



Meta-analysis of the effects of canopy removal on terrestrial salamander populations in North America

Joseph M. Tilghman, Shane W. Ramee, David M. Marsh*

Department of Biology, Washington and Lee University, Lexington, VA 24450, USA

ARTICLE INFO

Article history:

Received 30 November 2011
Received in revised form 22 March 2012
Accepted 27 March 2012
Available online 23 June 2012

Keywords:

Amphibian
Plethodan
Batrachoseps
Aneides
Forestry
Silviculture

ABSTRACT

Terrestrial salamander abundance in North American forests is closely associated with forest characteristics, and salamander populations typically decline following timber removal. However, salamander responses to timber harvest vary considerably from one study to the next – some studies have shown limited or no effects whereas others have found harvest-related declines of up to 95%. To estimate overall effect sizes of timber harvest on salamander populations and to examine factors that contribute to variation in salamander responses to harvest, we carried out a meta-analysis of published studies of the effects of timber harvesting on terrestrial salamander abundance. Based on 108 salamander species/treatment combinations from 24 studies, we found mean harvest-related declines ranged from 29% (95% CI = –2% to 51%) for long-term responses to partial canopy removal to 62% (95% CI = 29% to 80%) for short-term responses to clearcutting. Multivariate mixed models suggested that clearcutting had a modestly greater impact on salamander populations than partial harvest and that decreases following harvest were more pronounced at sites with warmer summer high temperatures. In addition, active sampling of salamanders (e.g., surface counts) led to greater apparent effects of timber harvest than passive sampling (e.g., cover boards or pitfall traps), suggesting that sampling methodology influenced the perceived effects of harvest. In the studies evaluated, salamander numbers almost always declined following timber removal, but salamanders were never extirpated and populations typically increased as forests regenerated.

© 2012 Elsevier Ltd. All rights reserved.

1. Introduction

Timber harvest can affect North American forest ecosystems through reduction of canopy cover, alteration of coarse woody debris, disturbance of soil on the forest floor, and numerous other processes (Aust and Blinn, 2004; Aikens et al., 2007; Vanderwel et al., 2009). These changes frequently affect abundance of forest-associated species. For mammals, effects of harvest may differ greatly among species, with some species decreasing in abundance and others increasing (Zwolak, 2009). Small scale harvest in North American forests also has heterogeneous effects for birds, with many species decreasing in abundance but some species increasing (Vanderwel et al., 2007; Forsman et al., 2010). For amphibians, timber harvest typically decreases both abundance and diversity (DeMaynadier and Hunter, 1995), and examples of species that benefit from harvesting are difficult to come by.

Among amphibians, reductions in abundance in response to harvest appear to be particularly common for terrestrial breeding salamanders (DeMaynadier and Hunter, 1995). Terrestrial breeding salamanders (hereafter “terrestrial salamanders”) are the most

abundant vertebrates in many North American forests; forests in the Appalachian range and Pacific Northwest can have terrestrial salamander densities exceeding 2000/ha (Burton and Likens, 1975; Petranks et al., 1993; Stebbins and Cohen, 1995). Given their abundance, terrestrial salamanders can influence the invertebrate composition in the detrital ecosystem of the forest floor (Wyman, 1998; Walton and Steckler, 2005). Forest enclosures in New York with predation by salamanders had significantly reduced invertebrate numbers compared to no-salamander treatments, and salamander foraging ultimately influenced decomposition rate (Wyman, 1998). Terrestrial salamanders are also consumed by other forest vertebrates, including snakes (Ducey and Brodie, 1983), birds (Brodie and Brodie, 1980), and small mammals (Brodie, 1977).

Abundance of terrestrial salamanders in forest ecosystems and their ecological importance makes salamanders a conservation concern. Because salamander abundance may depend on moisture (Jaeger, 1980; Grover, 1998), temperature (Jaeger, 1980), leaf litter (Jaeger, 1980; Welsh and Droege, 2001), and coarse woody debris (Grover, 1998; Butts and McComb, 2000), changes in forest characteristics through timber removal could have a substantial impact on salamander populations (Welsh and Droege, 2001). Terrestrial salamanders can be important indicators of forest health (Welsh

* Corresponding author. Tel.: +1 540 458 8176; fax: +1 540 458 8012.
E-mail address: marshd@wlu.edu (D.M. Marsh).

and Droege, 2001, but see Kroll et al., 2009), and terrestrial salamander populations are frequently monitored in this context (McKenny et al., 2006; Greenwald et al., 2008). In addition, many terrestrial salamander species have highly restricted distributions, and several (e.g., Shenandoah salamanders [*Plethodon shenandoah*], Desert Slender salamanders [*Batrachoseps aridus*], Red Hills salamanders [*Phaeognathus hubrichti*]) are listed as federally endangered in the United States. Others species (e.g., Peaks of Otter salamanders [*Plethodon hubrichti*], Cow Knob salamanders [*Plethodon punctatus*]) occur almost entirely on small areas of public land, and forestry practices in these areas are carried out in ways designed to limit impacts on salamander populations (USFS, 2005).

Many studies have attempted to gauge effects of canopy removal on terrestrial salamanders. These studies have varied in methodology, in time scale, and in type of harvest evaluated. Some studies have shown a substantial negative effect of even partial canopy removal on salamander abundance (Welsh and Lind, 1988; Knapp et al., 2003). Other studies, especially short term studies, have not found generalizable effects of timber harvesting on salamanders but have emphasized the importance of structural characteristics such as fallen debris and burrows (Cole et al., 1997; McKenny et al., 2006). Whereas the vast majority of clearcutting studies have found substantial negative effects on salamander abundance (Petranka et al., 1993; Dupuis et al., 1995; Ash, 1997), there are disparities in reported amounts of time required for salamander populations to recover to pre-disturbance levels. The interval estimated for the recovery of salamander populations varies between 25 years (Ash, 1997; Harper and Guynn, 1999) and 70 years (Petranka et al., 1993) in the southern Appalachians, and it may be between 30 and 100 years in the Pacific Northwest (Welsh et al., 2008).

To identify general patterns in the responses of terrestrial salamanders to timber harvesting, we carried out a meta-analysis of published studies that compared terrestrial salamander abundance between harvested and unharvested stands. Terrestrial salamanders are particularly well suited for a meta-analytic approach because species tend to be ecologically similar. Unlike birds and mammals, there are no species that are known to prefer gaps or open habitats. In fact, one distinguishing feature of this group is a high degree of diversification without corresponding morphological changes (Highton, 1995). As such, there are few “apple and orange” comparison problems (Arnqvist and Wooster, 1995) in analyzing data across terrestrial salamander species, and it is reasonable to believe that some common set of mechanisms could link timber removal to changes in terrestrial salamander populations.

Our meta-analysis had three major goals. First, we sought to estimate the means and confidence intervals for the effects of timber harvest on terrestrial salamander abundance. We estimated overall mean effects (averaged across all harvest methods and timescales), as well as effects for short-term salamander responses (<5 years post-harvest), for long-term responses (>10 years post-harvest), for responses to clearcutting, and for responses to partial canopy removal (e.g. group selection, individual selection, shelterwood, or thinning). Our second goal was to determine the factors that were associated with variation in observed effect sizes across studies. Factors examined included the degree of canopy removal, site-specific climate, stand size, and several aspects of study methodology such as sampling technique and whether the study was prospective or retrospective. We used multivariate mixed models to determine which collections of factors best explained why salamanders declined more in some studies than in others. Third, we carried out an analysis of the pattern and rate of salamander population increase over time following harvest. We fit both a linear increase model and a saturating model to determine whether salamander populations had recovered to pre-harvest levels by the end of the longest-term studies available.

