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Responses of the woodland salamander *Ensatina eschscholtzii* to commercial thinning by helicopter in late-seral Douglas-fir forest in northwest California

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ABSTRACT

We examined responses of the woodland salamander Ensatina (*Ensatina eschscholtzii*) to commercial thinning by helicopter in late-seral Douglas-fir forest in northwestern California, USA, using a before-after control-impact (BACI) design. We employed passive pitfall traps on eight (four each treatment and control) 100 trap grids over eight years (1996–2003), three years pre- and five years post-treatment. We conducted 3–11 weekly site visits within each of 10 trap periods depending upon weather over two spring and eight fall periods for a total of 50 visits to test for differences in surface counts and body condition. We standardized data to captures/1000 trap nights. Surface counts over the eight years were highly variable with less surface activity in spring compared to fall. Although the BACI design allows for initial differences among pre-treatment grids there were none. However, in the three years post-treatment (1999–2001) mean counts on treatment grids were significantly lower than on control grids. By 2002 and 2003, post-treatment counts on control and treatment grids both declined substantially, such that despite 47% more salamanders on control grids, variability was sufficient to preclude statistical significance. Recapture rates averaged 23.3% for three years pre-treatment, but increased to 51.4% for the five years post-treatment. Pre-treatment population estimates increased on control grids post-treatment, however, surface density estimates declined. On treatment grids both population and density estimates declined following treatment. Body condition analyses indicated no significant differences between controls and treatments for either sex prior to or post-treatment. The three years of significant differences in surface counts between controls and treatments post-treatment, followed by no differences in the last two years of the study, combined with no differences in BCIs, lead us to conclude that the surface activity of Ensatina on treatments grids was only temporarily impacted by the thinning. Declining population estimates on treatment grids also indicated at least a temporary reduction in those populations. We unexpectedly found declines in counts and density estimates on both sets of grids over the eight years, suggesting a wider effect may be causing reductions in the surface activity of these salamanders, and possibly in their populations.

1. Introduction

The negative impacts of commercial forestry practices on amphibian populations are well documented (e.g., Bury and Corn, 1988; deMaynadier and Hunter, 1995; Semlitsch et al., 2009). However, the type, severity, and duration of these impacts can vary greatly depending upon silvicultural prescription (e.g., Homyack and Haas, 2009; Semlitsch et al., 2009), as well as the life history attributes and physiological requirements of the resident species (e.g., Homyack and Haas, 2009; Connette and Semlitsch, 2013; Sutton et al., 2013). Further, few studies have addressed the impacts of different silvicultural techniques over sufficiently long time frames to quantify possible recovery trajectories (Hawkes and Gregory, 2012). Negative impacts to terrestrial salamanders in the family Plethodontidae are particularly well documented and of great concern (Wyman, 2003; Tilghman et al., 2012; Welsh and Hodgson, 2013). Woodland salamanders can occur in large numbers in temperate forests in North America, with estimates ranging up to 2950–18,000/ha (Burton and Likens, 1975a; Peterman et al., 2008; Petranka and Murray, 2001; Welsh and Lind, 1992). Their enormous biomass in healthy natural forest ecosystems (e.g., Burton and Limkens, 1975a) is indicative of their ecological dominance in trophic pathways, including linking

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aquatic and terrestrial environments (e.g., Greene et al., 2008; Schreiber and Rudolf, 2008), and modulating processes at the litter/soil interface where their predation on invertebrates facilitates nutrient cycling (Burton and Likens, 1975b), soil-building (e.g., humification [Prescott, 2010]) and carbon capture (Wyman, 1998; Best and Welsh, 2014). Maintaining these ecological processes in forests is vitally important because their compromise can adversely affect tree growth, extend recovery times of harvested stands, lower ecosystem resistance and resilience, restricting and reducing these essential ecological services (Likens and Franklin, 2009).

Alternative forestry prescriptions have been proposed that can provide for timber products without compromising the biota that sustain and perpetuate healthy resilient forest ecosystems (e.g., Kohm and Franklin, 1997; Maser, 1988). However, investigating the impacts of alternative silvicultural prescriptions on the herpetofauna is a relatively recent focus of research (e.g., Harpole and Haas, 1999; Semlitsch et al., 2009; Sutton et al., 2013), particularly in the western U.S. (e.g., Grialou et al., 2000; Suzuki, 2000; Karraker and Welsh, 2006; Olson et al., 2014). In this study we sought to test the effects of thinning from above with helicopters (see also Clawson et al., 1997; Perison et al., 1997), thereby eliminating the ground disturbing effects of tractor logging where felled logs are skidded along the forest floor, or cable yarding where logs are dragged up steep slopes; both approaches disturb soil layers and destroy microhabitats upon which fossorial and ground-dwelling herpetofauna depend (e.g., Kingsbury and Gibson, 2012). This study focused on Ensatina (*Ensatina eschscholtzii*), the most common woodland salamander in northern California forests (Welsh and Lind, 1991). Long-term studies of this highly abundant species are fairly rare (but see Staub et al., 1995; Stebbins, 1954), with little information available on the impacts of alternative forestry prescriptions on Ensatina populations. We sought to conduct this experiment over sufficient time to detect evidence of recovery should we find negative effects. Because of the limited impact on ground-level conditions, we predicted that helicopter thinning would have minimal effects on the salamanders, reasoning that five years post-treatment would suffice to document any such effects and subsequent recovery. The experiment was conducted in true reference forest (Foster et al., 2003; Pollack et al., 2012; Willis and Birks, 2006), a never-harvested, late-seral Douglas-fir (*Pseudotsuga menziesii*) dominated forest at a mid-elevation (~4000 ft. or 1220 m) site in northwest California.

Our objective was to compare surface counts and body condition of Ensatina on control and treatment pitfall trap grids (four each), before and after thinning to determine the effects, if any, of this light touch harvest approach on this common salamander. We tested the hypotheses that: (1) helicopter thinning would have little or no effect on surface counts or body condition of Ensatina, and (2) should we find negative effects on counts or body condition, it would be transitory and both metrics would recover in a reasonably short time (e.g., <5 years) on treatment grids to match those of the control grids.

2. Methods

2.1. Study location

This study was performed in conjunction with a commercial thinning project employing helicopter yarding conducted in the Pilot Creek watershed of the Mad River Ranger District of the Six Rivers National Forest in northwestern California (40°37′, 123°36′) (Fig. 1).

