^2) soil moistures (1.) and soil temperature (2.) 1 week prior to salamander surveys in 2010 and 2011, northern Lower Peninsula of Michigan.

1.



2.



.

Figure 1.3.

Proportion of marked salamanders recaptured at the enclosure-level (9 m^2) as a function of downed wood count, northern Lower Peninsula of Michigan, 2010-2011.

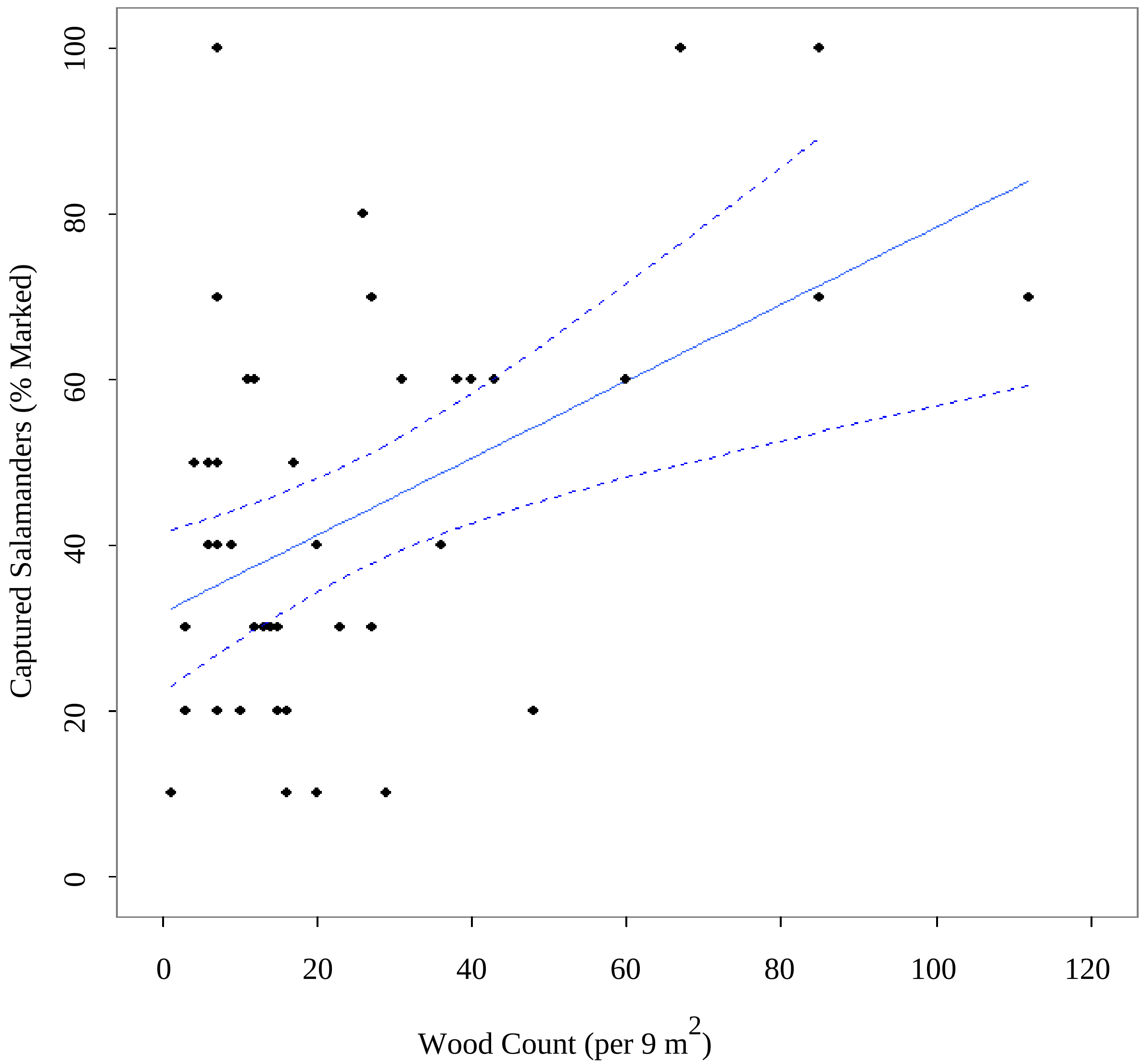
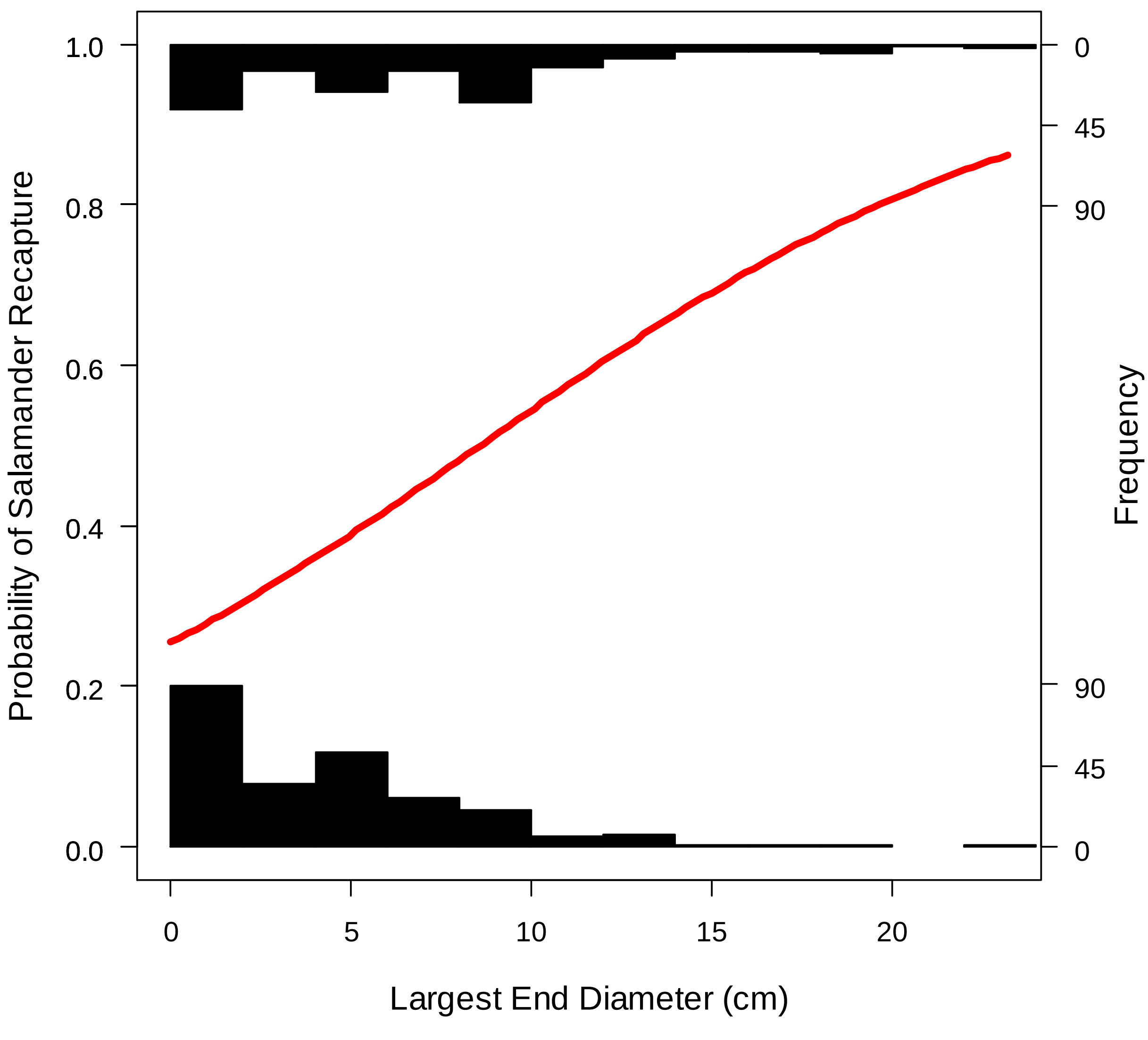


Figure 1.4.

