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Effects of experimental forestry treatments on a Maine amphibian community

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Abstract

Predicting how timber harvesting will influence sensitive taxa such as amphibians is of critical importance for sustainable management of forests. In 2004 and 2005, we studied the effects of four forestry treatments (clearcut with coarse woody debris [CWD] removed, clearcut with CWD retained, partial-cut of 50% of canopy cover, and an uncut control) on movement, habitat selection, and abundance of amphibians in Maine. Four landscape-scale replicates of these four forestry treatments were created with each replicate centered on a breeding pool. A total of 8632 emerging juvenile wood frogs were captured and marked at drift fences encircling breeding pools, with 1166 marked wood frogs (*Rana sylvatica*), and 13,727 unmarked amphibians captured in drift fence/pitfall arrays at 16, 50, 100, and 150 m from the pools. Our capture results in the different treatments were consistent with previous studies in showing that adult abundance and habitat use differed among species, with wood frogs, spotted salamanders (*Ambystoma maculatum*), and eastern red-backed salamanders (*Plethodon cinereus*) preferring uncut and partial-cut habitat, and adult green frogs (*Rana clamitans*) and American bullfrogs (*Rana catesbeiana*) being more tolerant of clearcutting. Spotted salamanders also showed reduced captures with partial canopy removal and increased captures with the retention of CWD. Our results for juvenile amphibians differed from previous research, with lower captures of all study species (statistically significant for seven of nine species) in clearcuts compared to uncut and partial-cut treatments. Clearcuts did not reduce habitat permeability for the low number of marked wood frogs that entered these treatments. Data from marked wood frogs also suggest that both density of conspecifics and habitat quality can influence habitat selection, and potentially dispersal of juvenile amphibians. The avoidance of clearcuts by juveniles of all study species suggests that this silvicultural technique may reduce both abundance and dispersal of many species, rather than just species where adults are known to be forest-dependent. Species may also be affected by partial as well as full canopy removal, and the retention of CWD may play a role in mitigating some of the effects of clearcutting.
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1. Introduction

When considering biodiversity in forest management planning it is crucial to understand how habitat changes will affect the distribution and abundance of species. Amphibians form a large part of the vertebrate biomass in forested ecosystems in north-eastern North America and play an important role in ecosystem processes (Burton and Likens, 1975a,b; Wyman, 1998). Furthermore there is a great deal of debate as to how forest management influences amphibians because of uncertainty in how severely practices such as clearcutting affect populations, and how long such effects may last following harvesting (Petranka et al., 1993, 1994; Petranka, 1994; Ash, 1997; Chazal and Niewiarowski, 1998; Harper and Guynn, 1999; Ford et al., 2002; Ash et al., 2003). There is also uncertainty as to the relative effects of different management practices on amphibians, for example the frequency and intensity of harvesting efforts (Bennett et al., 1980; Aubry, 2000; Bartman et al., 2001; Ryan et al., 2002) and the retention of biological legacies such as leaf litter and coarse woody debris (CWD) (Aubry, 2000; Moseley et al., 2004; Strojny, 2004).

Predicting the effects of habitat change on amphibian populations is complicated by the bi-phasic life history of most species. This makes them especially prone to changes in population dynamics caused by habitat alteration (Wilbur, 1980; Semlitsch, 1998). Previous amphibian population research has tended to focus on aquatic breeding habitat rather

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than the terrestrial environment used during the non-breeding season (Trenham and Shaffer, 2005; although see deMaynadier and Hunter, 1995; Regosin et al., 2003). Even within the terrestrial environment, habitat change may differentially affect each life-history stage. For example, juvenile amphibians have been shown to be the primary dispersing stage for many species, with adults often showing high philopatry (Vasconcelos and Calhoun, 2004; Berven and Grudzien, 1990). Because of this, changes in juvenile life history traits due to habitat alteration can have repercussions in terms of metapopulation dynamics (Green, 2003).

To understand and predict how alteration in forested habitat quality will affect amphibian community dynamics, we used a replicated experimental design with forestry treatments large enough to incorporate population processes (e.g., dispersal) that occur over a wide spatial scale, i.e., a landscape scale in terms of amphibian ecology. By blocking different treatments within the same location, we were able to account for temporal and spatial variation. Our experimental design allowed direct comparison of changes in abundance and habitat use by amphibians among treatments, and also allowed us to link movement and habitat selection paradigms, a critical step in understanding population dynamics in changing environments (Armstrong, 2005).

Our research had two foci. First, mark-recapture of emerging juvenile wood frogs was used to examine how differences in terrestrial habitat quality affect movement and habitat selection during dispersal, and the abundance of individuals in the different treatments during and following this period. Second, we looked at how the different forestry treatments influenced the use of habitat by most members of the amphibian community in the study area. This included examining potential differences in temporal patterns of use throughout the study period.