This watershed is approximately 55 km east of the Pacific Ocean in the Coast Range Mountains. Stand vegetation consisted of mixed-evergreen forest dominated by Douglas-fir, with white fir (*Abies concolor*) and oaks (*Quercus chrysolepis*, *Q. kelloggii* and *Q. garryana*) also common. The study stand was in late-seral forest not previously logged and dominated by 80–100 year old Douglas-fir trees (the species to be thinned) with scattered old-growth trees >200 years old that had survived previous fires. The Pilot Creek watershed is immediately due west of the Klamath Mountains Province which has a fire return cycle of 11.5–16.5 years (Taylor and Skinner, 2003). Prior to thinning the basal area of trees within the treatment area averaged 80.0 m^2/ha (range: 71.3–88.5 m^2/ha) with a canopy closure of 96%. The treatment pitfall grids were in a 26.3 ha polygon scheduled to be commercially thinned to 36.7–50.5 m^2/ha of basal area or about 70% canopy closure, with the intent to facilitate the development of old-growth characteristics while minimizing ground disturbance (L. Crippa, Six Rivers Natl. Forest, pers. com.). The study occurred over eight years (1996–2003), three before and five post-thinning. Elevations of both treatment and control pitfall trap grids ranged from 1100 to 1300 m located in areas of moderate slope near the ridge top relative to the surrounding steep and rugged landscape (Fig. 1). Salamander sampling consisted of traps spaced 6 m apart in rows and columns, with three 10×10 grids of 100 traps (0.29 ha) and one 8×12 grid of 96 traps (0.28 ha) in treatment and control areas; the later grid shape was required to fit all the grids in the stand with at least a 10 m buffer from any edge.

2.2. Salamander sampling

We used pitfall traps approximately 15 cm diameter × 18 cm deep to capture salamanders. Traps consisting of two stacked number 10 tin cans with plastic collars inserted at the top to prevent captured animals from escaping. Pitfall traps were buried so the open top was flush with the ground and covered with a wood shake propped up on pebbles or twigs to provide 1–3 cm of crawl space. A thin layer of moistened soil was added to the bottom of each trap to provide moisture; this was particularly important when ambient conditions were dry. Water was added as needed during trap checks to maintain suitable conditions for salamander survival. We established four pitfall grids in areas scheduled for thinning (treatment grids), and four grids in nearby areas in similar landscape positions with similar forest cover not scheduled for thinning (control grids) (Fig. 1). Grids were considerably larger than individual salamander home ranges (10–41 m; mean of 20 m for males; Stebbins, 1954) and were designed to estimate relative abundances (i.e. indices of the true populations [Johnson, 2008]) from captures on these grids. Although we did not adjust the data for detection probabilities less than one (Mazerolle et al., 2007), we considered that our passive sampling method rendered these probabilities relatively constant over the eight year study, and that surface counts and population estimates derived to be conservative approximations of the true numbers.

Salamanders were weighed and measured (snout-to-vent length [SVL]) with each animal individually toe-clipped. Elastomer implants were impractical given the logistic constraints of the project. We initially used individual numbers that were specific to each grid. However, these proved unreliable over the long-term due to toe regeneration and only the grid-specific batch marks were used for identifying recaptures in our analyses. We re-marked individuals whose toes had re-generated when previous marks were obvious. If there was any doubt about the identity of a captured salamander (i.e. new or recaptured) it was not included in the analyses. We determined sex and assessed whether females were gravid by visual inspection. Animals were released under cover objects within 2 m of the traps where captured.

A body condition index (BCI) was calculated following Peig and Green (2010), which determines a scaled mass index ($\widehat{M}_i$) from

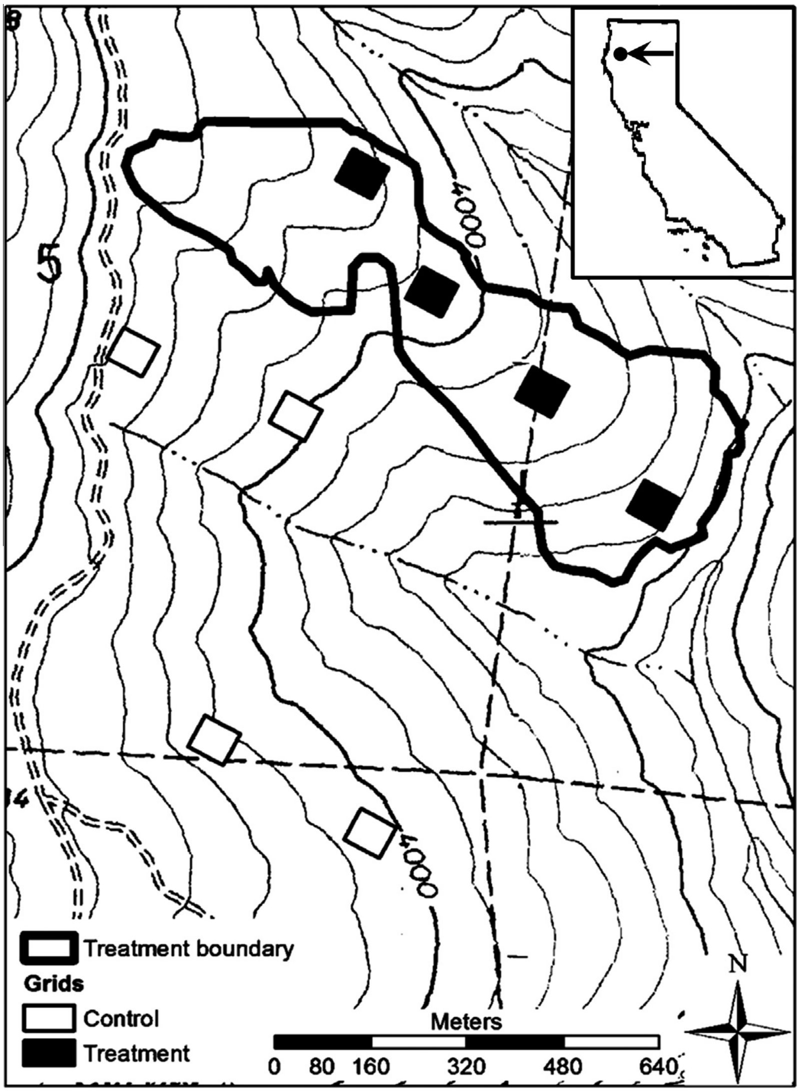

Fig. 1. Location of the study stand and area of treatment, and the distribution of the eight pitfall grids near the headwaters of Pilot Creek, Six Rivers National Forest, Humboldt County, northwestern California (40°37′, 123°36′).

salamander standardized body mass (weight) and snout-to-vent length (SVL). We used only adults of known sex (⩾30 mm SVL), with gravid females and animals with missing or re-generated tails eliminated from analyses due to their potential to bias the regression equations. Only initial captures in good condition were used, with analysis conducted separately for males and females to account for sexual dimorphism.