Likelihood of capturing marked individual salamanders as a function of downed wood diameter at the micro-site level (1 m^2), northern Lower Peninsula of Michigan, 2010-2011.



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CHAPTER 2

EFFECTS OF WOODY BIOMASS HARVESTS ON RED-BACKED SALAMANDERS (*Plethodon cinereus*) IN CLEARCUT ASPEN STANDS, MICHIGAN, USA

Abstract

Interest in woody biomass as a source of renewable energy is increasing. In response, managers have developed retention guidelines that are intended to mitigate the negative effects of biomass harvests on forest floor-dwelling wildlife, particularly species that depend on downed wood like terrestrial salamanders. I assessed changes in occupancy and abundance of Red-Backed Salamanders (*Plethodontid cinereus*) to the removal of woody debris in recently clearcut aspen (*Populus* spp.) stands in the northern Lower Peninsula of Michigan. I allocated 3 treatments (control, moderate, and high) of wood removal equally among 60 sites in the fall of 2011 and subsequently surveyed for *P. cinereus* in the spring and fall of 2012. Treatments were based on Michigan Department of Natural Resources biomass retention guidelines, where moderate and high removals corresponded to 66% and 83% reductions in wood count, respectively. I found that occupancy and abundance of *P. cinereus* declined following treatment in both seasons. Compared to control sites, average site occupancy probability was >1.6 and >2.4 times lower in moderate and high wood removals, respectively, regardless of season. Similarly, *P. cinereus* abundance estimates were >3.0 and >3.1 times lower in moderate and high removals, respectively. The results demonstrated that *P. cinereus* occupancy and abundance declined following biomass removal although the mechanism(s) associated with these declines are not clear. The results also indicated that moderate and high levels of wood removal had similar

effects on the *P. cinereus* population, suggesting the retention of more wood is needed if conservation of forest-floor dwelling wildlife is an intended outcome.

2.1. Introduction

Demand for renewable energy sources has increased interest in harvesting woody residues resulting from timber harvest (Becker et al., 2009; Janowiak and Webster, 2010; Rittenhouse et al., 2012). Harvest residues include tree tops, limbs, and snags that can potentially be used for the production of energy (Becker et al., 2009; Janowiak and Webster, 2010). The Great Lakes region of the United States has the potential to serve as a primary source of woody residue; the timber industry in Michigan produces an estimated 1.4 million dry tons of residue per year (Becker et al., 2009). Harvesting of woody residue could amplify the negative impacts some wildlife populations already experience as a result of timber harvest (Petranka et al., 1994; Harpole and Haas, 1999; Thompson et al., 2003; Semlitsch et al., 2009; Riffell et al., 2011; Otto et al., 2013a).

To promote sustainable forestry practices and mitigate the negative effects of clearcutting on some forest-dwelling wildlife, retention of harvested tree residues or woody biomass has been proposed (Franklin et al., 1997). Retention of woody biomass provides coarse woody debris that serves as refugia for some wildlife in harvested forests (reviewed by Riffell et al., 2011). Potential benefits provided by the retention of woody debris include forage and shelter sites for various species (Bunnell and Houde, 2010) and more stable microclimates (Franklin et al., 1997). The Michigan Department of Natural Resources (MDNR) recently developed guidelines for the retention of woody biomass during timber harvest (MDNR&E, 2010). However, quantitative evidence on the effectiveness of these guidelines for conserving wildlife is lacking.

Salamanders are important elements of terrestrial ecosystems (Burton and Likens, 1975) and can serve as indicators of ecosystem health (Welsh and Droege, 2001). Furthermore, terrestrial salamanders have been used as model organisms in past timber harvest studies and their negative responses to clearcutting have been documented (*e.g*., Petranka et al., 1993; Ash, 1997; deMaynadier and Hunter, 1998; Patrick, et al., 2006). These studies showed that salamander numbers decline rapidly following clearcutting, however the mechanisms of these observed declines are not fully understood. One potential mechanism is decreased survivorship resulting from habitat degradation and altered microclimate (Todd and Rothermel, 2006). The retention of appropriate amounts and types of woody debris can serve as immediate and future refuge sites (Bunnell and Houde, 2010), potentially improving survivorship.

Assuming that salamanders select habitat on a small scale, and that selection depends on the amounts, piece sizes, and decay class of woody debris (Bunnell and Houde, 2010; Otto, 2012; Thames 2013: Chapter 1), biomass harvesting could exacerbate the negative effects of timber harvest on localized terrestrial salamander populations (Otto et al., 2013a). However, evidence regarding appropriate retention amounts is lacking (Corn and Bury, 1991; Welsh and Lind, 1991; Butts and McComb, 2000; Bunnell and Houde, 2010; Otto et al., 2013a). While use of woody debris by salamanders varies geographically and by species, red-backed salamanders (*Plethodon cinereus*) in northern Michigan are known to rely on downed wood (Thames 2013: Chapter 1). Thames et al. (2013: Chapter 1) found that surface activity of *P. cinereus* populations was positively associated with piece counts of woody debris and that micro-site selection by individual salamanders was positively associated with size of the wood.

The objective of this project was to assess the effect of MDNR woody biomass retention guidelines on *P. cinereus* occupancy and abundance within recently clearcut forests. I hypothesized that occupancy and abundance would differ between control (no woody debris removal) and treatment sites (with woody debris removal). Furthermore, I predicted that occupancy and abundance estimates would positively associate with woody debris amount. Here I quantify the relationships between occupancy and abundance of a terrestrial salamander and woody debris amount to better inform biomass retention guidelines.

2.2. Methods

2.2.1. *Study Area*

This study was conducted in May and October 2012, on state-owned forest lands currently managed for aspen (*Populus* spp.) production in Wexford County, northern Lower Peninsula, Michigan. The study areas have well-drained, sandy soils characteristic of glacial outwash plains and moraines (Barnes and Wagner, 2004). Elevation in Wexford County ranges from 274-457 m with minimum and maximum temperatures averaging 1 to 12°C, respectively (NOAA, 2011). Average precipitation is 88 cm annually (NOAA, 2011). Dominant regenerating tree species in clearcuts was aspen, with overstory retention that included mixed oak (*Quercus* spp.), maple (*Acer* spp.), beech, (*Fagus* spp.), cherry (*Prunus* spp.), and white pine (*Pinus strobus*).