2. Study site and methods

2.1. Study area and experimental design

This study was conducted in the Dwight B. Demeritt and Penobscot experimental forests, Orono, Maine, as part of the Land-use Effects on Amphibian Populations project (LEAP) underway at the University of Maine, the University of Missouri-Columbia, and the University of Georgia, USA. We created four replicates of four forestry treatments with each replicate centered around a breeding pool approximately 10 m in diameter (Fig. 1). Treatments extended 164 m in radius from the pond, giving a total area of 2.11 ha for each treatment per site. The four treatments were a clearcut with coarse woody debris (CWD) >10 cm in diameter removed, a clearcut with CWD retained, a partial cut where the canopy was reduced by 50%, and an uncut control. All merchantable timber was removed from harvested treatments using a cable skidder. Harvesting was conducted between November 2003 and April 2004. Treatments were randomly assigned, with the caveat that the clearcut treatments were opposite one another. Breeding pools were constructed from naturally occurring forested wetlands in 2003 with the goal being to create the vernal breeding sites used by our focal study species, wood frogs and spotted salamander. Initially, three of our four sites were areas where less than 6 in. of surface water remained for 1–2 months following spring snow-melt, but no amphibians bred. The other site was a natural vernal pool where small numbers of wood frog and spotted salamander bred (<10 egg masses). Following deepening with a backhoe, the pools averaged 25–40 cm in depth and 10 m in diameter. A pond liner was also used at one site to extend the hydroperiod long enough for successful amphibian reproduction. Soils in the study area are a mosaic of glaciomarine hydric soils, with well-drained till soils in upland areas (Natural Resources Conservation Service, 1962).

Before the establishment of experimental treatments, forests in the study areas were mixed coniferous and deciduous stands, with the dominant tree species being balsam fir (*Abies balsamea*), eastern white pine (*Pinus strobes*), northern white cedar (*Thuja occidentalis*), red maple (*Acer rubrum*), eastern hemlock (*Tsuga canadensis*), red oak (*Quercus rubra*), and paper birch (*Betula papyrifera*). Understory tree species included American beech (*Fagus grandifolia*), bigtooth aspen (*Populus grandidenta*), quaking aspen (*P. tremuloides*), and balsam poplar (*P. balsamifera*). Stands were predominantly even-aged, with some stratified mixed stands (no more than

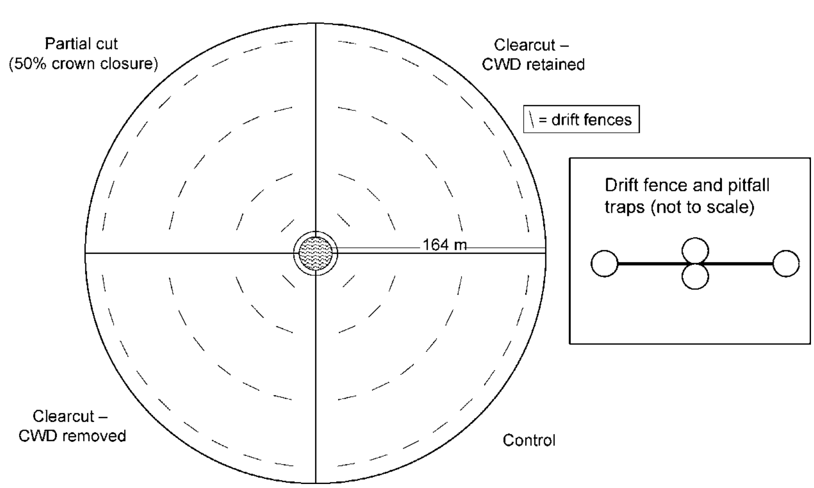

Fig. 1. Outline of the LEAP experimental array, showing locations of drift fences. The inset shows the design of each drift fence.

three age classes). Sites had a simple stand history, with two sites on regenerating agricultural lands (cleared at least 80–100 years prior to the study), and two sites in areas harvested at least 60 years prior to our study. Of the four sites, three were located in forested lowland areas, with the last being in an upland area. Sites were selected such that the vegetation was as homogeneous as feasible before the establishment of experimental treatments. None of the sites contained any additional natural breeding locations for the focal amphibian species during the duration of our study, although construction of experimental arrays did result in several depressions where egg masses were laid by wood frogs and spotted salamanders. These egg masses were removed. The nearest breeding ponds outside of the arrays were at least 50 m from the outer treatment edge.

At each pool, we used 1 m tall silt fencing to make a complete encircling drift fence approximately 1 m from the water's edge. Pitfall traps were placed at 5 m intervals on both the inside and outside of each fence. Drift fences/pitfalls were also constructed at 50, 100, and 150 m from the pool's edge (Fig. 1). In each treatment, there were 3 fences at 50 m, 6 at 100 m, and 9 at 150 m, with a total of 18 fences per treatment, and 72 per site. This allowed the same proportion (38%) of the circumference at each distance to be sampled. We constructed an additional drift fence in each treatment at 16.6 m from the pool in 2005 to allow an examination of short-distance dispersal.

Each drift fence consisted of four pitfalls and 10 m of silt fencing buried approximately 30 cm in the ground. Two number-10 aluminum cans were taped together to form each pitfall trap, with a plastic container used to make a 10 cm deep entrance funnel around the trap. A single pitfall trap was placed at the end of each fence, plus one on each side at the center of the fence. Trapping was conducted for 2 years following forest harvesting, from July 1 to October 27 in 2004, and June 24 to September 17 in 2005. The four sites were split into pairs of sites, with one pair being checked approximately every other day. During sampling, we removed water from traps using a hand bilge pump to reduce amphibian mortality.