2.3. Study design

We conducted a total of 50 site visits over ten trap periods in the eight years of the study, averaging five site visits per trap period (range: 3–11) (Table 1). Eight trap periods were in the fall and two in the spring. Both spring trap periods and three fall trip periods occurred prior to treatment (Table 1). The spring trap periods ran from 09 April to 18 June 1997, and 11 June to 02 July 1998. All fall trap periods ran from October to December in 1996 to 2003. Thinning occurred in summer 1999. We averaged 7.4 days between site visits. On eight occasions, traps ran for two weeks between visits due to inaccessibility of the study site, with the longest period lasting 17 days between visits due to snow on the higher elevation access road. We had no mortality over this period. While snow occasionally restricted our access to the site, salamanders were under ground during these cold winter periods so no data were lost.

Because we had prior knowledge of the thinning to take place, a technique intended to accelerate late-seral structure while minimizing ground disturbance, we were able to use a before-after control-impact (BACI) design (Smith, 2002). The eight pitfall grids were the primary units of analysis. Trees to be thinned were felled with chainsaws and removed by helicopter with slash left on the ground then hand-piled and burned during summer 2000. The burning was carefully controlled by using small discrete piles in order to eliminate new ground cover resulting from the thinning. The burning (like the thinning itself) occurred when resident salamanders were underground and aestivating so we assumed no direct impact. Salamander sampling continued for five years after the thinning treatment. Sampling commenced in the fall (with the exception of two spring trap periods) following the first significant rains of the season, and continued until access to the site was no longer possible due to snow and ice. The traps were closed with plastic lids following each fall sampling period.

Table 1
Schedule of pitfall trapping of Ensatina at Pilot Creek over the course of this study.

Trap period	Year	Season	# of visits per trap period	# of days open per trap period	Treatment
1	1996	Fall	6	42	Pre
2	1997	Spring	11	72	Pre
3	1997	Fall	7	44	Pre
4	1998	Spring	4	28	Pre
5	1998	Fall	3	22	Pre
–	1999	Summer	–	–	Harvest
6	1999	Fall	3	21	Post
–	2000	Summer	–	–	Slash/burn
7	2000	Fall	4	34	Post
8	2001	Fall	4	28	Post
9	2002	Fall	4	35	Post
10	2003	Fall	4	41	Post

2.4. Tree, canopy, and ground cover variables

All trees were counted and measured, percent canopy open was estimated with spherical densiometers (averaging four directions at 25 locations spaced systematically across each grid), and ground cover and litter were estimated (% of cover) in eight categories (above ground foliage, bare ground, Douglas-fir litter, forbs, hardwood litter, moss, pine litter, and woody debris) on treatment and control grids prior to treatment in summer 1999 and after thinning and slash burning was completed in summer 2002. We recorded tree species and diameter at breast height (DBH) for all live and dead trees $\geqslant 5$ cm DBH and <1.4 m height. Stump (harvested tree) diameters were measured (cm) at the top of each stump. Ground cover was estimated using a 1-M^2 quadrat positioned at the center of each 6×6 grid cell formed by 4 pitfall traps (77 or 81 cells per grid). We used Aspin-Welch unequal variance *t*-tests to test the hypothesis that there was no significant difference in the change over time on the control and treatment grids before and after the thinning treatment for each variable.

2.5. Analysis of the thinning treatment

Captures were standardized to captures per thousand trap nights on each grid (total captures per grid divided by sampling days multiplied by 1000). We used a BACI mixed effects ANOVA model (SAS Institute Inc., 2003) to test the effects of helicopter thinning on surface counts and body condition before and after treatment. Within the framework of a general linear mixed model the difference between the means of captures on the treatment and control grids in each time period is the change that comprised the statistic we used to assess the effect. Spring samples were not used in this analysis; and because we lacked body condition data across all eight grids for the first fall trap period (fall 1996), we used fall 1997 through fall 2003 to test for the main effect on body condition. All eight fall samples were used to test the effect on surface counts.The observed counts per thousand trap nights and the body condition index for grid type i (C for control and T for treated), time period j(j = 1, 3, 5, 6, 7, 8, 9, 10) at relative month t_j ($t_1 = -31$, $t_3 = -20$, $t_5 = -8$, $t_6 = 3$, $t_7 = 15$, $t_8 = 27$, $t_9 = 39$, and $t_{10} = 52$), and grid k (k = 1, 2, 3, 4) is y_{ijk} and modeled as follows:

$$y_{ijk} = \mu_{ij} + \alpha_{ik} + \epsilon_{ijk}$$

where μ_{ij} is the mean for grid type i and time period j, α_{ik} is a random effect of the k-th grid for the i-th grid type with $\alpha_{ik} \sim N(0, \sigma^2_G)$, and ϵ_{ijk} is the random error for grid type i, time period j and grid k with $\epsilon \sim N(0, \sigma^2)$ and $Cov(\epsilon_{ijk}, \epsilon_{i'j'k'}) = 0$ if $i \neq i'$ or $k \neq k'$ and otherwise $Cov(\epsilon_{ijk}, \epsilon'_{ijk}) = \rho^{|t_j - t_{j'}|}$. In other words we allowed for potential serial correlation over time.