2.2.2. *Study Design*

I selected 3 aspen stands 1-5 years post-harvest. Here, a stand refers to an area of relatively homogenous overstory vegetation that was harvested at approximately the same time. Selected stands ranged in size from 8-12 hectares. Using 1-m resolution 2009 and 2010 NAIP (National Agriculture Imagery Program) imagery, I digitized cover of retained overstory trees in a Geographic Information System (GIS; ArcGIS, Environmental Systems Research Institute, Redlands, CA; Otto, 2012). I divided each stand into 60x60 m grid cells in GIS and assigned a cover category for green tree retention; 1-10% or other. I only sampled the 1-10% cover cells to avoid potentially confounding the effects of overstory shading on my results. Also, areas with low retention cover (i.e., most of the overstory trees were harvested) were assumed to have higher amounts of woody residue available after timber harvest (Visser and Sherman, 2007; Patrick et al., 2006).

2.2.3. *Data Collection*

I randomly selected 20 - 60x60 m cells with low (1-10%) overstory cover within the 3 stands. In each cell, I located and marked 3 - 3x3 m sites (n=60) that included a control (no downed wood removal), a high downed wood removal (~83% removed), and a moderate downed wood removal (~66% removed), consistent with MDNR biomass retention guidelines (MDNR&E, 2010). The center of each 60x60 m cell was located in the field using GPS coordinates obtained from GIS. From the center of each cell an observer walked north, east, and south until a 3x3m location with 11-45% downed wood ground cover was identified; slash piles were avoided. I used 11-45% downed wood cover as a sample target based on a prior assessment that found this range of downed wood cover to represent a typical amount of logging residue in aspen clearcuts administered by MDNR (Otto, 2012). All 3x3 m locations were demarcated with flagging and were ≥20 m from forest edges, roads, wetlands, and other sample sites. I used spatial separation between sampling sites (i.e. ≥ 20 m) to help account for the assumption of independence. *P. cinereus* exhibit relatively small home ranges (average 18 m^2; Petranka, 1998) and coupled with localized variability in the vegetation I sampled the independence assumption was likely met. Northerly sites served as controls, southern sites as high downed wood removal, and eastern sites as moderate downed wood removal. For increased accuracy of meeting downed wood proportions I gridded each 3x3 m site into 9-1x1 m cells and created a correctly scaled overhead sketch of downed wood cover. I used a dot matrix on these sketches to verify that the percent cover of downed wood was within the 11-45% range. Overhead photographs were also taken during leaf-off using a digital camera attached to a telescoping poll. The camera was lifted to a height of 5 meters directly above the center of the sample site. I used a dot matrix on the photographs to verify the accuracy of sketches for quantifying the proportions of downed wood at each site. Using the sketches of treatment sites and a random number table, I numbered and randomly selected individual downed wood pieces for removal.

Debris (downed wood, leaf, and vegetation litter) in the outer 1 m area surrounding each 3x3 m cell was removed via raking. Downed wood protruding from the 3x3 m site was cut and the outer portion removed. Clearing the 1 m area around each 3x3 m cell was conducted to reduce the likelihood of salamanders moving into or out of the treatment area during our 3-4 day sampling. Individual downed wood pieces that were marked for removal were removed from treatment sites in August of 2011. After wood was removed, overhead photographs were again collected to quantify the reduction in downed wood cover.

The second week in May and fourth week in October, 2012, cover object surveys (i.e., where an observer rolls or searches under all available cover objects) were completed at each sample site. I monitored daily temperature and precipitation prior to and during surveys in an attempt to maximize capture rates by conducting surveys during warm moist weather (Reichenbach and Sattler, 2007; Otto and Roloff, 2011). I surveyed each site twice, with 2-3 days separating each survey. Two observers were assigned to each site and each surveyed half of the site. On subsequent surveys, observers switched halves to minimize observer bias on detecting salamanders. Observers searched sites by rolling pieces of downed wood >6 cm diameter. I recorded piece count, length, and diameter for all downed wood within sites and subsequently replaced wood to its original position in the survey area.

Salamanders captured during surveys were categorized as juvenile (<30 mm) or adult (≥30 mm) and morphometric data were collected (snout-vent length, total length, color phase, gravidity). Captured salamanders were held in moistened plastic bags in a cooler until the entire site had been surveyed. Once sampling at a site was completed salamanders were returned to the point of capture. All animal handling was done in compliance with Michigan State University's Institutional Animal Care and Use Committee (IACUC) procedures and guidelines (IACUC #03/12-057-00). All applicable state permits were obtained.

2.2.4. *Statistical Analysis*

I used Pearson correlation between cover estimates for sketches and photographs to confirm that sketches were a reasonable approximation of downed wood amounts. Box plots of downed wood ground cover pre- and post-treatment were used to confirm that the treatment had the intended effect on downed wood cover. I assumed that sites within a season (May and October) were closed to changes in occupancy during the surveys (MacKenzie et al., 2002). Research suggests that the closure assumption is valid for cover object surveys if the interval between sample events within a season is short (2-3 days in our study; Otto et al., 2013b). Multiple surveys within a season allowed inclusion of detection probabilities into occupancy and abundance estimates; I assumed that these probabilities were <1 because *P. cinereus* are known to use leaf litter and subterranean retreat to avoid inclement surface conditions (Petranka, 1998; Otto and Roloff, 2011).

I used single season occupancy models to quantify occupancy probability (MacKenzie et al., 2002). Single season models are suited for analyses where occupancy status in one season is not conditional on occupancy status in subsequent seasons and when the processes underlying occupancy status (i.e., extinction and colonization) are implied but not quantified (MacKenzie et al., 2002). Here, seasons corresponded to the May and October salamander surveys. I conducted occupancy analyses using program PRESENCE (vers. 5.8; J. E. Hines, Patuxent Wildlife Research Center, Laurel, MD). Site variables in the candidate models included treatment type, downed wood piece count, and downed wood dimensions (diameter and length; Table 1). Correlated variables were not included in the same candidate model. I used Akaike Information Criterion to rank and weight candidate models (Burnham and Anderson, 2002) and model averaging to estimate site-level occupancy (MacKenzie et al., 2006). I assessed model fit using 1000 parametric bootstrap iterations and the resulting goodness-of-fit statistic in program Presence.

I estimated salamander abundance at each site for each season using N-mixture models (Royle, 2004). Treatment type and downed wood variables were included as covariates in candidate models. I conducted the analysis using the pcount function in program R version 2.15.3 (RDCT, 2008), package unmarked. I assumed constant detection probability. Correlated variables were not included in the same candidate models. Akaike Information Criterion was used to rank and weight the candidate models (Burnham and Anderson, 2002).

2.3. Results

I captured 37 salamanders during the study, 25 and 12 in May and October, respectively. All but 4 captures were *P. cinereus* with other species observed including spotted salamander (*Ambystoma maculatum*) and 4-toed salamander (*Hemidactylium scutatum*). All non-*P. cinereus* observations were made during the May sampling periods. Three of the 33 *P. cinereus* captures were classified as juveniles.

Cover of downed wood estimated from sketches was correlated with photo estimates both before ($r = 0.76$, $P < 0.01$) and after ($r = 0.92$, $P < 0.01$) treatments, indicating that sketches were a reasonable approximation of surface-visible downed wood. The goal of 11-45% downed wood ground cover prior to wood removals was confirmed; the majority of sites had pre-treatment downed wood cover ranging between 20-30% (Figure 2.1.). After treatment, mean downed wood cover of control, moderate, and high removal sites was 23%, 8%, and 4%, respectively (Figure 2.1.). Site downed wood piece count ranged from 2-38 with a mean diameter of 16 cm and mean length 0.84 m (Table 2.1.); residual downed wood was generally small in diameter and short. Wood count was correlated with wood diameter and the change in downed wood cover resulting from treatment ($P<0.10$). Wood diameter was correlated with length ($P<0.10$). Only univariate occupancy models converged for May (Table 2.2.).