2.2. Study species

Our study focused on nine species of amphibians commonly found in Maine forests: wood frogs, green frogs, American bullfrogs, northern leopard frogs (*Rana pipens*), pickerel frogs (*Rana palustris*), spotted salamanders, blue-spotted salamanders (*Ambystoma laterale*), red-spotted newt (*Notophthalmus viridescens viridescens*), and eastern red-backed salamanders. These species cover a diversity of life-history strategies allowing evaluation of how such differences may influence the effects of forest management on amphibians (summarized in Table 1).

2.3. Data collection

2.3.1. Amphibians

In 2004, wood frog metamorphs emerging from the focal pools were individually marked at the encircling fence using a combination of a single toe clip and visible implant elastomer (VIE) (Heyer et al., 1994). In 2005 a single mark was given depending on the treatment the individual entered post-emergence. Age (juvenile or adult based on the presence of secondary sexual characteristics and/or size), sex of adults, and snout-vent length (SVL) were recorded for all captures of marked and unmarked amphibians at the terrestrial fences. We released captured animals on the opposite side of the fence to the point of capture.

2.3.2. Habitat sampling

We sampled habitat variables from 16 to 23 August 2004, and 5 to 26 August 2005 to assess how the forestry treatments influenced environmental factors. Sampling in each treatment was based on arrays of seven hexagonal plots, each hexagon being 1 m in length at the longest axis, with six plots encircling a seventh plot. Eighteen of these arrays were located in each treatment, with one array associated with each fence. The arrays were placed 25 m towards the focal pool from the central trap of each drift fence.

Variables sampled included percent canopy cover per array using a densiometer, leaf litter depth per plot, percent cover of standing water >1 cm in depth per plot, and vegetation as percent cover in two height classes per plot (0–50 and 50–100 cm). Variables sampled in 2005 were those that would have changed as a result of succession between years, with canopy cover and CWD only measured in 2004.

We sampled CWD using three 50 m line transects in each treatment. Each transect had a fixed starting point and random angle, with one transect originating between the 50 and 100 m fences, and two originating between the 100 and 150 m fences. Coarse woody debris >10 cm in diameter and within 2.5 cm of the ground intercepting this line was measured, including diameter at the point of intersection, length, and decay class (scale of 1–5) (Faccio, 2003). This allowed a calculation of the volume of CWD (m^3/ha) in each treatment (Bate et al., 2004).

2.4. Statistical analyses

Statistical analysis was conducted using SYSTAT 11.0. (Systat Software Inc.). For parametric tests, all data were assessed for normality and homogeneity of variance using Shapiro–Wilk and Bartletts tests, respectively, with data transformed via the square-root function where assumptions of normality were not met.

Differences in the number of wood frogs recaptured at successive distances from the pond were analyzed using three-factor analysis of variance (ANOVA) with site as a blocking factor, and site, treatment, and distance as the main factors. Recaptures of marked wood frogs were grouped by one-week intervals starting from the date of the first capture and analyzed graphically to determine temporal patterns. In 2004 a low sample size meant we could only compare changes in the total number of captures at all sites and treatments over the 1-week intervals. Sufficient recaptures in 2005 allowed assessment of both individual treatment recaptures and the overall totals.

Analysis of differences in unmarked captures of adults and juveniles of each species in the LEAP treatments were

Table 1
Life-history traits of amphibian species captured in the LEAP project, Maine, 2004–2005.

Trait	Wood frog[a]	Green frog[b]	American bullfrog[c]	Northern leopard frog[d]	Pickerel frog[e]	Spotted salamander[f]	Blue spotted salamander[g]	E. Red-backed salamander[h]	Red-spotted newt[i]
Life-cycle	Bi-phasic	Bi-phasic	Bi-phasic	Bi-phasic	Bi-phasic	Bi-phasic	Bi-phasic	Uni-phasic	Bi-phasic
Juvenile habitat	Forested wetlands	Wetlands	na	na	na	Forest	Forest	Forest	Forest
Juvenile dispersal habitat	Forest	Drainages/ vernal pools	Streams/ drainages	Streams/ drainages	na	na	na	na	na
Adult summer habitat	Forested wetlands	Pool edge, dense vegetation	Primarily near water	Forest, fields, and meadows	Forest, fields, and meadows	Underground in forest	Underground in forest	Forest in moist conditions	Aquatic (adult) forest (eft)
Adult Winter habitat	Upland forest	Underwater/ underground	Underwater/ underground	Underwater	Underwater	Underground in forest	Underground in forest	In forest soil	Terrestrial
Max. juv. dispersal distance (km)	2.530	4.800	0.914	5.200	na	na	0.92	na	na
Adult dispersal distance (km)	0.43	1.260	1.600	3.218	na	0.756	0.405	0.090	1.000