To be more convincing about determining the possibility of a treatment effect, the BACI design allowed us to look at the difference in the changes over time of the control and treated grid means. This isolates the comparison to the same time period and allowed for potential differences in the initial pre-treatment means. In this case we have two (body condition) or three (surface counts) pre-treatment measurements for both the control and the treated grids. We use the means of those pre-treatment measurements as the initial values for the control and the treated grids.The mean of the three pre-treatment means for grid type j is

$$\frac{\mu_{i1} + \mu_{i3} + \mu_{i5}}{3}$$

At post-treatment time period j (j = 6, 7, 8, 9, 10) we find the change from the initial mean:

$$\mu_{ij} - \frac{\mu_{i1} + \mu_{i3} + \mu_{i5}}{3}$$

The mean difference in the treatment change and the control change is

$$\Delta_j = \left(\mu_{Tj} - \frac{\mu_{T1} + \mu_{T3} + \mu_{T5}}{3}\right) - \left(\mu_{Cj} - \frac{\mu_{C1} + \mu_{C3} + \mu_{C5}}{3}\right)$$

Note that this is equivalent to the difference in the post-treatment difference and the pre-treatment difference for treated and control grids:

$$\Delta_j = (\mu_{Tj} - \mu_{Cj}) - \left(\frac{\mu_{T3} + \mu_{T5}}{2} - \frac{\mu_{C3} + \mu_{C5}}{2}\right)$$

We fit the above model with the residual maximum likelihood (REML) approach (using PROC MIXED in SAS) and found 95% confidence intervals for Δ_j for all post-treatment time periods to assess if there were treatment differences and if the treatment differences changed over time. We applied the same model to both captures per thousand trap nights and body condition index (BCI). In summary, we fit a linear mixed model accounting for potential serial correlation over time and then constructed the estimates of the parameter combinations of interest. Because we fit our linear model once for each time interval (year) looking for differences in captures between control and treatment grids in an exploratory (not confirmatory) analysis, we considered adjustments for multiple comparisons unnecessary and inappropriate (Roback and Askins, 2005; Waite and Campbell, 2006). The data were tested for normality. Alpha was set at 0.1 for all tests as is appropriate for ecological studies (Schrader-Frechette and McCoy, 1993).

2.6. Relative densities and population estimates

Terrestrial plethodontid salamanders spend much of their lives underground (e.g., Taub, 1961) which makes deriving accurate population estimates challenging (Bailey et al., 2004). The paucity of reliable population estimates in the literature is in large part due to the length of time required to derive reliable estimates, with accuracy incrementally enhanced over time as the proportion of recaptures increases with progressive re-sampling efforts. The eight year duration of this study provided a unique opportunity to derive estimates of the target populations of this abundant but secretive salamander based on long-term data with a high number of recapture events.

Surface density estimates, which were calculated based on initial captures only, differ from population estimates by providing evidence of changes in surface behavior or possible indications of declining numbers. We used the area of each sampling grid, surrounded by a 4-m buffer, a distance selected based on the low vagility of woodland salamanders (Welsh and Lind, 1992; Stebbins and Cohen, 1995; Liebgold et al., 2011), divided by the total number of initial captures in the five trap periods both prior to and after treatment, to estimate relative densities (i.e. we did not incorporate detection probabilities) before and after treatment on each pitfall grid. Estimates were then averaged for the four grids in each set (i.e. treatment, control, before, and after treatment) and converted to salamanders/ha.

The fact that we were not able to reliably use long-lasting individual marks for the salamanders limited our options for estimating population size. However, using the modified Schnabel method (Chapman, 1954; see Chao and Huggins, 2005) we used the ratio of recaptures to captures in trap periods before and after treatment to derive estimates of the population on each grid. We used only data from the fall samples, and only from those grids with two or more recaptures in a sample period to avoid over-inflating our estimates ($N = 20$); mean estimates were derived for the same grids as noted above (four treatment and four control, before and after treatment). We used the unbiased estimator for population size ($\widehat{N}$):

$$\widehat{N} = \frac{\sum_{t=1}^{S}(C_t M_t^2)}{\sum_{t=1}^{S}(R_t M_t)}$$

where C_t is the total number of individuals caught in sample t, R_t is the number of individuals already marked when caught in sample t, M_t is the number of individuals marked in the previous sample, and S is the number of the sample in the series. For this analysis we made the following assumptions: (1) sampling was random, (2) the population was closed (i.e. no immigration, emigration, birth, or death) within a trap period, (3) all animals had the same chance of being caught in the first sample, (4) marking individuals did not affect their catchability, (5) animals did not lose marks between sampling intervals, and 6) all marks were reported on discovery in the second sample. We recognize the limitations of this method (see Pollock et al., 1990) but our lack of confidence in individual marks greater than a year old due to regeneration precluded a more sophisticated analysis. Consequently, we consider these estimates conservative approximations of the Ensatina population sizes on the two sets of trap grids.

3. Results

We captured Ensatina a total of 3150 times (2375 captures and 775 recaptures), along with one Rough-skinned Newt (*Taricha granulosa*), and two Pacific Treefrogs (*Pseudacris regilla*) over eight years.

3.1. Trees, canopy, and ground cover

Vegetation sampling showed that prior to the thinning the basal area of Douglas-fir trees within our treatment grids averaged 80.0 m^2/ha (range: 71.3–88.5 m^2/ha) with a canopy closure of 96%; post-thinning the volume was decreased to 54.7 m^2/ha (range: 43.7–64.2 m^2/ha) (Fig. 2), with a canopy closure of 85%. The control sites averaged 81.6 m^2/ha (range: 54.7–101.0 m^2/ha) with a canopy closure of 94%. Basal area of Douglas-fir was similar on control and treatment grids prior to treatment; however, following thinning it was reduced such that significant differences were evident between grid types ($T = 8.47$, $p = 0.003$, df = 3.24; Table 2). Accordingly, the canopy was significantly reduced on treatment grids compared to the control grids post-treatment ($T = -3.65$, $p = 0.03$, df = 3.35; Table 2). With the exception of significant differences in bare ground, a variable that amounted to a very small percent of the total ground and thus can be justifiably ignored, no other ground cover variables differed between grid types post-treatment (Table 2). Thus it appears that the removal of basal area, in conjunction with the increase in open canopy, were the only structural changes we measured that might reasonably be linked to changes in salamander counts or body condition following treatment.