Depending on the model formulation, detection probability for *P. cinereus* ranged from 0.23-0.33 and 0.15-0.24 in May and October, respectively. The top-ranked occupancy model for May (77% weight) included the treatment factor; no competing models (i.e., Δ AIC < 2.0) were identified, however weight of evidence >0.01 existed for 3 additional models (Table 2.2.). Site-level occupancy estimates from model averaging in May were higher for controls (0.94) than for moderate (0.27) or high (0.24) treatments (Figure 2.2.).

The top ranked occupancy model for October (23% weight) included wood diameter, however multiple competing models (i.e., Δ AIC < 2.0) were identified (Table 2.3.). Additionally, weight of evidence >0.01 existed for all candidate models (Table 2.3.). Site-level occupancy estimates from model averaging in October were higher for controls (0.63) than for moderate (0.39) or high (0.26) treatments (Figure 2.3.). Occupancy models for May exhibited poor fit (chi square test, $P<0.01$) whereas the October models fit better ($P>0.07$). The results suggest strong AIC support for a treatment effect on spring and fall occupancy estimates for *P. cinereus* but I caution that models exhibited characteristics of poor fit.

Detection probabilities for abundance modeling were low (<0.03) in both seasons however the candidate models successfully converged. There was strong evidence in support of a single top-ranking model during both seasons. In May, the top ranked model (91% weight) included wood diameter and the treatment factor; no competing models were identified (Table 2.4.). Average site-level abundance in controls was 4.1 and 3.1 times higher than in moderate and high treatments, respectively (Figure 2.4.). On average, home ranges for 24 detectable *P. cinereus* overlapped our control sites, whereas <8 home ranges overlapped our treated sites (Figure 2.4.).

The top-ranked abundance model in October (71% weight) included diameter and an absolute measure of percent change in wood cover; no other competing models were identified (Table 2.5.). Average abundance in controls was 3.0 and 4.4 times higher than in moderate and high treatment sites, respectively (Figure 2.5.). On average, approximatley 16 detectable *P. cinereus* home ranges overlapped our controls in October, whereas <6 overlapped our treatments (Figure 2.5.).

2.4. Conclusion

My results demonstrated that *P. cinereus* populations are sensitive to woody biomass removals. On average, *P. cinereus* occupancy probability was >1.6 times lower at wood removal sites, regardless of season; abundances were >3.0 times lower. Even though all sites had retained downed wood following treatment, my hypothesis that occupancy and abundance would differ between control and treatment sites was verified. Given the downed wood covariates I sampled, support for wood count (or proxies for wood count) and log diameter were identified in all top-ranking models; length was not important. These results are consistent with Thames (2013; Chapter 1) who found that wood count and diameter influenced surface activity and small-scale habitat selection for marked *P. cinereus* in the same study system but at different survey sites. I found that both biomass treatment levels (i.e., 66% and 83% wood removal) had comparable negative effects on *P. cinereus* populations. Within the range of logging residue sampled (i.e., 11-45% cover pre-treatment), my findings indicate that more (i.e., >34%) of the residual downed wood should be retained to mitigate the negative effects of biomass removal on localized *P. cinereus* populations.

Although I saw declines in occupancy and abundance for woody removal sites, the mechanism(s) causing these declines is not well understood (*e.g.*, Petranka et al., 1993; Ash, 1997; Homyack and Hass, 2009). A combination of the main hypotheses (mortality, retreat, and evacuation) as summarized by Semlitsch et al. (2008), are most likely associated with apparent salamander population declines following timber harvest. The causal factor(s) to these hypotheses likely relates to the loss of important habitat elements such as leaf litter and downed wood, which provide necessary microclimate, food, and shelter (Petranka et al., 1993; Ash, 1997; deMaynadier and Hunter, 1998; Moorman et al., 2011; Peterman et al., 2011). Consistent with other studies that found close relationships between salamander populations and downed wood (e.g., Heatwole, 1962; Patrick et al., 2006; Bunnell and Houde, 2010; Thames 2013: Chapter 1), my results indicate that wood characteristics (e.g., amount, size) affect how that wood functions as habitat. Downed wood following timber harvest is generally small (e.g., this study; Rittenhouse et al., 2012) and thus retention recommendations often focus on providing larger pieces (e.g., Thames 2013: Chapter 1). Consideration also should take into account decay rates as McKenney et al. (2006) found that density of well-decayed wood was a stronger predictor of *P. cinereus* abundance than downed wood amount alone. Thames (2013: Chapter 1) similarly found some evidence in support of decay class as an important downed wood characteristic.

Data on species occupancy alone may misinform management because presence of a species is not always correlated with habitat quality (Yoccoz et al., 2001; Cushman, 2006; Welsh et al., 2008). Stronger inference is provided if multiple metrics of population performance exhibit similar trends to habitat modification. I found consistent negative responses in *P. cinereus* occupancy and abundance to woody removals, suggesting that the treatment effect was consistent across study sites and levels of wood removal. These findings, collectively with other results on occupancy (Otto and Roloff, 2011; Otto, 2012), abundance (Petranka et al., 1994; deMaynadier and Hunter, 1998; Morneault et al., 2004; McKenny et al., 2006), and apparent survival (Otto et al., 2013a), substantiate the importance of downed wood to population demographics of *P. cinereus*.

Although I purposefully designed this experiment to isolate the effects of wood removal, I caution that my results apply to localized areas within harvested stands. As amphibians generally display a patchy spatial distribution linked to microhabitat (Heyer et al., 1994), I previously recommended leaving patches (25 m^2) of downed wood throughout harvest units (Thames, 2013: Chapter 1). Commercial woody biomass harvests will likely be integrated directly into normal timber harvest operations at the stand-level (Benjamin et al., 2010), and given current harvesting and processing efficiencies resultant stands can be homogenously devoid of downed wood. I contend that small-scale management provisions can benefit wildlife through retention practices and that these practices be explicitly integrated into timber harvesting contracts. Predictions made on the effects of biomass harvests on wildlife will be tentative until we better understand how operational harvests actually change downed wood availability over long time periods and larger scales (Riffell et al., 2011; Otto et al., 2013a).

My study is the first to quantitatively assess the impacts of woody biomass retention guidelines (MDNR&E, 2010) on terrestrial salamanders. My results potentially apply to other forest floor-dwelling wildlife that depends on downed wood (Semlitsch et al., 2009; Bunnell and Houde, 2010; Moorman et al., 2011; Riffell et al., 2011) as *P. cinereus* is often recognized as a useful indicator species (Welsh and Droege, 2001). The retention of appropriate amounts of downed wood that can serve as refuge sites for terrestrial salamanders following timber and biomass harvests will be conditional on management objectives. If conservation of forest floor-dwelling wildlife is an important management outcome, my results suggest that quantity, size, and likely spatial arrangement of downed wood are important. Although additional biomass harvesting may amplify the negative impacts terrestrial salamander populations are having in response to harvest of overstory trees, retention of >34% of the residual downed wood, coupled with preference for larger piece sizes (i.e., >20cm diameter; Thames 2013: Chapter 1) can provide benefits towards conservation of *P. cinereus* populations.

2.5. Acknowledgements

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APPENDIX

APPENDIX

Occupancy and Abundance Modeling

Table 2.1.