2. Materials and methods

2.1. Studies and inclusion criteria

We performed a comprehensive search for data from all published studies and technical reports that compared terrestrial salamander abundance in harvested areas with abundance in unharvested areas. These included cross-sectional studies, which compared stands with different histories of timber removal, and prospective studies, where abundance was measured before and after harvest. Studies of edge effects, the effect of riparian buffer zones, or the effect of burning or herbicide treatment were not included in our analysis. We defined terrestrial salamanders as salamanders without an aquatic larval stage. Terrestrial salamanders included all species of the genera *Plethodon*, *Ensatina*, *Batrachoseps*, *Phaeognathus*, and *Aneides*, as well as direct developing species of *Desmognathus* (*D. wrighti* and *D. aeneus*).

We used several methods to identify relevant studies. First, we searched Scopus and Google Scholar using combinations of the following terms: salamander, amphibian, forestry, *Plethodon*, stand age, *Desmognathus*, silviculture, terrestrial, logging, forest, population response, and harvest. We then used the reference sections of these papers to find additional studies. As a final check, we sent our compiled list to several experts in the field to inquire about missing references. The full list of studies used is given in the Supplementary materials.

2.2. Data extraction

For each study, a number of variables related to site location, climate, study design, harvest type, sampling method, and species were extracted and added to a database (Table 1, see Supplementary materials for the complete database). Not all covariates were available for every study, so when information was missing we attempted to contact the authors to get this information. In some cases, data from the same longitudinal studies were published in more than one paper; in these situations, we used data only from the most complete paper.

For an effect size measurement, we used the log response ratio (Ln RR) of salamander abundance to timber removal (Hedges et al., 1999). Ln RR is calculated as $\ln(\text{treatment mean}/\text{control mean})$, where the treatment mean reflects the mean salamander abundance in each harvested treatment and the control mean reflects the mean in unharvested or pre-harvest sites. Abundance measures from the various studies included counts, population indices, and density estimates from mark-recapture. There were no significant differences in effect size across these categories of abundance estimates (likelihood ratio = 0.60, $p = 0.78$), though there were only two sets of density estimates from mark-recapture available. Because treatment and control values were always calculated based on the same data type, response ratio can be interpreted as the proportional reduction in apparent salamander abundance in harvested sites. Ln RR is expected to have normally distributed error, and our effect size residuals did not deviate from this expectation (Kolmogorov–Smirnov test, $p = 0.63$). The variance of Ln RR is approximated by:

$$\frac{(SD_E)^2}{n_E \bar{X}_E^2} + \frac{(SD_C)^2}{n_C \bar{X}_C^2}$$

where \bar{X}_E and SD_E denote the mean and standard deviation of the experimental group, \bar{X}_C and SD_C denote the mean and standard deviation of the control group, and n_E and n_C denote the number of replicates in each group (Hedges et al., 1999).

Many studies produced multiple response ratios either because they recorded data for multiple species or because they compared

Table 1

Summary of variables used in the multivariate analysis and their sources. Table shows variables related to study sites, study methodology, forestry techniques, and species. "Info from individual studies" indicates that the information came from the same publication as the relevant salamander data.

Variable	Type	Source
<i>Site variables</i>		
Annual precipitation	Continuous	NOAA Weather Station Data
Elevation	Continuous	Info from individual studies
Max. mean monthly high temp	Continuous	NOAA Weather Station Data
Min. Mean monthly low temp.	Continuous	NOAA Weather Station Data
Mean high temp., sampling period	Continuous	NOAA Weather Station Data
Mean low temp., sampling period	Continuous	NOAA Weather Station Data
Mean temp diff., sampling period	Continuous	NOAA Weather Station Data
Region	Categorical	Info from individual studies
<i>Methodological variables</i>		
Pre-harvest salamander data?	Yes/no	Info from individual studies
Cross-sectional study?	Yes/no	Info from individual studies
Randomization of treatments?	Yes/no	Info from individual studies
Passive/active sampling	Categorical	Info from individual studies
<i>Forestry variables</i>		
Clearcut/partial removal	Categorical	Info from individual studies
Proportion canopy removal	Continuous	Info from individual studies
Mean stand area	Continuous	Info from individual studies
<i>Species variables</i>		
Species group	Categorical	Info from individual studies
Species size	Categorical	Petranka (1998)

multiple methods of timber harvest. We calculated all possible response ratios for each study and then used a study-specific random effect to account for multiple data points from the same study. We excluded all response ratios based on fewer than 10 individual salamanders in controls (unharvested or pre-treatment) because we considered these estimates to be unreliable.

2.3. Statistical methods

Linear mixed effects models are the most commonly used tool for meta-analysis of published data (Gurevitch and Hedges, 1999; Sutton et al., 2000). Mixed effects models for meta-analysis typically include fixed effects for factors that might influence the effect size (e.g. harvest intensity, stand size) and random effects that can account for random differences among studies. Random effects can also be used to account for effect size measurements that are non-independent because they come from the same study or the same research group. Mixed effects models are conservative in that they assume heterogeneity among effect size estimates beyond sampling error. In ecological research spanning different species and study sites, this sort of heterogeneity is expected (Gurevitch and Hedges, 1999).

Studies included in our analysis varied greatly in terms of salamander counts and the number of replicate plots. Typically, response ratios in meta-analysis are weighted to account for these sources of variation (Gurevitch and Hedges, 1999; Sutton et al., 2000). Ideally, effect size estimates are weighted by the inverse

of the variance in the effect size estimate. This method has the greatest theoretical justification, but requires data on the standard deviation of treatment and control samples, which are sometimes unreported. Variance weighting also excludes studies with no replication (which are not infrequent in forestry), as these studies produce response ratios with zero variance. A more inclusive alternative to variance weighting is to weight response ratios by the number of treatment replicates (Hedges and Olkin, 1985; Rosenberg et al., 1997). Replicate-weighting allows for inclusion of more studies because papers almost always report numbers of replicates and because unreplicated studies are not excluded. However, weighting by replicates assumes that sampling variance is independent of the number of replicates. In practice, smaller studies may tend to sample more intensively, so weighting by the number of replicates can overweight larger studies. To account for these tradeoffs, we performed our primary analyses using replicate weighting but then repeated our analyses using variance weighting.

We used weighted mixed-effects models in three sets of analyses. The first set of analyses estimated summary effect sizes across studies and their 95% confidence intervals. Rather than compute a single effect size estimate, we computed a series of estimates based on different assumptions and different subsets of studies. We computed overall effect size for all studies in four ways: (1) weighting by the number of replicates; (2) weighting by the inverse of the variance; (3) not weighting at all; and (4) including only randomized, prospective studies (i.e., the highest quality studies) but not weighting. Because we expected effect sizes to differ between sites that underwent clearcutting and sites that underwent partial canopy removal, we also computed effect sizes separately for these classes of studies. In addition, we divided response ratios based on whether they came from short-term measurements (<5 years after harvest) or long-term measurements (>10 years after harvest), as an initial decline followed by an increase is the expected response to timber harvest (Petranka et al., 1993). Thus, we present a range of effect size estimates based on different weighting schemes, different levels of canopy removal, and different timescales.