[a] Based on data from Heatwole (1961), Bellis (1965), Howard and Kluge (1985), Berven and Grudzien (1990), deMaynadier and Hunter (1998), Gibbs (1998), Guerry and Hunter (2002), Petranka et al. (2003), Regosin et al. (2003), Vasconcelos and Calhoun (2004) and Baldwin (2005).
[b] Based on data from Martof (1953, 1956), Schroeder (1976), Hunter et al. (1999), Carr and Fahrig (2001), Guerry and Hunter (2002), Lamoureux et al. (2002) and Livingston Birchfield (2002).
[c] Based on data from Raney (1940), Ingram and Raney (1943) and Willis et al. (1956).
[d] Based on data from Force (1933), Merrell (1970), Dole (1971), Seburn et al. (1997), Hunter et al. (1999), Pope et al. (2000) and Carr and Fahrig (2001).
[e] Based on data from Hunter et al. (1999).
[f] Based on data from Douglas and Monroe (1981), Kleeberger and Werner (1983), Madison (1997), Semlitsch (1998), Guerry and Hunter (2002), Rothermel and Semiltsch (2002), Faccio (2003) and Vasconcelos and Calhoun (2004).
[g] Based on data from Douglas and Monroe (1981), Semlitsch (1998) and Faccio (2003).
[h] Based on data from Vernberg (1953), Heatwole (1962), Burton and Likens (1975b), Gill (1978), Pough et al. (1987) and deMaynadier (2000).
[i] Based on data from Gill (1978), Jaeger (1980), Jaeger et al. (1995), Kleeberger and Werner (1982), Pough et al. (1987), Gibbs (1998) and Hunter et al. (1999).

conducted using chi square tests of the observed number captured in the 2 years combined. Captures of the two most numerous species of unmarked amphibians (wood frogs and spotted salamanders) were assessed via two-factor ANOVA with site and treatment as the main effects, excluding sites with fewer than five individuals captured in any treatment (Zar, 1996). Captures were compared for the 2 years combined, as patterns of captures remained consistent between years. Only adults of six species, wood frogs, green frogs, American bullfrogs, northern leopard frogs, spotted salamanders, and eastern red-backed salamanders, yielded sufficient data for analysis. We did not have sufficient data for analyses on blue-spotted salamander and pickerel frog juveniles.

Seasonal changes in abundance of unmarked animals in each treatment were evaluated graphically using the mean proportion (±S.E.) of the total captures per site per year, caught in each 2-week interval. To compare the mean size of juvenile amphibians captured, we used two-way analysis of variance (ANOVA), with site and treatment as the main factors.

3. Results

3.1. Marked wood frogs

In 2004, 2547 emerging juvenile wood frogs were individually marked from the 2 July to 14 August. Eighty-two wood frog juveniles were recaptured, with only 16% of these recaptures in the clearcuts (28 in the control, 41 in the partial-cut, 8 in the clearcut with CWD removed, and 5 in the clearcut with CWD retained). The first individual was recaptured on the 17 July, and the peak recaptures occurred 2–6 August (Fig. 2a).

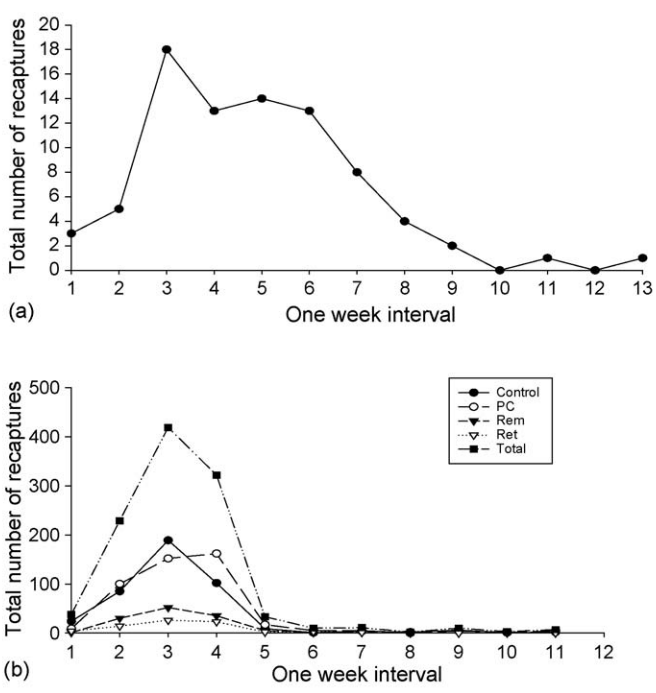

Fig. 2. Total number of recaptures of marked juvenile wood frog over one week time intervals in (a) 2004 ($n = 82$), with individual LEAP treatments total shown for (b) 2005 ($n = 1084$).

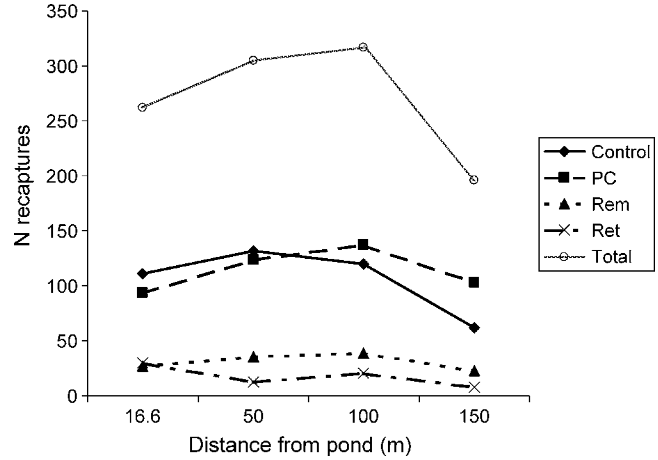

Fig. 3. Total number of recaptures of marked juvenile wood frogs in the LEAP treatments at successive distances from the pools in 2005 ($n = 1084$).