Site level covariates, post-treatment, used in candidate models for evaluating the response of *P. cinereus* to downed wood removals in recently clearcut aspen forests of the northern Lower Peninsula of Michigan, 2012.

Downed Wood Variable	Mean (SE)	Range	Definition
Wood Count	10 (0.8)	2-38	Tally of wood pieces >6 cm diameter.
Diameter (cm)	16.2 (0.3)	6.1 – 65.5	Diameter at the largest end of each wood piece.
Length (m)	0.84 (0.09)	0.10 – 8.30	Length of wood piece.
Wood Change (%)	12 (1)	0-30	Change in percent cover after wood removal treatment.
Treated			Binary variable denoting whether the site was treated or not.

Table 2.2.

Ranking of candidate models for *P. cinereus* occupancy probability based on downed wood attributes, treatment, and change in wood cover resulting from downed wood removals in recent aspen clearcuts in the northern Lower Peninsula of Michigan, May 2012.

Candidate Model	AIC[a]	ΔAIC	AIC_{wt}	k	-2l
psi(Treated),p(.)[b]	89.66	0.00	0.77	3	83.66
psi(Diameter),p(.)	92.97	3.31	0.15	3	86.97
psi(Wood Change),p(.)	95.44	5.78	0.04	3	89.44
psi(Wood Count),p(.)	96.10	6.44	0.03	3	90.10
psi(.),p(.)	101.28	11.62	<0.01	2	97.28
psi(Length),p(.)	101.74	12.08	<0.01	3	95.74

[a]Lowest AIC value = top ranked model, ΔAIC=difference from best model, AIC_{wt} = weight of evidence in support of model, k = number of parameters, -2l = 2 times the negative log likelihood.

[b]Psi= occupancy, p(.)= constant detection probability.

Table 2.3.

Ranking of candidate models for *P. cinereus* occupancy probability based on downed wood attributes, treatment, and change in wood cover resulting from downed wood removals in recent aspen clearcuts in the northern Lower Peninsula of Michigan, October 2012.

Candidate Models	AIC[a]	ΔAIC	AIC_{wt}	k	-2l
psi(Diameter),p(.)[b]	63.65	0.00	0.2258	3	57.65
psi(Diameter + Treated),p(.)	64.31	0.66	0.1623	4	56.31
psi(Diameter + Wood Change),p(.)	64.57	0.92	0.1426	4	56.57
psi(Wood Change),p(.)	64.80	1.15	0.1271	3	58.80
psi(Diameter + WoodChange + (Diameter * Wood Change),p(.)	65.07	1.42	0.1110	5	55.07
psi(Treated),p(.)	65.54	1.89	0.0878	3	59.54
psi(Length),p(.)	65.71	2.06	0.0806	3	59.71
psi(.),p(.)	66.85	3.20	0.0456	2	62.85
psi(Wood Count),p(.)	68.80	5.15	0.0172	3	62.80

[a]Lowest AIC value = top ranked model, ΔAIC = difference from best model, AIC_{wt} = weight of evidence in support of model, k = number of parameters, -2l = 2 times the negative log likelihood.

[b]Psi= occupancy, p(.)= constant detection probability.

Table 2.4.

Ranking of candidate models for *P. cinereus* abundance models based on downed wood attributes, treatment, and change in wood cover resulting from downed wood removal in recent aspen clearcuts in the northern Lower Peninsula of Michigan, May 2012.

Candidate Model	AICc[a]	Δ AIC	AIC_{wt}	ML	k
r(Diameter + Treated), p(.)[b]	121.246	0.00	0.91	-56.25	4
r(Diameter + Wood Change), p(.)	126.312	5.06	0.07	-58.79	4
r(Diameter), p(.)	130.170	8.92	0.01	-61.87	3
r(Treated), p(.)	132.537	11.29	0.00	-63.05	3
r(Wood Change), p(.)	136.649	15.40	0.00	-65.11	3
r(Length), p(.)	138.312	17.06	0.00	-65.94	3
r(Wood Count), p(.)	140.778	19.53	0.00	-67.17	3
r(,), p(.)	140.880	19.63	0.00	-68.33	2

[a]AICc=takes sample size into account, ΔAIC=difference from best model, AIC_{wt}=weight of evidence in support of model, ML= maximum model likelihood, k= number of parameters.

[b]r=abundance, p(.)=constant detection probability.

Table 2.5.

Ranking of candidate models for *P. cinereus* abundance models based on downed wood attributes, treatment, and change in wood cover resulting from downed wood removal in recent aspen clearcuts in the northern Lower Peninsula of Michigan, October 2012.

Candidate Model	AICc[a]	ΔAIC	AIC_{wt}	ML	k
r(Diameter + Negative Wood Change), p(.)[b]	78.673	0.00	0.71	-34.97	4
r(Diameter), p(.)	82.936	4.26	0.09	-38.25	3
r(Negative Wood Change), p(.)	82.989	4.31	0.08	-38.28	3
r(Diameter + Treated), p(.)	83.109	4.43	0.07	-37.19	4
r(,), p(.)	86.584	7.91	0.01	-41.18	2
r(Treated), p(.)	86.814	8.14	0.01	-40.19	3
r(Length), p(.)	87.614	8.94	0.00	-40.59	3
r(Wood Count), p(.)	88.076	9.40	0.00	-40.82	3

[a]AICc=takes sample size into account, ΔAIC=difference from best model, AIC_{wt}=weight of evidence in support of model, ML= maximum model likelihood, k= number of parameters.

[b]r=abundance, p(.)=constant detection probability.

Figure 2.1

Site-level downed wood cover (%), by treatment, pre and post wood removal in aspen clearcuts, northern Lower Peninsula, Michigan. Removals were completed in autumn of 2011 prior to site sampling in spring of 2012. High treatment sites received 83% wood removal; moderate treatment sites received 66% wood removal.