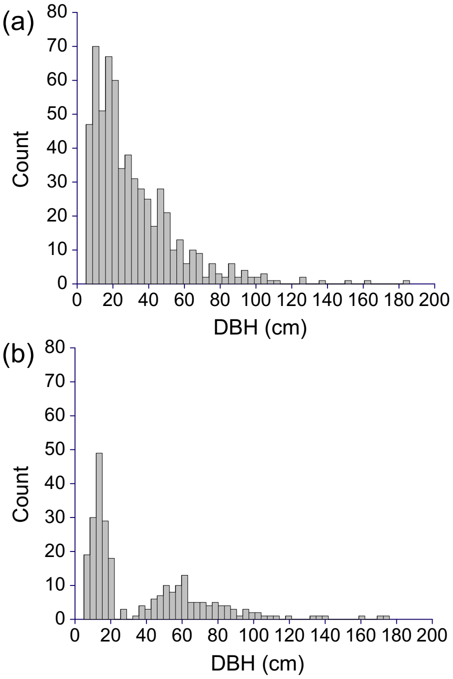

Fig. 2. Numbers of Douglas-fir trees measured in centimeters at their diameters at breast height (DBH) on the treatment grids before (a) and after (b) thinning. The thinning was focused primarily on the 20–30 cm DBH size class of trees.

3.2. Helicopter thinning effects on surface counts of Ensatina

The surface counts of male and female Ensatina were analyzed separately due to the possibility of finding differences in surface behavior by the two sexes; however, no differences were found so the data were combined in further analyses. Spring data, which were not used in the analysis of the treatment effect, showed markedly reduced Ensatina surface activity compared to the fall (Fig. 3). Using the seven fall sampling periods (1997–2003) to test for the treatment effect we found high variability in Ensatina surface counts among periods (Fig. 4), with the highest counts in the falls of 1998 and 1999, followed by the falls of 2001, 1997, and 2000, respectively (Fig. 4). The trap periods after the treatment indicate consistently higher captures on the control grids, but with a declining trend in the difference. The test of the effects of helicopter thinning on Ensatina surface activity was not unduly influenced by the high variability in counts among trap periods because the linear model tested for differences between grid types within each time interval rather than between them. After treatment the differences in counts between the two sets of grids increased significantly (Table 3; Fig. 4), with the ANOVA model revealing a

Table 2
Tests for differences in ten vegetation and ground cover variables estimated in 1998 and 2002 (before and after treatment) on grids where Ensatina were sampled. We tested the hypothesis that the difference between the two years for each variable was the same on treatment and control grids; finding of a significant difference refuted this hypothesis. A positive difference in means indicates that 2002 values were higher than 1998 values; a negative difference in means indicates the opposite.

Variable	Difference in means between yrs for control grids (difference of SD)	Difference in means between yrs for treatment grids (difference of SD)	*T*	*p*	df
Basal area (total in m^2)	0.11 (0.26)	−5.51 (1.30)	8.47	0.003	3.24
Open canopy (%)	−0.63 (1.31)	11.03 (6.20)	−3.65	0.03	3.35
Above ground foliage (%)	2.33 (1.65)	2.46 (4.80)	−0.05	0.96	3.70
Bare ground (%)	2.03 (0.85)	4.25 (1.57)	−2.48	0.06	4.61
Douglas fir litter (%)	9.04 (11.94)	18.88 (6.40)	−1.45	0.21	4.59
Forbs (%)	5.49 (5.53)	2.15 (2.80)	1.08	0.34	4.44
Hardwood litter (%)	−1.76 (4.75)	−6.59 (14.11)	0.65	0.55	3.67
Moss (%)	0.99 (0.70)	3.37 (2.16)	−2.10	0.11	3.62
Pine litter (%)	1.82 (3.64)	−8.71 (10.12)	1.96	0.13	3.76
Woody debris (%)	5.91 (2.69)	5.42 (1.80)	0.30	0.77	5.24

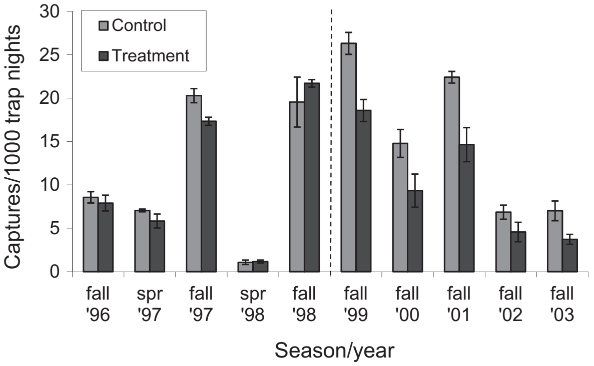

Fig. 3. Ensatina salamander captures (captures per 1000 trap nights) by trap period. The vertical dashed line indicates when thinning occurred. Gray bars are control grid and black bars are treatment grid captures. The first trap periods in 1997 and 1998 were in the spring and were not included in the analysis of the main effect; all other trap periods were in the fall. The error bars are standard errors.

highly significant interaction effect between treatment and time ($F = 214.33$; $p < 0.0001$; df = 32.9); reflecting the changes in the differences in surface counts between control and treatment grids across the sampling periods before and after treatment (Fig. 4). There were no significant differences in surface activity between treatments and controls prior to treatment ($T = -0.56$; $p = 0.579$; Table 3), with the treatment effect becoming evident in the sixth through eighth trap periods (1999 through 2001; Table 3; Fig. 4). However, by the ninth and tenth trap periods (2002 and 2003) salamander numbers on both treatment and control grids had diminished, with those on control grids declining to closely match those on treatment grids. By four and five years post-thinning the smaller means on both sets of grids reduced the difference between the two sets; this along with high variability resulted in a lack of statistical significance (Table 3).