In 2005, 6085 emerging juveniles wood frogs were marked between 30 June and 7 August. Recaptures totaled 1084 individuals, again with relatively few (18%) captures in the clearcuts (425 in the control, 460 in the partial-cut, 125 in the clearcut with CWD removed, and 74 in the clearcut with CWD retained). The first recapture was on the 2 July, and the peak recaptures occurred 16–22 July (Fig. 2b). There was a significant difference in the number of recaptures at different distances from the pool (d.f. 3, 3, 3, $F = 3.177$, $P = 0.031$) and no significant interaction between treatment and distance indicating that differences in captures at different distances remained consistent between treatments (d.f. 3, 3, 3, 9, $F = 0.633$, $P = 0.645$) (Fig. 3). The highest number of recaptures was at 100 m, with a peak in the captures in the partial-cut and clearcut with CWD removed treatments at this distance.

3.2. Unmarked study species

We captured 7379 unmarked amphibians in 2004, and 6350 in 2005, representing 11 species (Table 2). Wood frogs, green frogs, and spotted salamanders were found in high abundance at all four of the sites, and these species collectively constituted 90.4% of the total captures during the study. Traps did not adequately sample gray tree frog (*Hyla versicolor*) and spring peeper (*Pseudacris crucifer*), which were excluded from future analyses. Four-toed salamanders (*Hemidactylium scutatum*) and American toads (*Bufo americanus*) were rarely captured, and therefore were also excluded from analyses. Data for pickerel frog and blue-spotted salamander are presented but only discussed qualitatively.

Adults made up a smaller proportion of the total captures for all species except for blue-spotted and eastern red-backed salamanders (Table 2). Four species (wood frogs, northern leopard frogs, spotted salamander, and eastern red-backed salamanders) showed consistently higher adult captures in uncut and partial-cut treatments than in clearcuts, with patterns

Table 2
Captures of unmarked amphibians in the LEAP treatments in 2004 and 2005[a]

Species	Chi-square value[a]		Total juvenile captures		Total adult captures		Adults in both seasons combined[b,c,d] (%)				Juveniles in both seasons combined [b,c,d] (%)			
	Adult	Juvenile	2004	2005	2004	2005	Con	PC	Rem	Ret	Con	PC	Rem	Ret
Wood frog	313.22*	1375.34*	4097	3033	262	466	51.2^{A}	26.5^{B}	11.3^{C}	11.0^{C}	40.2^{A}	30.8^{A}	14.3^{B}	14.7^{B}
American bullfrog	15.30*	15.30*	137	238	35	34	37.7	13.0	27.5	21.7	32.8	25.3	18.9	22.9
Green frog	11.53*	79.95*	582	1160	181	153	25.1	16.8	32.3	19.8	32.8	27.0	21.1	19.1
Pickerel frog	na	na	33	24	8	7	40.0	6.7	33.3	20.0	36.8	36.8	15.8	10.5
Northern leopard frog	20.40*	19.11*	132	142	24	6	30.0	46.7	16.7	6.7	32.8	29.6	21.5	16.
Blue-spotted salamander	na	na	10	21	13	2	40.0	20.0	6.7	33.3	58.1	9.7	9.7	22.6
Spotted salamander	39.18*	1653.29*	1303	871	279	25	37.2^{AB}	28.9^{A}	13.2^{B}	20.7^{AB}	61.9^{A}	20.1^{B}	7.0^{C}	11.0^{B}
Red-spotted newt	na	57.157*	75	52	5	11	25.0	43.8	12.5	18.8	52.8	23.6	13.4	10.0
E. red-backed salamander	19.49*	11.79*	67	27	122	69	33.5	30.9	22.5	13.1	38.3	27.7	18.1	16.0
Total			6444	5570	929	773								

[a] Calculated from captures in both seasons combined. The critical value of the chi-square distribution with 3 d.f. and α of 0.05 is 7.815. Significant results are indicated by *.
[b] For wood frogs and spotted salamanders, pairwise comparison of significant ANOVA results ($p < 0.05$) are indicated by superscript letters (A–C) grouping similar data.
[c] Con = control, PC = partial cut, Rem = clearcut coarse woody debris removed, and Ret = clearcut coarse woody debris retained, na = insufficient data.
[d] Peak captures were measured in weeks from the start of the field season.

being less clear for the remaining species (Table 2). Significantly more wood frog adults were captured in the control forest compared to the partial-cut, and in the partial-cut compared with the clearcut treatments (ANOVA: 3, 9, d.f. $F = 16.520$, $P = < 0.001$, Tukey pairwise comparisons $P = 0.045$, $P < 0.001$, and $P < 0.001$, respectively). Spotted salamanders showed higher number of adult captures in the control, partial-cut, and clearcut with CWD retained compared to the clearcut with CWD removed (ANOVA: 3, 7 d.f., $F = 5.279$, $P = 0.032$, Tukey pairwise comparison 0.034).