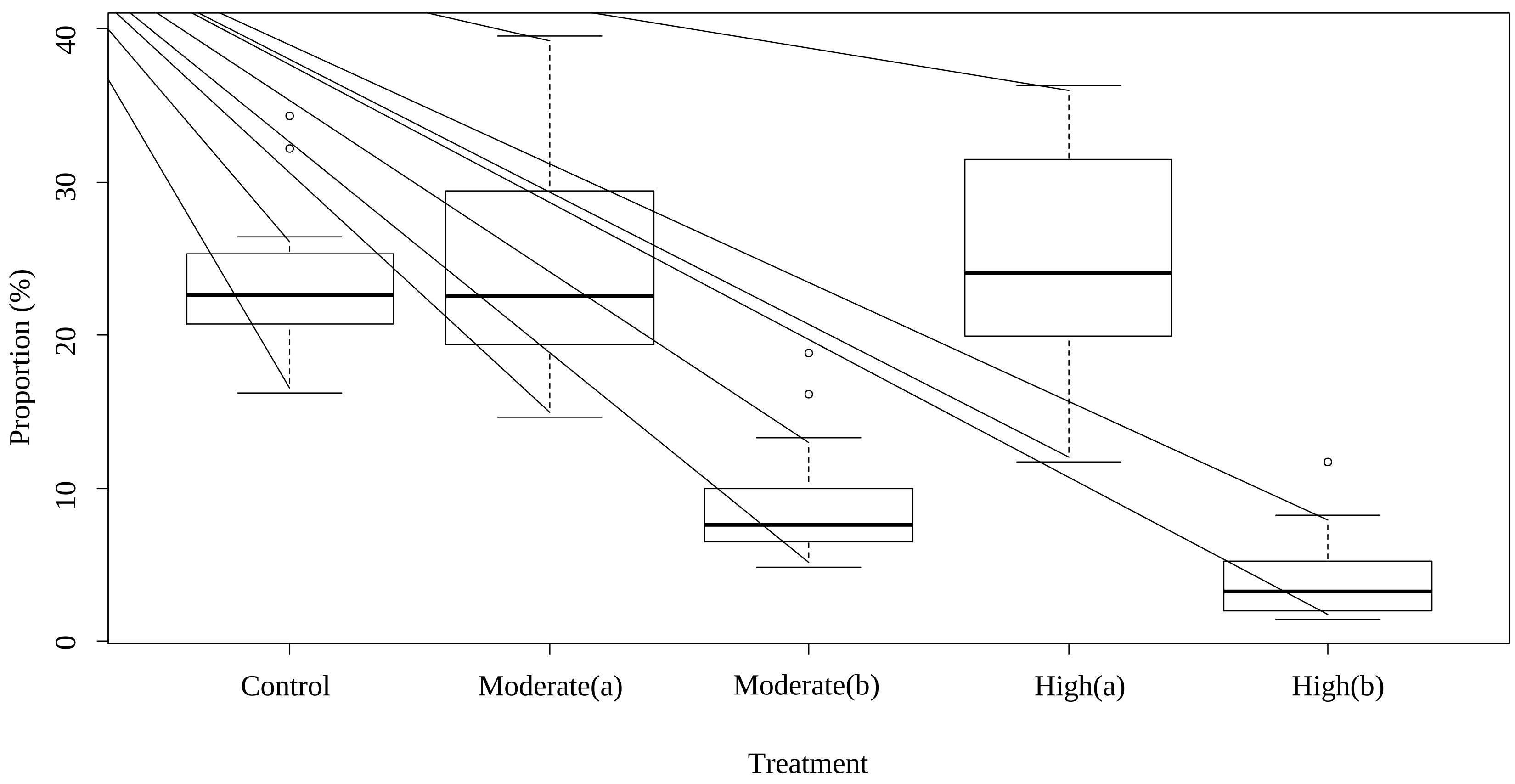


Figure 2.1. (cont'd)

[a]Proportion of site covered by downed wood pre-removal.

[b]Proportion of site covered by downed wood post-removal.

Figure 2.2.

Estimated occupancy probability by wood removal treatment for *P. cinereus* in northern Lower Peninsula, Michigan, May 2012.

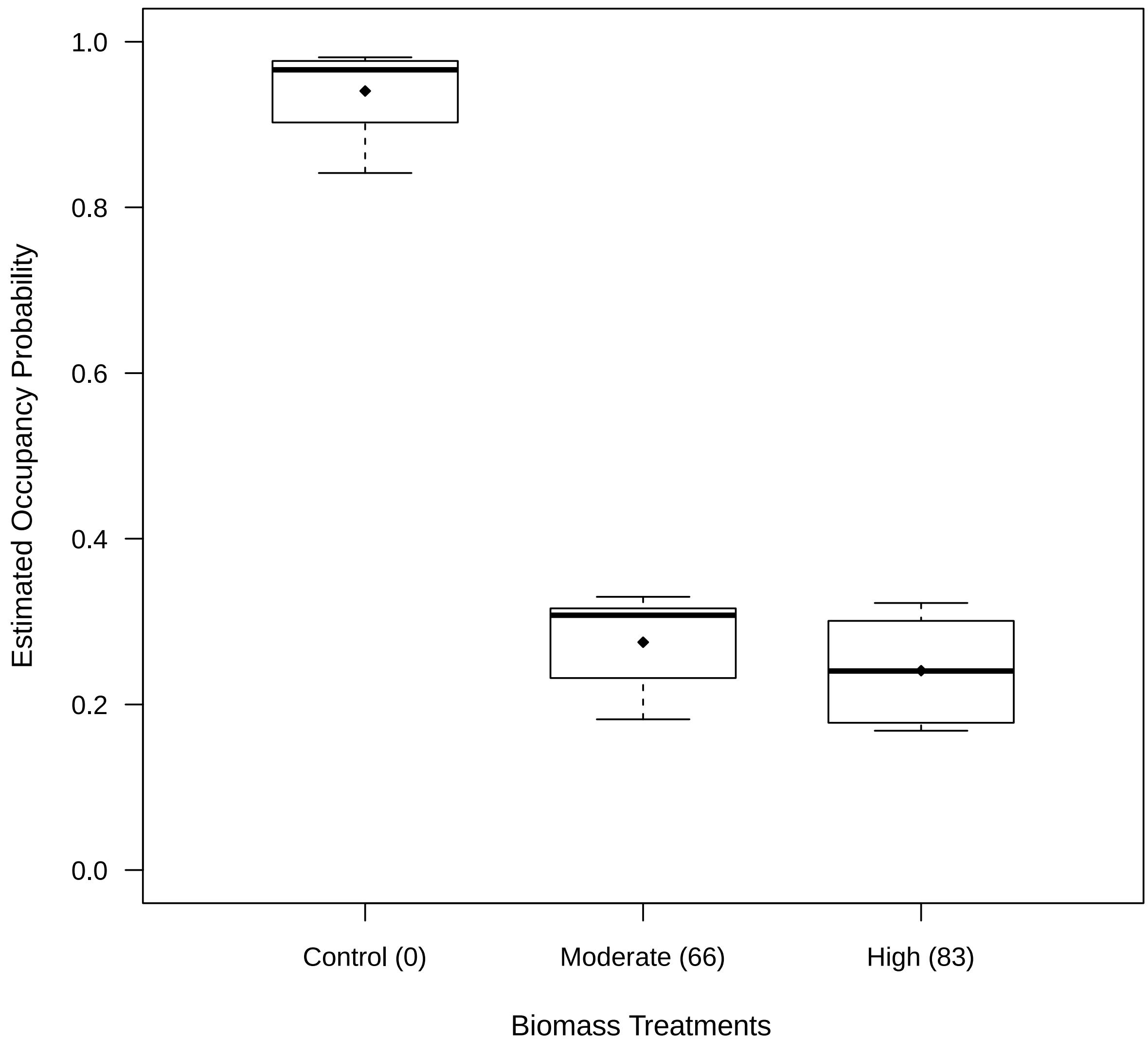


Figure 2.3.

Estimated occupancy probability by wood removal treatment for *P. cinereus* in northern Lower Peninsula, Michigan, October 2012.