Our second analysis focused on identifying factors that explained variation among studies in effect size estimates (Table 1). Variables that had strong *a priori* empirical or theoretical justification (clearcut versus partial removal, salamander body size, taxonomic group, and study region) were passed directly to a final model comparison. However, for variables without *a priori* support (i.e. climate variables and study design variables), we first used variable reduction strategies to identify a set of variables that might be related to effect size. To decrease the number of variables considered at once, we evaluated variables related to climate in one analysis and variables related to study design in a second analysis. For each of these variable reduction analyses, we started with a full model and dropped variables sequentially in order of lowest contribution to the model likelihood. Variables that made at least a marginal contribution to the likelihood ($p < 0.25$ in a likelihood ratio test) were retained for the next stage of analysis. Although sequential procedures can produce unreliable results (Burnham and Anderson, 2002), in this case, both reverse and forward sequential procedures identified a single climate variable (high temp – the mean high of the warmest month) and a single study design variable (active versus passive sampling) that were plausibly related to effect size. The temperature variable was calculated from high temperature data at the nearest NOAA weather station, and the active versus passive search variable distinguished active search techniques, which we defined as surface counts or searches under natural cover, from passive capture techniques, which involved placing sampling units (e.g. pitfall traps or cover boards) in the field for salamanders to naturally colonize.

Following variable reduction, we compared a series of models for response ratios of terrestrial salamanders to timber harvest. To allow for maximum inclusion of data, we used the response ratio at the conclusion of each study with number of years since harvest as a covariate. We compared models with and without each of the primary factors being considered (clearcut versus partial removal, salamander size, taxonomic group, region, maximum temperature, and active versus passive sampling), with several constraints. First, size and taxonomic group could not be entered together because some groups were uniformly large or small. Second, region and group could not be entered together because some groups are found exclusively in the eastern or western United States. Finally, we note that we did not correct body size for phylogenetic relatedness because correlated errors cannot easily be accounted for within mixed models. Our full model took the form: $\ln(\text{RR}) \sim \text{clearcut} + \text{salamander size} + \text{hightemp} + \text{region} + \text{sampling} + 1|\text{study}$.

Combining explanatory variables yielded a total of 40 models, and these models were compared using Akaike's Information Criteria (AIC) adjusted for small sample sizes (AIC_c; Burnham and Anderson, 2002). We calculated AIC_c model weights to represent the relative evidence in favor of each model in the set. Finally, we used the full set of models to calculate model-averaged parameter estimates for each of the primary factors being considered (clearcutting, salamander size, region, hightemp, and survey method). We repeated the analysis for the smaller set of response ratios that could be variance-weighted ($n = 53$) and for a separate set of response ratios reflecting only short-term responses to harvest (i.e., <5 years post-treatment, $n = 55$).

For two variables, mean area logged in each treatment (i.e., stand size) and proportion of canopy removed in partial removal, we had only limited data from published studies. Because mixed models cannot easily account for missing data, we examined each of these variables in a separate set of analyses. These targeted analyses compared models with and without area logged and proportion of canopy removed in both the presence and absence of covariates from the multivariate analysis. Likelihood ratio tests were used to determine the statistical significance of each of the two variables (i.e., stand size and proportion canopy removed).

Our third analysis was an examination of the rate and pattern of salamander population increase following canopy removal. Using the best model from previous model comparisons, we compared a linear increase following harvest (as incorporated in the primary model comparison) to a saturating function that asymptotes at a response ratio of one ($1 - a * e^{(-bt)}$). This model starts at time zero with an initial response to harvest (determined by the constant "a"), rises as populations recover, but then flattens out to unity as the effect of past harvest disappears. Thus, this comparison asks whether there is evidence that sites have fully recovered in the longest term studies for which we have abundance data. In addition, we examined overall response ratios for subsets of studies at least 40 years post-harvest and ≥ 80 years post-harvest to determine whether response ratios supported the idea that salamander populations had recovered over these time intervals. All analyses were performed in R 2.12 package nlme (R Development Core Team, 2008).

3. Results

3.1. Mean effect sizes

We initially compiled 131 response ratios from 26 studies. Of these, 23 response ratios were excluded because total number of salamanders in the controls was less than 10 ($n = 15$) or because forestry techniques were not clearly articulated ($n = 8$). That left 108 response ratios from 24 studies for use in estimating overall

effect sizes. For the multivariate analyses, additional studies were excluded because they were missing data for one or more of the explanatory variables. In the replicate-weighted analysis, 86 response ratios from 20 studies contained complete data. The variance weighted analysis eliminated a further 33 response ratios because studies were unreplicated or because within-study variance was not reported and could not be obtained from the authors. Thus, variance weighted analyses were based on 53 response ratios from 13 studies.

Mean effect size estimates for timber harvest ranged from a 29% reduction ($\ln \text{RR} = -0.35$) in salamander abundance for long-term studies of partial canopy removal to a 62% reduction ($\ln \text{RR} = -0.97$) for short-term studies of clearcutting (Table 2). Weighting methodology had a moderate influence on mean effect sizes; including all harvest techniques, variance weighting yielded a mean reduction in salamander abundance of 38%, replicate weighting yielded a mean reduction of 43%, and no weighting yielded a mean reduction of 46% (Table 2). Using only the highest quality studies (i.e., randomized, prospective studies) produced a slightly higher effect size overall (49% reduction) but a somewhat smaller effect size for clearcutting (54% reduction). In general, these decreases were statistically significant – only long-term studies of partial removal had a confidence interval that overlapped zero (95% CI = -2% to 51%).

3.2. Multivariate analysis of response ratios

For the multivariate analysis using replicate weighting, the best model included all of the five factors (clearcutting, salamander size, survey type, high temp, and region, see Table 3). Models that excluded either region, clearcutting, or survey type had only slightly lower support ($\Delta \text{AIC}_c = 0.42, 0.82, \text{ and } 0.94$ respectively). In terms of the individual parameters, greater responses to harvest were associated with increased high temperatures, larger-bodied salamanders, clearcutting, the Western North America region (primarily the Pacific Northwest), and active sampling techniques (Table 4). The temperature effect was equivalent to a 15% greater harvest-related decline for every 5 °C increase in maximum monthly high temperature, and the size effect corresponded to a 47% greater decrease in small bodied versus large bodied species. Both of these effects had confidence intervals that did not overlap zero. In addition, clearcutting produced declines 24% greater than did partial canopy removal, active sampling yielded declines 27% larger than did passive sampling, and declines were 27% greater in the western US than in the eastern US. The 95% confidence intervals for these latter coefficients did overlap zero (Table 4).