3.3. Recapture rates

We found no differences in recapture rates on treatment and control grids over the course of the study ($F = 0.04$, $p = 0.854$, df = 17), and they did not diverge post-treatment on the two sets

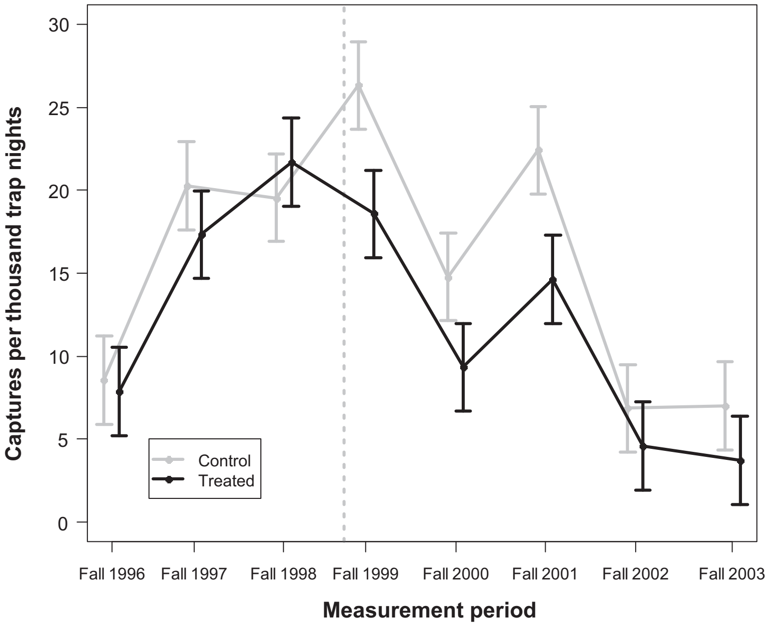

Fig. 4. Ensatina salamander captures (captures per 1000 trap nights) by fall trap period. Individual dots represent the means of the four grids in each set (control and treatment) by trap period. The error bars are plus and minus 1.96 standard errors (i.e. 95% confidence intervals) from the results of the linear mixed model. The vertical dotted line represents the thinning treatment which occurred between trap periods five and six.

Table 3
Mixed-effects ANOVA test of pre- and post-treatment effects of helicopter thinning on surface counts of Ensatina. The means are the numbers of Ensatina per 1000 trap nights per set of control and treatment grids. The SE (standard error) is an estimate of the variability in the estimates of the mean. Also reported are the percent differences in Ensatina/1000 trap-night between treatment and control grids for each trap period.

Year	Phase	Treatment mean (SE)	Control mean (SE)	Difference	*T*	*p*	95% lower	95% upper	Percent difference (%)
1996–98	Pre	15.64 (0.61)	16.13 (0.61)	−0.49	−0.56	0.579	−2.28	1.30	−3.0
1999	Post 1	18.57 (1.32)	26.31 (1.32)	−7.74	−4.15	0.000	−11.49	−3.98	−29.4
2000	Post 2	9.34 (1.32)	14.78 (1.32)	−5.44	−2.91	0.005	−9.19	−1.69	−36.8
2001	Post 3	14.64 (1.32)	22.41 (1.32)	−7.77	−4.16	0.000	−11.52	−4.01	−34.7
2002	Post 4	4.57 (1.32)	6.86 (1.32)	−2.29	−1.22	0.227	−6.04	1.47	−33.3
2003	Post 5	3.72 (1.32)	7.01 (1.32)	−3.29	−1.76	0.084	−7.05	0.46	−47.0

of grids (Fig. 5). Over the five trap periods pre-treatment recapture rates averaged 27.3% and 26.7% on control and treatment grids, respectively. Over the five trap periods post-treatment, recapture rates increased to 49.4% and 51.4% on control and treatment grids, respectively (Fig. 5).

3.4. Surface density and population estimates

Relative density estimates for Ensatina on the four sets of grids based on the initial captures ranged from a high of 456.58/ha (SE = 12.66) on the control grids before treatment, to a low of 257.23/ha (SE = 22.11) on the treatment grids post-treatment (a 56.3% difference) (Table 4). Treatment grids prior to treatment had the second highest relative density estimates 407.82/ha (SE = 18.99), followed by the control grids after treatment (393.06/ha) (SE = 19.87) (Table 4). The density of salamanders on treatment grids declined 36.9% following treatment.

The highest population estimate was 690.94/ha (SE = 131.38) on control grids following treatment (Table 4); these grids provided the most sampling increments without a treatment effect and so probably represent a more accurate estimate of what would constitute a reference population for this area. The lowest population estimate was 314.68/ha (SE = 45.91) on the treatment grids post-treatment (21.7% lower than the pre-treatment estimate), which is consistent with the lowest density estimate; both values indicating a distinct treatment response. The control grids before treatment had the second highest estimate (510.90/ha) (SE = 40.94), followed by the treatment grids prior to treatment (401.84/ha) (SE = 86.51) (Table 4).

Table 4
Population and relative density estimates. Standard errors are in parentheses and ranges are min – max. Population estimates were calculated using the modified Schnabel method (Chapman, 1954); relative density estimates were based on raw counts of initial captures of salamanders on each grid over the entire study. Before values are based on three years of data prior to treatment (trap periods 1–5), after values on the five years following treatment (trap periods 6–10).

	Ensatina per hectare [per m^2]	
	Before	After
Population estimates		
Control	510.90 (40.94) [0.05] 432.9–622.9	690.94 (131.38) [0.07] 245.8–1335.5
Treatment	401.84 (86.51) [0.04] 137.5–725.3	314.68 (45.91) [0.03] 222.9–362.1
Density estimates		
Control	456.58 (12.66) [0.05] 418.9–473.5	393.06 (19.87) [0.04] 348.6–437.0
Treatment	407.82 (18.99) [0.04] 364.2–452.7	257.23 (22.11) [0.03] 210.7–313.5

3.5. Body condition

Overall, body condition indices (BCI) declined moderately for females, with a downward trend most evident in the last two fall periods post-treatment (Fig. 6). Male BCIs remained relatively stable over the eight years of the study (Fig. 6). The ANOVA revealed significant interactions (female: $F = 174.06$, $p < 0.0001$, df = 30.1; male $F = 214.13$, $p < 0.0001$, df = 29.6), indicating that the change in treatment means differed from the change in control means in at least one of the time periods (time × BCI interaction). The greatest differences in mean BCI values between the two sets of grids for the females was during the last sample period, so the significant interaction is likely a response to this difference, however the variability was too great for the pairwise test to be significant (Table 5). For the males, the greatest difference between grids also occurs in the last trap period (Fig. 6), but the high variability among the control grids is likely why the pairwise test was not significant (Table 5). After treatment the male and female BCI values were not different between control and treatment grids (Table 5).