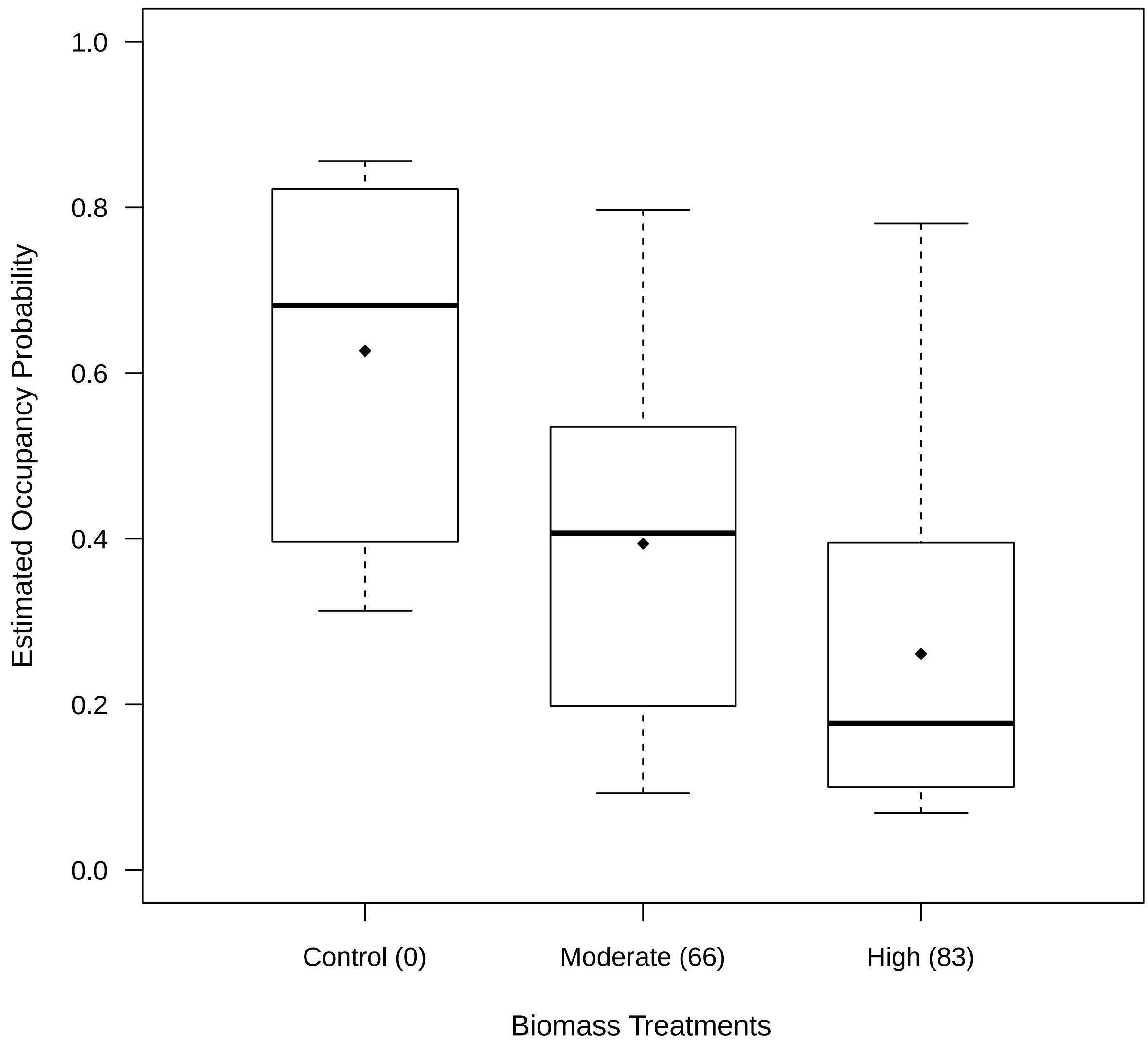


Figure 2.4.

Site level abundance estimates by wood removal treatment for *P. cinereus* in northern Lower Peninsula, Michigan, May 2012.

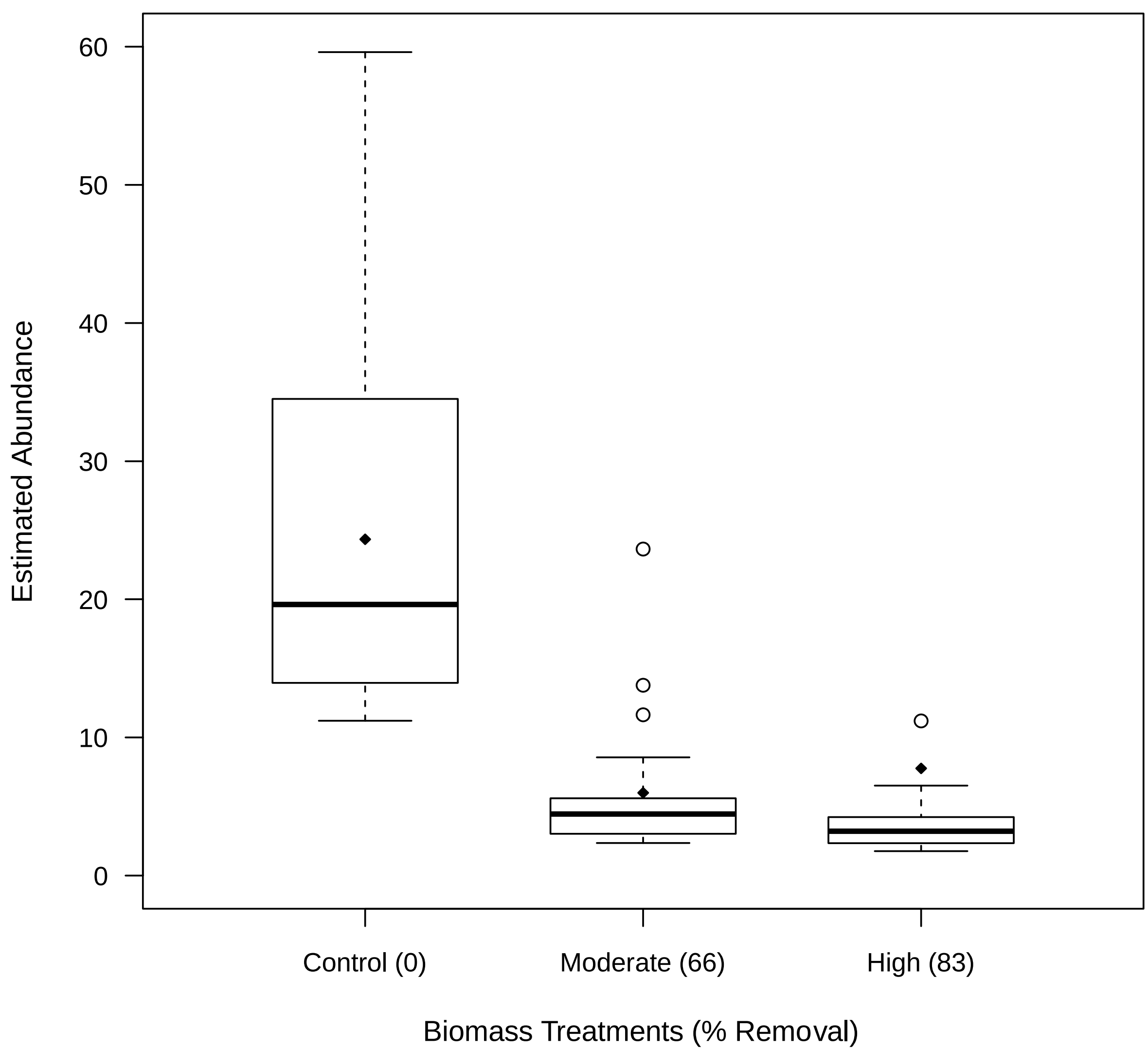
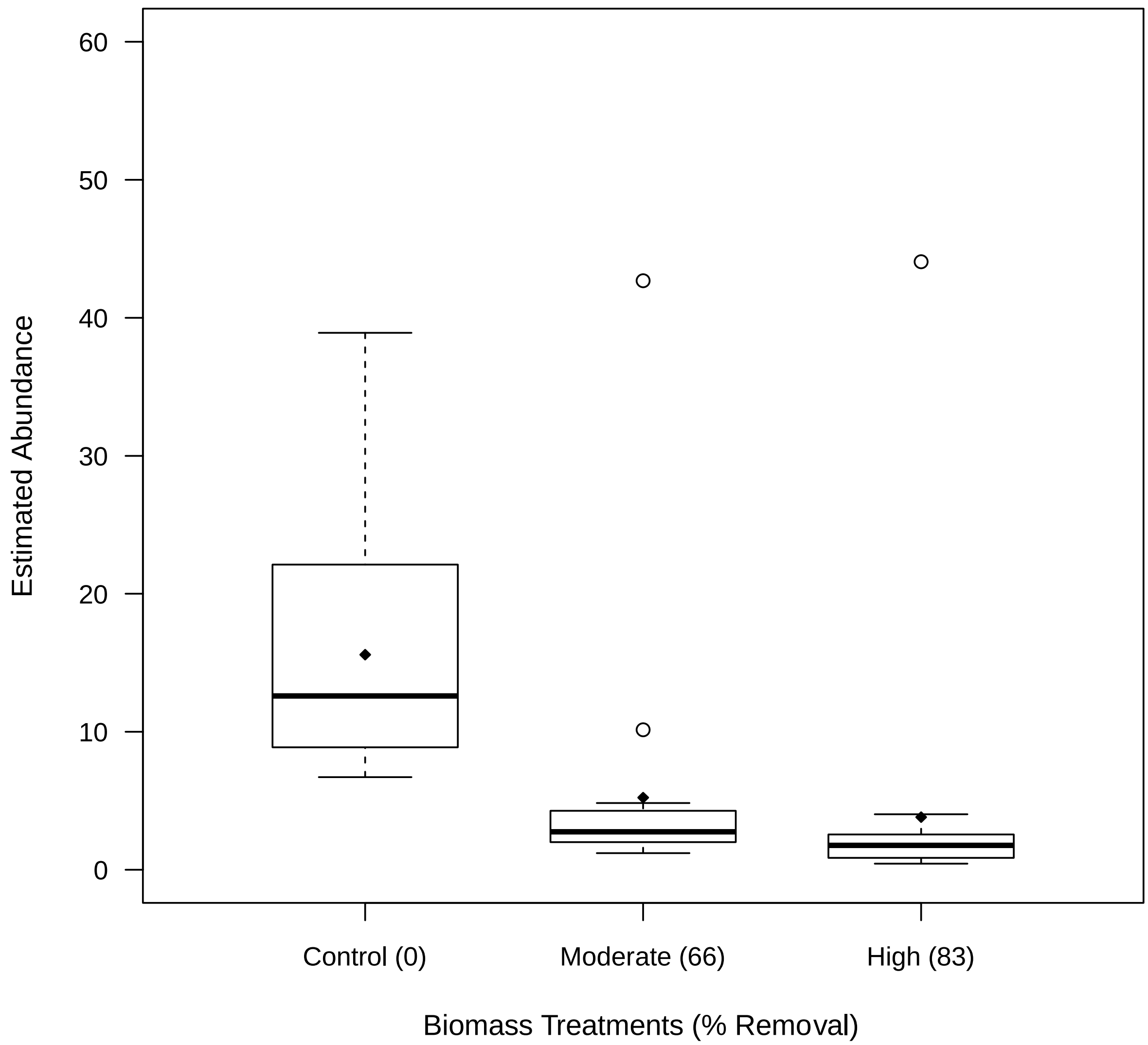