Although species group was a less supported variable than the combination of salamander size and region, it is nevertheless useful to examine the results for the various species groups (Fig. 1). Overall, the greatest reductions with timber harvest were seen in the *Plethodon vehiculum* group (*P. vehiculum*, *P. elongatus*, *P. dummi*, *P. vandykei*, and *P. stormi*), which showed a significantly greater reduction (mean = 62%) than the other groups. The weakest effects were found in the *Batrochoseps* group (*B. attenuatus*) and the *Aneides* group (*A. ferreus*, *A. lugubris* and *A. flavipunctatus*), both of which had response ratios near zero. Other species groups showed intermediate responses.

The variance-weighted analysis on the subset of 53 response ratios generally supported much simpler models and differences among model fits were small (Table 5). All of the models in the best set included survey type, and some also included combinations of clearcutting, region, and salamander size (Table 5). In terms of the individual parameters (Table 4), active surveys showed a mean salamander decline 47% larger than did passive surveys, and clearcutting produced a 35% decrease beyond what was seen in studies of partial canopy removal – both of these coefficients had 95% CIs that

Table 2

Summary of effect size estimates for subsets of studies delineated by forestry type (clearcutting, partial canopy removal, or all approaches), the time scale at which salamander responses were measured, and the weighting approach used for effect size estimation. Mean effect sizes (ln response ratios) are shown along with their standard errors and the associated percent reduction in salamander abundance.

Forestry	Time-scale	N	Weighting	Effect size	SE	Reduction (95% CI)
All	All	108	None	−0.62	0.10	46% (34–56%)
All	All	108	Replicates	−0.59	0.13	43% (29–57%)
All	All	76	1/Variance	−0.47	0.13	38% (20–51%)
All	All	28	High quality	−0.67	0.16	49% (30–63%)
Clearcut	All	49	Replicates	−0.87	0.18	58% (41–70%)
Clearcut	All	7	High quality	−0.77	0.30	54% (17–74%)
Clearcut	Short (<5 years)	22	Replicates	−0.97	0.32	62% (29–80%)
Clearcut	Long (>10 years)	28	Replicates	−0.86	0.23	50% (34–73%)
Partial cut	All	55	Replicates	−0.37	0.15	31% (8–48%)
Partial cut	All	21	High quality	−0.65	0.18	48% (26–63%)
Partial cut	Short (<5 years)	29	Replicates	−0.71	0.30	51% (11–73%)
Partial cut	Long (>10 years)	39	Replicates	−0.35	0.19	29% (−2% to 51%)

Table 3

Replicate-weighted models for the effects of timber harvesting on salamander abundance. The table shows all models within 7 AIC_c of the best model, a model containing all variables, and a model containing only an intercept and a covariate for time since timber removal. K is the number of parameters in each model, $\ln(L)$ is the log-likelihood of the data given the model, ΔAIC_c is the difference between each model and the best model in the set, and model weight represents the relative evidence in favor of each model.

Model	K	$\ln(L)$	AIC_c	ΔAIC_c	Model weight
Full model	9	−88.20	195.44	0	0.19
Clearcut + hightemp + size + survey type	8	−89.52	195.86	0.42	0.16
Hightemp + size + region + survey type	8	−89.72	196.26	0.82	0.13
Clearcut + hightemp + size + region	8	−89.78	196.38	0.94	0.12
Hightemp + size + region	7	−91.06	196.75	1.31	0.10
Hightemp + size + survey type	7	−91.33	197.29	1.85	0.08
Clearcut + hightemp + size	7	−91.58	197.78	2.34	0.06
Hightemp + size	6	−93.11	198.69	3.25	0.04
Clearcut + hightemp + group + survey type	13	−85.32	198.77	3.33	0.04
Hightemp + group + survey type	12	−86.51	198.83	3.39	0.04
Time and intercept only	4	−103.74	215.68	20.23	0.00

Table 4

Model-averaged parameter estimates from both replicate weighting and inverse variance weighting. Values shown are parameter estimates and standard errors averaged across candidate models weighted by their AIC weights. Standard errors and absolute percent decreases in harvest-related salamander abundance associated with each parameter value are also shown.

Parameter	Value	SE	Percent decrease	Weighting
Clearcut versus partial removal	−0.28	0.17	24	Replicate
Clearcut versus partial removal	−0.43 ^a	0.20	35	Variance
Maximum monthly high temp	−0.035 ^a	0.01	15 per 5 °C increase	Replicate
Maximum monthly high temp	−0.032	0.02	14 per 5 °C increase	Variance
Large versus small bodied	−0.63 ^a	0.17	47	Replicate
Large versus small bodied	+0.20 ^b	0.19	−18 ^b	Variance
Western region versus Eastern region	−0.31	0.19	27	Replicate
Western region versus Eastern region	−0.59	0.40	44	Variance
Active versus passive surveys	−0.31	0.16	27	Replicate
Active versus passive surveys	−0.60 ^a	0.20	45	Variance

^a Parameters with 95% confidence intervals that do not overlap zero.

^b Small bodied salamanders showed greater decreases than large bodied salamanders with variance weighting.

did not overlap with zero. The hightemp effect corresponded to a 14% decline for every 5 °C increase in maximum monthly high temperature, smaller bodied salamanders declined by 18% more than large-bodied salamanders, and salamanders in the Western region declined by 44% more than did salamanders in the Eastern region – these three coefficients had 95% CIs that included zero.

For response ratios from short-term studies (i.e., <5 years post-harvest), the best replicate-weighted models were a model with survey type only and a null model containing only an intercept to reflect an overall decrease in salamander abundance with harvest (Table 6). In general, model support was negatively related to the number of variables included, and no parameter estimates were significantly different from zero. With variance weighting, a model with only clearcutting versus partial removal had the greatest support (Table 6), and models with clearcutting and one

additional variable (region, size, or survey type) were only slightly less supported ($\Delta AIC_c < 2$). The large clearcut effect in the variance-weighted models corresponded to a mean decline of 85% in short-term studies of clearcuts versus a decline of only 18% in short-term studies of partial canopy removal.

3.3. Analysis of proportion canopy removal, stand size, and time

Data on the proportion of canopy removed in partial harvests and the mean stand size were only available from a selection of studies ($n = 27$ and $n = 61$, respectively), so these variables were considered separately. Although proportion of canopy removed was associated with response ratio ($\beta = -0.57$), this result was not significant in either univariate ($LR = 1.24$, $p = 0.26$) or multivariate analyses ($LR = 1.64$, $p = 0.20$). Mean stand size, which ranged

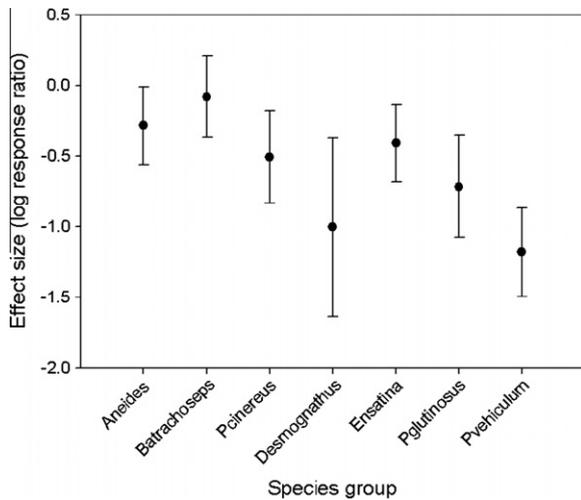


Fig. 1. Effect size across species groups based on replicate-weighting. Groups listed correspond to genera except Pcinerereus = *Plethodon cinereus* group, Pglutinosus = *Plethodon glutinosus* group, Pvehiculum = *Plethodon vehiculum* group.

from 0.02 ha to 113.5 ha, was unrelated to response ratio ($\beta = 0.002$, Fig. 2), and stand size did not approach significance in either univariate (LR = 0.05, $p = 0.83$) or multivariate analyses (LR = 0.49, $p = 0.48$). In addition, there was no evidence of interactions between stand size and clearcutting (e.g., effects of stand size for clearcutting but not for partial removal, LR = 1.29, $p = 0.52$) or between stand size and region (e.g. different effects of stand size across regions, LR = 1.03, $p = 0.60$). For both proportion canopy removal and mean stand area, results obtained with variance weighting or no weighting at all were similar to those obtained from replicate-weighting.