All of the study species showed higher juvenile captures in the uncut and partial-cut treatments compared to the clearcuts, although the results were not statistically significant for pickerel frogs and blue-spotted salamanders (Table 2). Wood frog juveniles showed significantly higher captures when comparing the uncut and partial-cut treatments to the clearcuts,

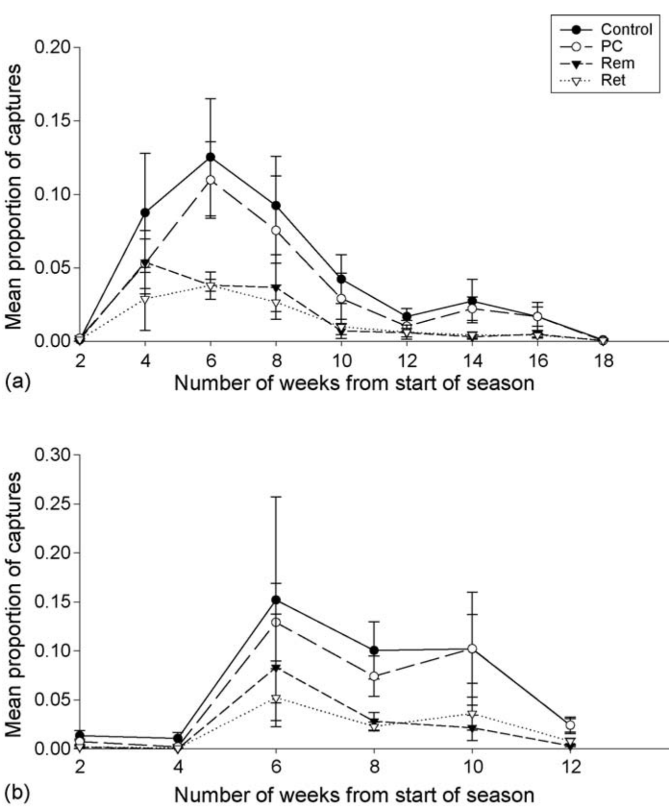

Fig. 4. Temporal changes in the mean proportion of the total number of captures of juvenile wood frogs (n sites = 4). (a) 2004 and (b) 2005.

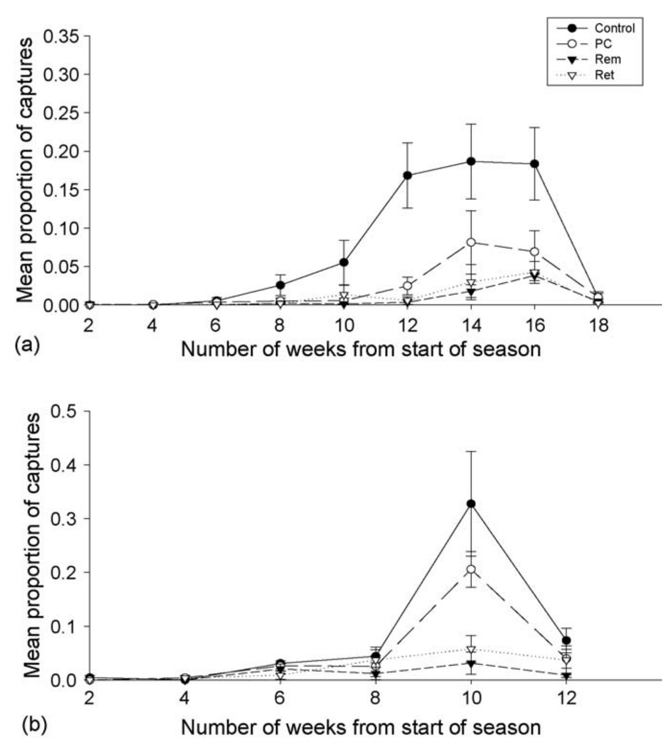

Fig. 5. Temporal changes in the mean proportion of the total number of captures of juvenile spotted salamanders (n sites = 4). (a) 2004 and (b) 2005.

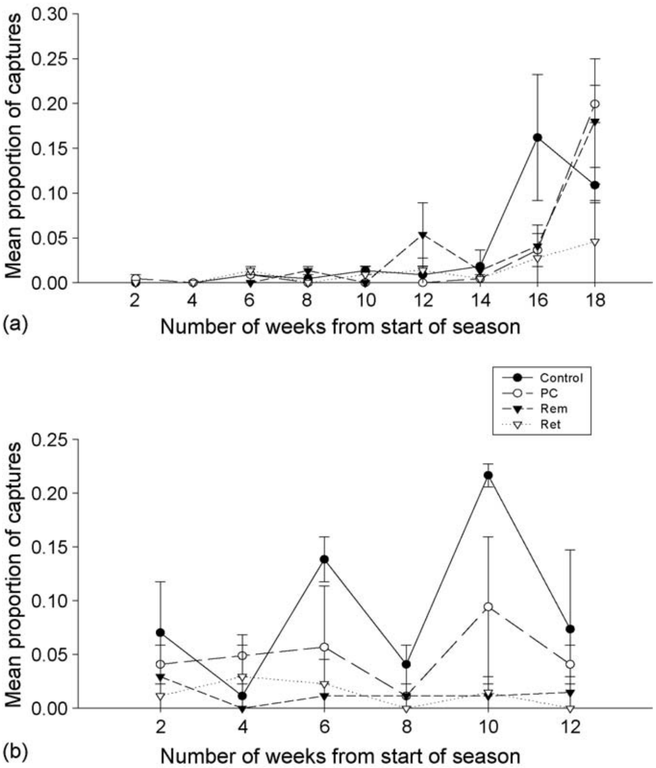

Fig. 6. Temporal changes in the mean proportion of the total number of eastern red-backed salamander captures grouped by two week intervals from the start of the field season (n sites = 2). (a) 2004 and (b) 2005.