Figure 2.5.

Site level abundance estimates by wood removal treatment for *P. cinereus* in northern Lower Peninsula, Michigan, October 2012.



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CONCLUSIONS

The theme of my thesis was how woody biomass harvest may affect a prevalent terrestrial salamander species (*P. cinereus*). My work was an extension of broader work conducted by the MDNR to better understand how retaining habitat elements in clearcut aspen forests helps to conserve wildlife. I specifically focused my work on the effects of the MDNR's woody biomass retention guidelines on *P. cinereus* to provide practical guidelines for managing downed wood in clearcut areas. Strengths of my work include: 1) combination of manipulative and correlative experimental designs that result in stronger inference, 2) assessments at different levels of biological organization (i.e., a population of *P. cinereus* and individual animals), and 3) a direct link to forest management activities as implemented by the MDNR. Limitations of my study include: 1) relatively small spatial scale (9 m^2) compared to the scale of timber management activities, 2) short duration (2 years in Chapter 1; 1 year with 2 seasons in Chapter 2), and 3) the inability to identify a causal mechanism for the observed responses by *P. cinereus*. Future research should include recommendations made by Otto et al. (2013) such as how biomass removal will impact salamander demography and dispersal, and what long-term effects may occur from continuous harvest rotations changing the availability of downed wood. Research is also needed on: 1) how salamanders use different levels of decay related to various seasons and life cycles, 2) how prey populations have changed in harvest areas versus mature forests, and 3) when habitat selection changes between leaf litter and downed wood occur, related to how prey populations temporally change.

In Chapter 1, I used linear and logistic regression modeling to evaluate differences in *P. cinereus* habitat selection based on downed wood and other environmental characteristics at the population and individual levels. My findings confirm that downed wood functions as refugia for terrestrial salamanders in clearcut environments. I found that surface activity of the *P. cinereus* population was positively related to the amount of downed wood in a clearcut area and that individual *P. cinereus* selected micro-sites based on size of the wood that was retained. My results suggest that downed wood functions differently depending on the level of biological organization; a concept consistent with theories on hierarchical habitat selection by wildlife (Johnson et al., 1980). My findings also have implications for future research on the effects of forest management on terrestrial salamanders. Specifically, for studies measuring a population-level parameter (i.e. abundance) over a larger area the amount of downed wood should be accounted for. For studies measuring individual habitat selection at the micro-site scale, studies should account for size of downed wood. Without controlling for downed wood characteristics in studies on terrestrial salamander response to timber harvest, the effects of wood characteristics are likely confounded with effects of canopy removal. Through incorporating knowledge of downed wood characteristics into the scale of the experimental design and response variable(s), results of future studies will be more likely to identify cause and effect and limit bias.

In Chapter 2, I used occupancy and abundance modeling to assess MDNR woody biomass retention guidelines. My findings illustrated that regardless of season, occupancy and abundance declined as a result of wood removals, even though some wood was retained on each treated site. Similar to Chapter 1 findings in regards to habitat selection, wood count and diameter were found to be influential determinants of *P. cinereus* occupancy and abundance within sites. Based on my findings and given that each of my study sites had 11-45% cover of downed wood prior to treatment, I proposed that retention of >34% of existing downed wood, coupled with 6-12 pieces >20 cm diameter in 25 m^2 patches, would help ameliorate the negative effects of biomass removal on an already disturbed population. However, I cautioned that my small-scale results should not be extrapolated to more than a localized *P. cinereus* population.

Making predictions on the effects of biomass harvests on wildlife is still uncertain until more is known about how operational harvests actually change downed wood availability over long time periods and larger scales (Riffell et al., 2011). I contend that adjusting habitat retention practices based on monitoring data is needed, particularly as forest management objectives change in response to shifting environmental and societal demands. This research, coupled with past studies on retention of habitat elements as part of timber harvest, underscores the importance of evidence-based research on the effectiveness and implications of management actions on conserving species.

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