A follow-up analysis of years since harvest was used to investigate population recovery after timber removal. Years since harvest was negatively associated with response ratio using both replicate weighting (LR = 6.74, $p = 0.009$) and variance weighting (LR = 7.08, $p = 0.008$), indicating that salamander populations tended to increase over time following harvests (Fig. 3). The rate of population increase was about 3.3% per 10 years, meaning that a 33% decline would require 100 years for recovery. A saturating function for time (i.e., recovery that asymptotes at zero effect size) did not yield a better fit than a simple linear time effect ($\Delta AIC_c = 4.4$ for the saturating model with two additional parameters). In addition, we found no evidence for an interaction between time and clearcutting (i.e., different rates of recovery for clearcutting versus partial removal, LR = 0.31, $p = 0.56$) nor for an interaction between

time and region (i.e. different rates of recovery across regions, LR = 0.02, $p = 0.89$). For surveys occurring at least 40 years post-harvest ($n = 24$), effect size was not significantly different from zero ($p = 0.28$), though it was still negative (ln RR = -0.27 ± 0.24 SE). A similar result was observed for surveys at least 80 years post-harvest ($n = 11$, ln RR = -0.22 ± 0.26 SE). These response ratios correspond to respective declines of 24% and 20% at 40 years and 80 years post-harvest.

4. Discussion

Several results from our meta-analysis confirm patterns previously reported in individual studies of canopy removal and terrestrial salamanders. In particular, clearcutting reduced salamander abundance somewhat more (on average, 6–27%) than did partial canopy removal, and salamander populations tended to increase with time since harvest. For these results, the estimation of mean effect sizes and their confidence intervals is probably more notable than the results themselves. Several other results were novel findings that only emerged when we analyzed all studies collectively. First, we found that a site's maximum mean monthly high temperature was potentially important in determining the magnitude of salamander declines following harvest. Second, we found that active sampling for salamanders (e.g., active search or surface counts) consistently produced greater estimates of the effects of timber harvest than did passive sampling techniques (e.g., pitfall traps and cover boards).

The relationship between summer high temperatures and the effects of canopy removal are consistent with several recent findings about the thermal biology of terrestrial salamanders. High temperature increases the risk of desiccation, but it also increases energy requirements for salamander body maintenance (Gifford and Kozak, 2012). These energy requirements are further increased in recent timber harvests, by approximately 33% for *Plethodon cinereus* (Homyack et al., 2011). The higher energy requirements at increased temperatures could ultimately result in reduced abundance (Homyack et al., 2011) and could contribute to the establishment of elevational range limits (Gifford and Kozak, 2012). As suggested in Homyack et al., 2011, harvest techniques should maximize the retention of refugia such as coarse woody debris and promote regrowth of understory vegetation to reduce negative effects of heating on salamander energetics. Our finding that higher summer temperatures may be associated with increases in the effects of timber harvest is also potentially relevant to predicting the combined effects of forestry and climate change on salamander populations (Milanovich et al., 2010). However, it should be noted that 50 and 100-year forecasts for climate change at mid-latitudes (IPCC, 2007) are much less than the variation

Table 5
Variance-weighted models for the effects of canopy removal on salamander abundance. The table shows all models within 2 AIC_c of the best model, a model containing all variables, and a model containing only an intercept and a covariate for time since timber removal. K is the number of parameters in each model, $\ln(L)$ is the log-likelihood of the data given the model, ΔAIC_c is the difference between each model and the best model in the set, and model weight represents the relative evidence in favor of each model.

Model	K	$\ln(L)$	AIC_c	ΔAIC_c	Model Weight
Survey type	5	-57.89	126.32	0	0.10
Clearcut + region + survey type	7	-55.65	126.35	0.03	0.10
Clearcut + survey type	6	-56.92	126.61	0.30	0.09
Region + survey type	6	-57.04	126.86	0.54	0.08
Clearcut + size + survey type	7	-56.00	127.04	0.72	0.07
Clearcut + size + region + survey type	8	-54.88	127.11	0.79	0.07
Size + survey type	6	-57.46	127.68	1.36	0.05
Clearcut + hightemp + survey type	7	-56.47	127.96	1.65	0.04
Clearcut + region	6	-57.63	128.04	1.72	0.04
Hightemp + survey type	6	-57.71	128.19	1.87	0.04
Clearcut + hightemp + region	7	-56.60	128.23	1.92	0.04
Full model	9	-54.86	129.41	3.10	0.02
Time and intercept only	4	-62.65	133.30	7.33	0.00

Table 6

Replicate and variance-weighted models for the short-term (<5 years) effects of canopy removal on salamander abundance. The table shows a subset of the best fitting models in each set. *K* is the number of parameters in each model, *Ln(L)* is the log-likelihood of the data given the model, ΔAIC_c is the difference between each model and the best model, and model weight is the relative evidence in favor of each model.

Model	<i>K</i>	<i>Ln(L)</i>	AIC_c	ΔAIC_c	Model weight
<i>Replicate-weighted models</i>					
Survey type	4	-79.01	166.54	0	0.19
Intercept only	3	-80.19	166.61	-0.08	0.18
Region	4	-79.39	167.3	-0.76	0.13
Hightemp	4	-79.51	167.53	-0.99	0.12
Survey type + region	5	-78.59	167.95	-1.42	0.09
Region + hightemp	5	-78.79	168.35	-1.81	0.08
Survey type + hightemp	5	-78.8	168.38	-1.85	0.08
Size	4	-79.95	168.42	-1.89	0.07
Clearcut	4	-80.16	168.83	-2.29	0.06
Full model	8	-78.14	174.24	-7.7	0.00
<i>Variance weighted models</i>					
Clearcut	3	-66.54	141.81	0	0.5
Clearcut + size	5	-65.88	143.69	-1.88	0.19
Clearcut + hightemp	5	-66.11	144.17	-2.36	0.15
Clearcut + survey type	5	-66.53	144.99	-3.18	0.1
Full model	7	-65.26	148.39	-6.58	0.02
Survey type	4	-70.03	149.3	-7.49	0.01
Intercept only	3	-71.41	149.54	-7.73	0.01
Hightemp	4	-70.48	150.21	-8.4	0.01
Size	4	-70.56	150.36	-8.56	0.01

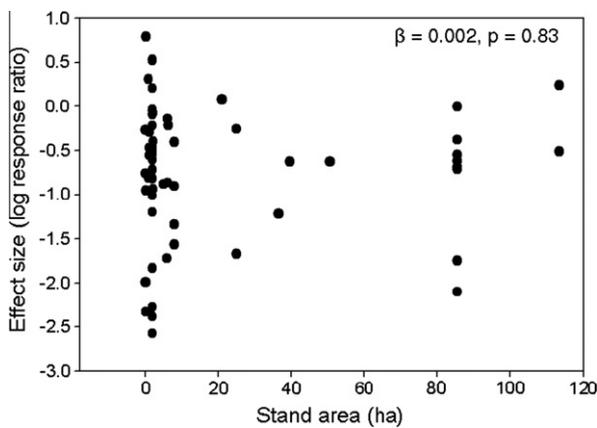


Fig. 2. Effects of stand area on response ratio. Stand area is the mean area of logged stands associated with each response ratio.

between our coolest sites (e.g., in Maine) and our warmest sites (e.g., in California).