but no significant differences within these groups (Table 2) (ANOVA 3, 8 d.f., $F = 17.711$, $P = <0.001$, Tukey pairwise comparisons $P = 0.001$ for control compared to both clearcuts, $P = 0.022$ for partial-cut compared to clearcut with CWD removed, and $P = 0.019$ for partial-cut compared to clearcut with CWD retained). Significantly more juvenile spotted salamanders were captured in the clearcut with CWD retained compared to the clearcut with CWD removed (ANOVA 3, 7 d.f., $F = 27.544$, $P = <0.001$, Tukey pairwise comparison $P = 0.028$). Captures of juveniles of this species were also significantly lower in the partial-cut compared to the control treatments (ANOVA 3, 7 d.f., $F = 27.544$, $P = <0.001$, Tukey pairwise comparison $P = <0.001$) (Table 2).

Temporal patterns in juvenile captures were generally similar among treatments for all species: representative figures for wood frogs and spotted salamanders are shown in Figs. 4 and 5, respectively. The temporal peaks in these captures also remained quite consistent between both field seasons for all species except green frogs. A distinct peak in eastern red-backed salamander captures (adults and juveniles combined) was seen at the end of the 2004 field season, but traps were closed before this period in 2005 (Fig. 6). This difference in field season duration may also have lead to the lack of selection seen for any treatment in 2004, with strong selection for the control treatment seen in 2005.

Unmarked juvenile wood frog showed a significant size difference, with larger animals found in the uncut and partial-cut treatments compared to the clearcuts (3, 1574 d.f., $F = 8.858$, $P < 0.001$). Individual mean sizes (mm $\pm$ S.E.) were 24.5 (0.2) for the control, 24.9 (0.2) for the partial-cut, 23.4 (0.3) for the clearcut with CWD removed, and 23.5 (0.3) for the clearcut with CWD retained.

3.3. Habitat

Mean canopy cover in the uncut forest was 73.8%, with harvesting reducing this to 53.0% in the partial-cut and 0% in the clearcuts (Table 3). Volume of CWD differed dramatically between treatments, with the greatest amount in the clearcut with CWD retained (Table 3). The uncut and partial-cut treatments had a greater mean leaf litter depth than the clearcuts in both years, with a reduction in this depth in both clearcuts in 2005. Regeneration of ground vegetation in the clearcuts was rapid, with approximately a 36% increase in cover in the 50–100 cm height category in both clearcuts from 2004 to 2005. Much of this regeneration was in the form of dense stands of red maple (*A. rubrum*), growing from cut stumps, and balsam poplar (*Populus balsamifera*), with the latter having reached heights of up to 3 m in 2 years of growth.

4. Discussion

Our results corroborate findings of previous studies on the effects of forest management practices on amphibians, with lower overall abundance of amphibians in clearcuts (Pough et al., 1987; Raymond and Hardy, 1991; Petranka et al., 1993, 1994; Ash, 1997; Harpole and Haas, 1999; Grialou et al., 2000; Ash et al., 2003; Knapp et al., 2003; Renken et al., 2004). As previously found, adult habitat use differed among species (deMaynadier and Hunter, 1998; Strojny, 2004), with wood frogs, spotted salamanders, and eastern red-backed

Table 3
Habitat variables sampled in LEAP treatments in 2004 and 2005

Treatment	Leaf litter depth (mm)		Cover of vegetation <0.5 m (%)		Cover of vegetation 0.5 –1 m (%)		Standing water (%)		CWD (m^3/ha)	Canopy cover (%)
	2004	2005	2004	2005	2004	2005	2004	2005		
Control	30 ± 5.8	18.9 ± 4.6	8.4 ± 1.0	0 ± 0	4.8 ± 2.2	10.5 ± 3.2	2.2 ± 1.3	2.6 ± 1.0	22.9 ± 11.8	73.8 ± 22.7
Partial cut	28 ± 5.9	13.5 ± 1.1	11.9 ± 4.4	0.05 ± 0.0	3.6 ± 1.9	14.0 ± 1.2	4.3 ± 2.51	5.2 ± 1.2	33.9 ± 7.3	53.0 ± 33.5
Clearcut (CWD removed)	24 ± 5.7	8.8 ± 2.5	10.6 ± 0.5	2.82 ± 2.3	2.1 ± 0.5	38.6 ± 7.2	5.3 ± 2.1	15.0 ± 3.2	12.7 ± 7.5	0
Clearcut (CWD retained)	19 ± 4.5	5.9 ± 1.0	10.1 ± 2.2	2.59 ± 1.5	1.1 ± 0.6	36.0 ± 5.0	3.0 ± 2.63	12.9 ± 1.9	45.6 ± 21.6	0

Values shown represent treatment means ± one standard error.

salamanders preferring uncut or partially cut forest, and adult green frogs and American bullfrogs being more tolerant of canopy removal. The reported sensitivity of ambystomatid salamander species to reduced canopy cover (deMaynadier and Hunter, 1998; Cromer et al., 2002; Guerry and Hunter, 2002; Rothermel and Semiltsch, 2002), and to the retention of CWD in clearcuts (Moseley et al., 2004) was also seen in our results. Eastern red-backed salamanders showed a low number of captures during summer when individuals are territorial and limited in movement (Jaeger et al., 1995). During the late fall movement of this species documented in 2004 it appears that eastern red-backed salamanders were moving through all four treatments (Fig. 6).