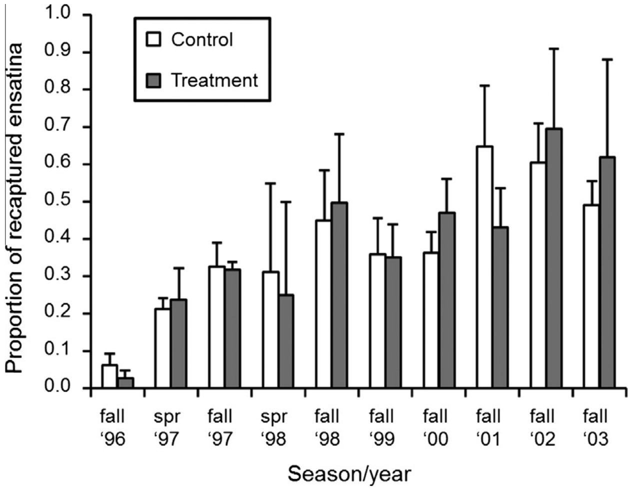

Fig. 5. Proportion of Ensatina salamanders that were recaptures in each trap period on treatment and control grids. Error bars indicate standard errors.

4. Discussion

Most members of plethodontid salamander populations are subterranean with typically only 2–32% of individuals present on the forest floor even under optimum conditions (Taub, 1961). This means that surface sampling methods repeated over short time periods typically yield few recaptures, resulting in population estimates with a high degree of variability (Bailey et al., 2004). Hyde and Simons (2001) found that active night sampling under climatic conditions favorable for woodland salamander surface activity (moderate temperatures and high humidity) was the most effective of the four methods they examined in the Appalachian Mountains (see also Buderman and Liebgold, 2012). However, these workers did not evaluate pitfall traps. Pitfall traps are a passive night sampling method because it is primarily the nocturnal movements of salamanders that yield captures; captures that are highest under favorable climatic conditions. By using large numbers of pitfall traps per trap grid over an extended period of time (eight years),

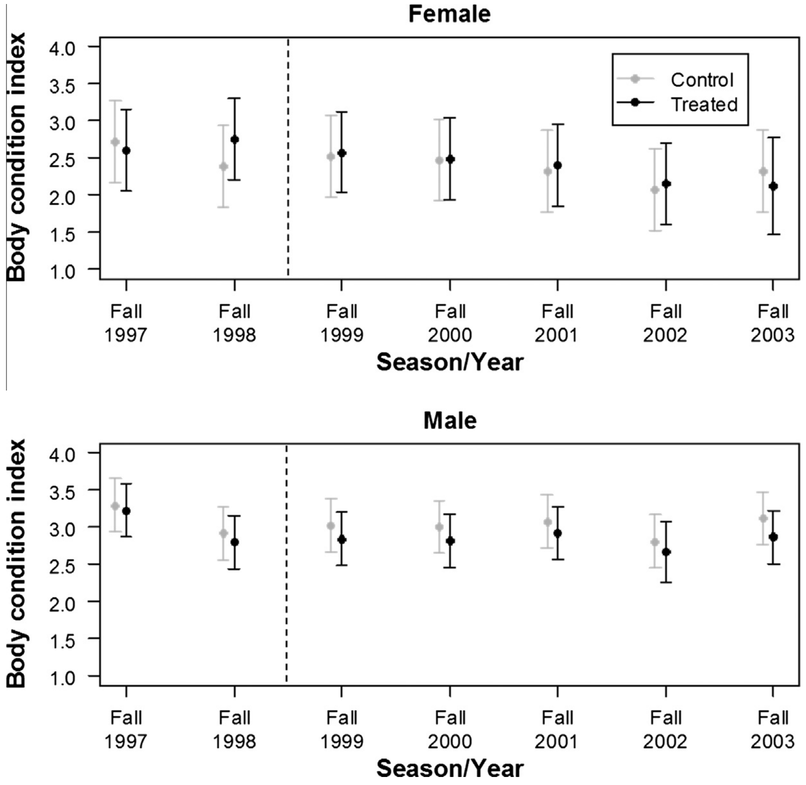

Fig. 6. Differences in fall body condition indices (BCI) for: females and males between control and treatment grids in each year of the eight year study. The error bars are plus and minus 1.96 standard errors (=95% confidence intervals).

Table 5
Results of the BACI ANOVA comparing body condition indices (BCI) for male and female Ensatina on treatment and control grids before (1996–98) and after (1999–2003) treatment. BCI was calculated by the scaled mass index method (Peig and Green, 2009) using weight and snout vent length. The first trap period was not included because salamander weights were not taken in the first year. The *t*-test signs reflect the changes in the treatment grids minus the changes in the control grids, not the differences between the means.

Year	Treatment mean (SE)	Control mean (SE)	Difference	*T*	*p*	95% lower	95% upper	Percent difference (%)
Males								
1996–98	3.02 (0.14)	3.10 (0.12)	0.089	−0.47	0.644	−0.302	0.479	−2.9
1999	2.85 (0.18)	3.03 (0.11)	−0.091	−0.32	0.750	−0.661	0.480	−5.9
2000	2.82 (0.18)	3.01 (0.11)	−0.099	−0.35	0.728	−0.670	0.472	−6.2
2001	2.92 (0.18)	3.08 (0.15)	−0.066	−0.23	0.816	−0.637	0.504	−5.0
2002	2.69 (0.21)	2.81 (0.17)	−0.055	−0.19	0.854	−0.660	0.549	−4.4
2003	2.87 (0.18)	3.12 (0.34)	−0.163	−0.58	0.566	−0.734	0.407	−8.1
Females								
1996–98	2.68 (0.13)	2.56 (0.13)	−0.470	−1.66	0.103	−1.039	0.100	4.7
1999	2.58 (0.18)	2.53 (0.18)	−0.246	−0.52	0.604	−1.196	0.704	2.2
2000	2.49 (0.18)	2.47 (0.18)	−0.360	−0.75	0.459	−1.332	0.613	0.9
2001	2.41 (0.18)	2.32 (0.18)	−0.290	−0.61	0.548	−1.259	0.678	4.0
2002	2.16 (0.18)	2.07 (0.18)	−0.134	−0.28	0.781	−1.103	0.834	4.0
2003	2.12 (0.21)	2.32 (0.18)	−0.633	−1.32	0.194	−1.160	0.336	−8.2

in combination with multiple trap grids, we attained relatively high recapture rates (Fig. 5), producing relatively robust population estimates (Table 4). These results also gave us high confidence in our tests of the main question, the impacts of thinning.