The observed difference between effect size estimates from passive and active surveys was not predicted, though it is not surprising in retrospect. Because habitat changes accompany timber removal, active techniques that involve searching under coarse woody debris will necessarily differ between logged and unlogged sites. Also, increased use of subsurface retreats by salamanders in logged areas could lead to a greater apparent decrease with active searches in these areas. In addition, active search adds the additional possibility of confirmatory bias in searching (i.e., researchers would not expect to find as many salamanders in clearcuts, and this could influence their search intensity). However, while passive surveys are potentially less problematic than active surveys, passive surveys could also be biased by changes in habitat use. For example, cover boards added to sampling sites might be more attractive to salamanders in logged areas which may lack natural cover. Additionally, if timber harvest causes increased movement by salamanders (Ash and Bruce, 1994), salamanders may be more

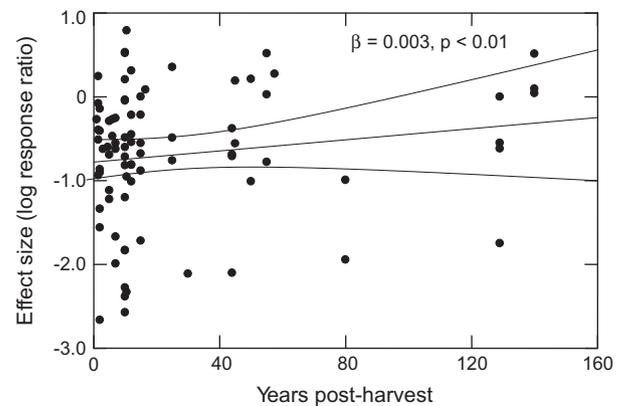


Fig. 3. Change in salamander populations over time following harvesting. Confidence bands show 95% CIs on the regression line. Effects sizes continued to decrease over time, but a saturating model did not provide a better fit, suggesting that in most cases, complete recovery had not been achieved over the longer-duration studies.

likely to end up in pitfall traps in logged areas. Welsh and Lind (1988) used both active, time-constrained searches and pitfall traps and found that a higher proportion of more motile salamander species were captured with pitfall traps compared with active searches. Studies in which individual salamanders are marked and capture probabilities are directly estimated in harvested and unharvested areas would be very helpful in determining the factors underlying the discrepancies between passive and active surveys.

Some of our negative results were both robust and potentially relevant to salamander conservation. For one, we found no effect of stand size on response ratio for stands ranging from <1 ha to more than 100 ha. Terrestrial salamanders typically have very small home ranges – in many cases only a few square meters (Kleeberger and Werner, 1982; Marvin, 1998). Thus, even stands of only a few hectares may be large enough that local effects of habitat change predominate over emigration and immigration in determining response to timber harvest (Cushman, 2006). From a methodological standpoint, we found no overall differences in mean effect sizes between prospective studies of canopy removal and cross-sectional studies that compared forest areas harvested at different times in the past. Although prospective experimental studies undoubtedly have advantages with respect to predictive inference, correlative studies do not appear to produce strongly biased estimates of salamander response to timber harvest.

In general, we found that effect sizes tended to decrease over time following harvest. For surveys >40 years post-harvest or >80 years post-harvest, mean response ratios were not significantly different from zero but were still negative in both cases (corresponding to a 24% and 20% decline). Overall, our findings are roughly consistent with recovery intervals suggested in individual papers – 70 years in Petranka et al. (1993) and 30–100 years in Welsh et al. (2008) – though the combined data do not necessarily show evidence for complete recovery. While viable salamander populations might exist without a complete recovery, a return to pre-disturbance levels could serve as a good index for forest recovery. Likens et al. (1978) reported a recovery time for forest floor organic matter in a northern hardwood forest of 65 years, which is similar to the recovery times reported for terrestrial salamander populations.

Meta-analyses typically rely on a single approach to weighting individual studies. We were thorough in applying various criteria for weighting, and we found some results that depended on the weighting approach. In particular, the effect of salamander body size differed between the weighting schemes, with large-bodied salamanders estimated to be more sensitive to harvests using

replicate-weighting but appearing to be less-sensitive using variance weighting. Given this discrepancy, we suggest that any inference about body size from our study would be untenable. The effects of the other factors were much more consistent between the weighting approaches. Though maximum monthly mean high temperature was significant only with replicate weighting, the associated parameter value was almost identical under variance weighting (i.e. -0.032 versus -0.035). For survey method, region, and clearcutting, effects were always in the same direction using both weighting methods, though they differed somewhat in magnitude.

One limitation of our results is that they are largely based on count data from in the original studies. Count data can be problematic because raw counts of animals confound actual abundance with detection rates (MacKenzie and Kendall, 2002; Anderson, 2003). If detection rates differ between logged and unlogged stands, count data will yield response ratios that are biased with respect to true differences in abundance. This sort of problem might be particularly acute with terrestrial salamanders, since most of the population is underground most of the time (Taub, 1961; Bailey et al., 2004; Chelgren et al., 2011). Thus, some authors have argued that count data for terrestrial salamanders have little value (Kroll et al., 2009), whereas others suggest that they should be used cautiously and in concert with other population metrics (Welsh et al., 2008). Only two studies in our meta-analysis provided data from both raw counts and mark-recapture estimates that would allow response ratios to be compared. Bartman et al. (2001) presented data for *Plethodon jordani* before harvest and for 2 years following shelterwood harvest. In the first year, In response ratios from raw counts and mark-recapture were nearly identical (-0.59 versus -0.60) whereas in the second year, counts produced a higher In response ratio (-1.03 versus -0.36). Sattler and Reichenbach (1998) presented 2 years of post-harvest data for *P. hubrichti* from both surface counts and Jolly-Seber estimates before and after shelterwood or clearcut harvests. For shelterwood sites, In response ratios from counts and mark-recapture estimates were respectively -0.71 and -0.24 in the first year and 0.19 and -0.15 in the second year. For clearcut sites, In response ratios (counts and mark-recapture estimates) were -0.44 and -0.64 in the first year and -0.22 and -1.34 in the second year. These results illustrate that counts and mark-recapture data can yield substantially different estimates for response to harvest, though effect sizes from counts did not appear to be uniformly high or low relative to estimates from mark-recapture.