Much of the research on terrestrial habitat use of amphibians to date has focused on adults (although see deMaynadier and Hunter, 1999; Rothermel and Semiltsch, 2002; Vasconcelos and Calhoun, 2004), with the ranid species in our study (except wood frogs) typically being described as generalists rather than forest-dependent species (Table 1). This highlights the importance of our results showing that juvenile habitat use differed from that of adults, with seven of nine species showing statistically more juvenile captures in the uncut and partial-cut treatments and lower in clearcuts. In other words, our results clearly show that the habitat selection of adult amphibians does not necessarily make a good surrogate for that of juveniles of the same species, and that the majority of juvenile amphibians will choose to move through forest rather than open-canopy areas. The results also suggest that partial canopy removal may reduce the relative abundance of many species (all species except pickerel frogs had fewer juvenile captures in the PC compared to the control, although a statistical difference could only be shown for spotted salamander), and that the retention of CWD may serve to mitigate some of the effects of clearcutting for ambystomatid salamanders.

Our experimental design assessed two components of habitat selection during movement of marked juvenile wood frogs. The first of these was the initial choice made as to which treatment is entered. The second component related to how treatments such as clearcuts affect habitat resistance, i.e., movement through the habitat following this initial selection (Ricketts et al., 2005; Rothermel and Semiltsch, 2002; Mazerolle and Desrochers, 2005). Recaptures did not decline until 150 m from the pond in any of the treatments suggesting that for the few juvenile wood frogs that chose to move through clearcuts, the habitat did not offer greater resistance. Although this suggests that clearcuts do not present a significant barrier to movement and potentially to dispersal and connectivity between populations, we are hesitant to draw this conclusion. Clearcuts have been shown to increase dehydration and reduce survival of juvenile amphibians (Rothermel and Semiltsch, 2002). Our study did not address such effects, and further research is clearly needed to understand how clearcuts may affect long-term survival.

The marked wood frog data also show that the highest total number of recaptures was at 100 m from the pond. This suggests that there were more recaptures of the same individuals at 100 m (assuming that efficacy of the fences did not change with distance), which could indicate that the animals had settled in an area suitable for summer foraging and were not actively dispersing. In other words, juvenile wood frogs may have a predisposition to move some minimum distance from the source pools. Such a predisposition has been suggested for adult female wood frogs (Regosin et al., 2003), but to the best of our knowledge this is the first time that a similar pattern has been shown for juvenile wood frogs. This finding has important implications when protecting terrestrial habitat near pools, as it suggests that the population may not be most concentrated directly adjacent to the pool.

The marked wood frog data also suggest that habitat selection during movement is not purely a function of habitat quality, given that some juvenile wood frogs chose to remain in clearcuts. Competitive exclusion by a high density of conspecifics in the high-quality (uncut and partial-cut) treatments might explain this result (Fretwell and Lucas, 1969). The significantly larger mean sizes of unmarked juvenile wood frog captured in the uncut and partial-cut treatments in 2005 supports this idea.

5. Conclusion

The sensitivity to clearcutting of juvenile amphibian species in our study may have important implications when considering the linkage between forest management and amphibian populations. Juveniles have been shown to be the dispersing life-history stage for many amphibian species (Gill, 1978; Breden, 1987; Berven and Grudzien, 1990). Reductions in abundance and changes in dispersal patterns can have critical effects on population viability and processes such as the probability of recolonization of extinct populations, and gene flow between populations (Frankham et al., 2002). Although our results do not explicitly measure the effects of forest management on juvenile dispersal, our data on habitat selection, abundance, and long-distance movement of marked wood frogs provides a surrogate measure of these effects. If fewer juvenile amphibians choose to enter clearcuts, then the probability of successful dispersal through these habitats is obviously reduced when compared to dispersal through uncut or partially cut habitat. Similarly, if juvenile amphibians avoid settling in clearcuts following dispersal, the available habitat is reduced, along with the population abundance. To critically assess the importance of these patterns we would need to have information on many other factors, notably the extent of clearcutting in the region and the duration of any responses to clearcutting (i.e., how soon would regeneration restore habitat for juvenile amphibians).

Although our study species are common and probably not jeopardized by the limited clearcutting that currently occurs in Maine, these results suggest that biologists should investigate the effects of major habitat change on juveniles of other amphibian species, especially those at risk of local or global extinction. Furthermore, diminished abundance of common species could compromise their ecological role (Wyman, 1998).

Future research efforts should focus on understanding the long-term patterns of juvenile abundance and how they affect the viability of amphibian populations. Such an understanding will need to include factors such as the survival of juveniles to adulthood in different treatments, as well as the effects on subsequent life-history stages for example adult survival and reproduction. By understanding such effects, forest management can be designed to incorporate both connectivity between areas of suitable habitat, and sufficient areas of habitat to maintain population viability.

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