The harvest technique of thinning individual trees from forest stands, while generally having negative effects on salamander populations (e.g., Karraker and Welsh, 2006), the effects often appear to be temporary, with numerous studies documenting minimal effects and relatively rapid recovery (e.g., Homyack and Haas, 2009; Semlitsch et al., 2009; Olson et al., 2014). Such results however, can only be assured given particular harvest thresholds are not exceeded (e.g., Burivalova et al., 2014). We are aware of two previous studies of the impacts to amphibians where helicopters were used to thin or harvest timber, both in the southeast and both represented a range of treatments (Clawson et al., 1997; Perison et al., 1997). Clawson et al. (1997) in a 2-yr study found that following initial reductions, the numbers recovered but the community composition shifted, with salamander densities reduced while anuran densities increased post-treatment. Perison et al. (1997) also found salamander numbers reduced on treatment sites two years after treatment. In this much longer study of helicopter thinning on Ensatina surface counts the salamanders were significantly reduced for the first three years post-treatment; however, by the fourth year changes on control plots did not differ from changes on treatment plots. Despite this apparent convergence, however, prior to thinning the treatment grids averaged 3.0% fewer Ensatina compared to the control grids, while four years after thinning treatment grids averaged 33.3% fewer Ensatina than control grids, with differences at the end of the study reaching 47.0%. Regardless of the lack of statistical significance these differences were sufficiently large to question any conclusion that there was recovery on treatment plots. Rather they suggested that an unanticipated effect has reduced surface activity across all eight grids, resulting in low counts on both treatment and controls not attributable to the thinning.

Given what is known about the requirements of plethodontid salamanders for specific surface microclimatic conditions (e.g., Crawford and Semlitsch, 2008; Peterman and Semlitsch, 2013; Welsh and Hodgson, 2013) reductions in their surface activity is not unusual. Further, such changes in surface conditions can negatively influence surface activity without any evidence of long-term impacts on fitness. Consequently, the low counts on both sets of grids in 2002 and 2003 clearly did not resolve the question of whether or not there was recovery. The convergence in counts on control and treatment grids at the lowest fall numbers of the entire study (Fig. 4), in conjunction with the high percent difference between the two sets of grids four and five years post-treatment (−33.3% and −47.0%, respectively; Table 3), suggested a biologically significant effect had reduced counts across all grids by the last two censuses, rendering the surface count data equivocal evidence of recovery.

To further explore this key question we turned to the body condition data. Body condition (BCI) can serve as a highly informative indicator of population status given it is a proxy for fitness (Peig and Green, 2009; Rohr and Palmer, 2013). Furthermore, with an organism whose populations are mostly below the surface at any time (Taub, 1961), a parameter that can help to establish their overall fitness from a relatively small sample of individuals has its advantages. Given the lack of significant differences in BCI values for either sex between control and treatment grids post-treatment (Table 5), we interpreted the body condition data as supporting the conclusion that the thinning project had minimal short-term effects on the populations on treatment grids. Contrarily, the one signal we did find in the BCI data was the approximately 50% increase for both sexes in the percent differences between control and treatment grids in the last sample period, a difference that while not statistically significant may be biologically significant, and may suggest a possible lag effect on BCI from the treatment that our study was not sufficiently long to unequivocally demonstrate (e.g., Hawkes and Gregory, 2012).

The only effect of thinning on Ensatina we demonstrated unequivocally was to reduce the counts of individuals active on the surface on the treatment grid from 1999 through 2001. This result is consistent with a reduction in canopy, an action that incurs more light reaching the ground thereby increasing temperatures and lowering moisture (e.g., Rambo and North, 2009). While the effects of canopy reduction on amphibians can vary by species (e.g., Felix et al., 2010), there is little debate that the overall effects on woodland salamanders is negative (Tilghman et al., 2012). Surface activity, while vital for foraging and reproduction, can none-the-less be substantially reduced because of the physiological constraints on these salamanders (Feder, 1983; Homyack et al., 2011). However, the body condition analysis supported the conclusion that the treatment was not immediately detrimental to individual fitness, even though the reduction in the population estimates on the treatment grids (Table 4) suggests at least a temporary negative impact on those populations.

Considering our three metrics together, we interpret the results of our experiment as evidence that the thinning had short-term effects on Ensatina surface activity, and possibly on population numbers on the treatment grids at Pilot Creek. However, surface counts more closely match those on control grids within a few years post-thinning, with the similarities in body condition supporting a conclusion of minimal treatment effects. These results were consistent with other studies on the impacts of thinning on woodland salamanders that demonstrated short-term reductions in their numbers, and steeper recovery trajectories than are typical of those harvest techniques that remove greater amounts of canopy (e.g., Homyack and Haas, 2009; Semlitsch et al., 2009; Olson et al., 2014). It is appropriate in this regard to view the range of silvicultural techniques as a continuum, with the relative effects on particular species likely to vary not only by technique and taxa, but also by region (Burivalova et al., 2014). However, small poikilotherms such as herpetofauna, and particularly terrestrial amphibians requiring surface moisture, are the most sensitive to alterations of forest structure that directly affect their requisite microclimates (see Homyack et al., 2011).

Three hypotheses have been proposed to explain declines in woodland salamanders post-harvest: (1) mortality, (2) retreat, or (3) evacuation (Semlitsch et al., 2008). Our finding of increased recapture rates post-thinning regardless of treatment best matches the retreat hypothesis for some members of the populations on both sets of grids. However, the evidence of declines across both sets suggests mortality at a wider scale unrelated to the thinning treatment, and indicating that these three hypotheses are not necessarily mutually exclusive. Consequently, perhaps the more interesting result, and one where we can only speculate as to cause, is this reduction of surface counts across all the grids over the later part of this study. This may be evidence of a greater negative effect at a regional or larger scale (e.g., Emmerson et al., 2005; Rohr and Palmer, 2013). Similar phenomena have been observed to negatively influencing plethodontid salamanders in other regions (e.g., Highton, 2005; Caruso and Lips, 2013; Caruso et al., 2014). Furthermore, recent studies have linked physiological constraints to susceptibility to global warming in other montane plethodontids (Bernardo and Spotila, 2006; Bernardo et al., 2007). If the causes are similar, the scale at which they are operating may be continental or greater, and a possible indication of planet-wide perturbations (e.g., Wake and Vredenburg, 2008; Wake, 2012).

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