Combining results in meta-analysis creates some inherent challenges. Most importantly, meta-analysis assumes that the data being compared across studies are in fact comparable. Given that salamander surveys were done in a variety of ways (e.g., night transects, cover object surveys, pitfall trapping), it is possible that different metrics of population status represent fundamentally different aspects of salamander populations. Additionally, because of incomplete descriptions of harvests and temporal changes in the use of terms such as “selective logging,” we lumped a number of different harvest techniques together as partial canopy removal. If different techniques (e.g., shelterwood versus group selection) produced very different effects on salamander populations, these differences would be missed by our approach. Similarly, calculation of summary effect sizes across studies assumes some similar underlying effect on all species. Although terrestrial salamanders have a basic ecological similarity – no one has yet found a species that is consistently more abundant in open habitats – population or species-level differences in harvest effects would nevertheless complicate interpretation of overall effect sizes. Finally, meta-analysis assumes that all studies on a topic are in fact published. If, for example, studies showing no effects of harvest were less likely to be published, meta-analysis would over-estimate the true effects

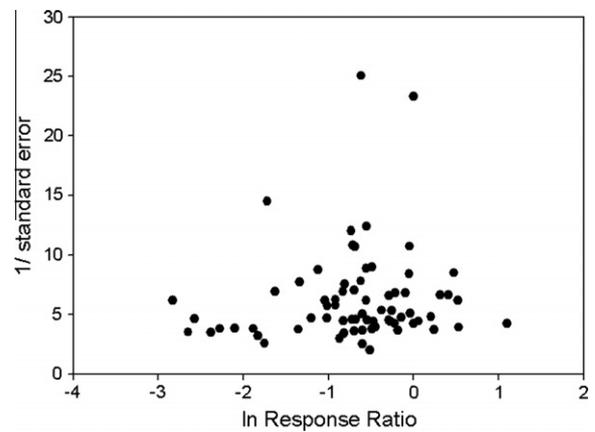


Fig. 4. Funnel plot of effect sizes relative to $1/\text{standard error}$, a measure of the within-study variance. The plot is largely symmetrical, though the left tail (studies showing strong negative effects of harvest) is longer than the right tail (studies showing positive effects of harvest).

of canopy removal. Diagnostics for publication bias showed little evidence for publication bias in our dataset. A funnel plot (Sutton et al., 2000) of effect size versus $1/SE$ was largely symmetrical (Fig. 4), and correlation between within-study variance and effect size was not significant ($r_s = -0.18$, $p = 0.14$). These results do not rule out more complex forms of publication bias, but they do suggest that no single class of studies (e.g., studies showing unusually small or large effects of harvest) was systematically missing from our analysis.

Our results have a number of implications for salamander conservation in North American forests. Most importantly, our results serve to bracket the expectations for salamander responses to harvest. In general, we find that with partial removal, short-term reductions in salamander abundance of approximately 50% can be expected (95% CI = 11–73%). With clearcutting, a moderately larger short term reduction should be anticipated (mean = 62%, 95% CI = 29–80%). Effects of timber removal will likely be more severe for sites subject to warm summer temperatures and for the *P. vehiculum* group and less severe for sites with cooler summer temperatures and for the genera *Aneides* and *Batrachoseps*. Based on our results, monitoring to assess long-term recovery of salamander populations is warranted, but short-term monitoring may not provide new information beyond what is known – i.e., small-scale harvests will decrease salamander populations, probably by about half, but will not eliminate them if the logged area is permitted to regenerate. When monitoring is carried out, our results suggest either that both passive and active sampling should be employed or that capture probabilities should be directly estimated along with raw counts.

Acknowledgements

We thank Carola Haas, Bruce Bury, Bob Brooks, Andrée Morneau, and Jean-David Moore for providing unpublished data and/or clarification of published data. Hart Welsh contributed several references we had initially missed, and A.J. Kroll provided helpful comments on an earlier draft of the manuscript. This research was funded by a Howard Hughes Medical Institute award to Washington & Lee University under the Undergraduate Science Education Program and an H.F. Lenfest Grant to D. Marsh.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.biocon.2012.03.030>.

References

- Aikens, M.L., Ellum, D., McKenna, J.J., Kelty, M.J., Ashton, M.S., 2007. The effects of disturbance intensity on temporal and spatial patterns of herb colonization in a southern New England mixed-oak forest. *For. Ecol. Manage.* 252, 144–158.
- Anderson, D.R., 2003. Response to Engeman: index values rarely constitute reliable information. *Wildlife Soc. Bull.* 31, 288–291.
- Arnqvist, G., Wooster, D., 1995. Meta-analysis: synthesizing research findings in ecology and evolution. *Trends Ecol. Evol.* 10, 236–240.
- Ash, A.N., 1997. Disappearance and return of plethodontid salamanders to clearcut plots in the southern Blue Ridge Mountains. *Conserv. Biol.* 11, 983–989.
- Ash, A.N., Bruce, R.C., 1994. Impacts of timber harvesting on salamanders. *Conserv. Biol.* 8, 300–301.
- Aust, W.M., Blinn, C.R., 2004. Forestry best management practices for timber harvesting and site preparation in the eastern United States: an overview of water quality and productivity research during the past 20 years (1982–2002). *Water, Air, Soil Pollut.* 4, 5–36.
- Bailey, L.L., Simons, T.R., Pollock, K.H., 2004. Estimating detection probability parameters for plethodontid salamanders using the robust capture–recapture design. *J. Wildlife Manage.* 68, 1–14.
- Bartman, C.E., Parker, K.C., Laerm, J., McCay, T.S., 2001. Short-term response of Jordan's salamander to a shelterwood timber harvest in Western North Carolina. *Phys. Geogr.* 22, 154–166.
- Brodie Jr., E.D., Brodie III, E.D., 1980. Differential avoidance of mimetic salamanders by free-ranging birds. *Science* 208, 181–182.
- Brodie Jr., E.D., 1977. Salamander antipredator postures. *Copeia* 1977, 523–535.
- Burnham, K.P., Anderson, D.R., 2002. *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*. Springer, New York, NY.
- Burton, T.M., Likens, G.E., 1975. Energy flow and nutrient cycling in salamander populations in the Hubbard brook experimental forest, New Hampshire. *Ecology* 56, 1068–1080.
- Butts, S.R., McComb, W.C., 2000. Associations of forest-floor vertebrates with coarse woody debris in managed forests of western Oregon. *J. Wildlife Manage.* 64, 95–104.
- Chelgren, N., Adams, M.J., Bailey, L.L., Bury, R.B., 2011. Using multilevel spatial models to understand salamander site occupancy after wildfires. *Ecology* 92, 408–421.
- Cole, E.C., McComb, W.C., Newton, M., Chambers, C.L., Leeming, J.P., 1997. Response of amphibians to clearcutting, burning, and glyphosate application in the Oregon coast range. *J. Wildlife Manage.* 61, 656–664.
- Cushman, S.A., 2006. Effects of habitat loss and fragmentation on amphibians: a review and prospectus. *Biol. Conserv.* 128, 231–240.
- DeMaynadier, P.G., Hunter, M.L., 1995. The relationship between forest management and amphibian ecology: a review of the North American literature. *Environ. Rev. – Ottawa – Natl. Res. Council* 3, 230–261.
- Ducey, P.K., Brodie Jr., E.D., 1983. Salamanders respond selectively to contacts with snakes: survival advantage of alternative antipredator strategies. *Copeia* 1983, 1036–1041.
- Dupuis, L.A., Smith, J.N., Bunnell, F., 1995. Relation of terrestrial-breeding amphibian abundance to tree-stand age. *Conserv. Biol.* 9, 645–653.
- Forsman, J.T., Reunanen, P., Jokimäki, J., Mönkkönen, M., 2010. The effects of small-scale disturbance on forest birds: a meta-analysis. *C. J. For. Res.* 40, 1833–1842.
- Gifford, M.E., Kozak, K.H., 2012. Islands in the sky or squeezed at the top? Ecological causes of elevational range limits in montane salamanders. *Ecography* 35, 193–203.
- Greenwald, K.R., Petit, L.J., Waite, T.A., 2008. Indirect effects of a keystone herbivore elevate local animal diversity. *J. Wildlife Manage.* 72, 1318–1321.
- Grover, M.C., 1998. Influence of cover and moisture on abundances of the terrestrial salamanders *Plethodon cinereus* and *Plethodon glutinosus*. *J. Herpetol.* 32, 489–497.
- Gurevitch, J., Hedges, L.V., 1999. Statistical issues in ecological meta-analyses. *Ecology* 80, 1142–1149.
- Harper, C.A., Guynn Jr., D.C., 1999. Factors affecting salamander density and distribution within four forest types in the Southern Appalachian Mountains. *For. Ecol. Manage.* 114, 245–252.
- Hedges, L.V., Gurevitch, J., Curtis, P.S., 1999. The meta-analysis of response ratios in experimental ecology. *Ecology* 80, 1150–1156.
- Hedges, L.V., Olkin, I., 1985. *Statistical Methods for Meta-Analysis*. Academic Press, San Diego, CA.
- Highton, R., 1995. Speciation in eastern North American salamanders of the genus *Plethodon*. *Annu. Rev. Ecol. Syst.* 26, 579–600.
- Homyack, J.A., Haas, C.A., Hopkins, W.A., 2011. Energetics of surface-active terrestrial salamanders in experimentally harvested forest. *J. Wildlife Manage.* 75, 1267–1278.
- IPCC, 2007. *Climate Change 2007: Synthesis Report. Contribution of Working Groups I, II and III to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. Pachauri, R.K., Reisinger, A. (Eds.), Intergovernmental Panel on Climate Change, Geneva, Switzerland.
- Jaeger, R.G., 1980. Microhabitats of a terrestrial forest salamander. *Copeia* 1980, 265–268.
- Kleeberger, S.R., Werner, J.K., 1982. Home range and homing behavior of *Plethodon cinereus* in northern Michigan. *Copeia* 1982, 409–415.
- Knapp, S.M., Haas, C.A., Harpole, D.N., Kirkpatrick, R.L., 2003. Initial effects of clearcutting and alternative silvicultural practices on terrestrial salamander abundance. *Conserv. Biol.* 17, 752–762.
- Kroll, A.J., Runge, J.P., MacCracken, J.G., 2009. Unreliable amphibian population metrics may obfuscate more than they reveal. *Biol. Conserv.* 142, 2802–2806.
- Likens, G.E., Bormann, F.H., Pierce, R.S., Reiners, W.A., 1978. Recovery of a deforested ecosystem. *Science* 199, 492–496.
- MacKenzie, D.I., Kendall, W.L., 2002. How should detection probability be incorporated into estimates of relative abundance? *Ecology* 83, 2387–2393.
- Marvin, G.A., 1998. Interspecific aggression and spatial relationships in the salamanders *Plethodon kentucki* and *Plethodon glutinosus*: evidence of interspecific interference competition. *Can. J. Zool.* 76, 94–103.
- McKenny, H.C., Keeton, W.S., Donovan, T.M., 2006. Effects of structural complexity enhancement on eastern red-backed salamander (*Plethodon cinereus*) populations in northern hardwood forests. *For. Ecol. Manage.* 230, 186–196.
- Milanovich, J.R., Peterman, W.E., Nibbelink, N.P., Maerz, J.C., 2010. Projected loss of a salamander diversity hotspot as a consequence of projected global climate change. *PLoS One* 5, 1–10.
- Petranks, J.W., Eldridge, M.E., Haley, K.E., 1993. Effects of timber harvesting on southern appalachian salamanders. *Conserv. Biol.* 7, 363–370.
- R Development Core Team, 2008. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. <<http://www.R-project.org>>.
- Rosenberg, M.S., Adams, D.C., Gurevitch, J., 1997. *MetaWin: Statistical Software for Meta-Analysis with Resampling Tests*. Version 1.0. Sinauer Associates, Sunderland, Massachusetts.
- Sattler, P., Reichenbach, N., 1998. The effects of timbering on *Plethodon hubrichti*: short-term effects. *J. Herpetol.* 32, 399–404.
- Stebbins, R.C., Cohen, N.W., 1995. *A Natural History of Amphibians*. Princeton University Press, Princeton, New Jersey, USA.
- Sutton, A.J., Abrams, K., Jones, D., Sheldon, T., Song, F., 2000. *Methods for Meta-Analysis in Medical Research*. John Wiley, New York, NY.
- Taub, F.B., 1961. The distribution of red-backed salamanders, *Plethodon c. cinereus*, within the soil. *Ecology* 42, 681–698.
- United States Forest Service, 2005. *George Washington and Jefferson National Forests: Detailed Monitoring and Evaluation Report for Fiscal Year 2004–2005*. US Department of Agriculture, Forest Service Southern, Region, pp. 36–37.
- Vanderwel, M.C., Malcolm, J.R., Mills, S.C., 2007. A meta-analysis of bird responses to uniform partial harvesting across North America. *Conserv. Biol.* 21, 1230–1240.
- Vanderwel, M.C., Mills, S.C., Malcolm, J.R., 2009. Effects of partial harvesting on vertebrate species associated with late-successional forests in Ontario's boreal region. *For. Chron.* 85, 91–104.
- Walton, B.M., Steckler, S., 2005. Contrasting effects of salamanders on forest-floor macro- and mesofauna in laboratory microcosms. *Pedobiologia* 49, 51–60.
- Welsh Jr., H.H., Droegge, S., 2001. A case for using plethodontid salamanders for monitoring biodiversity and ecosystem integrity of North American forests. *Conserv. Biol.* 15, 558–569.
- Welsh Jr., H.H., Lind, A.J., 1988. *Old Growth Forests and the Distribution of the Terrestrial Herpetofauna*. General Technical Report – US Department of Agriculture, Forest Service, pp. 439–458.
- Welsh Jr., H.H., Pope, K.L., Wheeler, C.A., 2008. Using multiple metrics to assess the effects of forest succession on population status: a comparative study of two terrestrial salamanders in the US Pacific Northwest. *Biol. Conserv.* 141, 1149–1160.
- Wyman, R.L., 1998. Experimental assessment of salamanders as predators of detrital food webs: effects on invertebrates, decomposition and the carbon cycle. *Biodivers. Conserv.* 7, 641–656.
- Zwolak, R., 2009. A meta-analysis of the effects of wildfire, clearcutting, and partial harvest on the abundance of North American small mammals. *For. Ecol. Manage.* 258, 539–545.