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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

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ARTICLE INFO

Article history:
Received 10 May 2007
Received in revised form
24 January 2008
Accepted 12 February 2008
Available online 24 March 2008

Keywords:
Source-sink dynamics
Forest management
Demographic profile
Body condition index
Terrestrial salamanders
Plethodon elongatus
Plethodon stormi

ABSTRACT

Investigations to determine stable or source-sink animal population dynamics are challenging and often infeasible for most species due to the time and expense of mark-recapture studies and the challenge of life histories attributes that result in low detectability and low recapture probabilities. Often, managers rely solely on occupancy or relative abundance patterns to assess a species' sensitivity to environmental changes. Greater insight into population-level responses to environmental change can be gained by consideration of a combination of readily obtainable metrics, including occupancy, relative abundance, demographic structure and body condition. We examined how these metrics can improve our understanding of population-level responses to forest disturbance, using datasets for two exemplar species of terrestrial salamanders resident to the Pacific Northwestern USA. We compared population metrics for the Del Norte salamander (*Plethodon elongatus*) and the Siskiyou Mountains salamander (*Plethodon stormi*) across the seral continuum represented by four forest age classes: pre-canopy, young, mature, and old-growth. We compared these data with those collected from reference stands in mature (*P. stormi*) or old-growth (*P. elongatus*) forest containing robust populations. *P. elongatus* was twice as common as *P. stormi*. Both occupancy and salamander counts were lowest at pre-canopy sites for both species. Although there were numerous *P. elongatus* detections in young forests, higher proportions of these individuals were juveniles and sub-adults when compared to populations in late-seral forests. We found a negative relationship between the proportion of immature animals and total counts at a site, indicating that the high proportion of young animals in young forest stands is likely due to dispersal of young salamanders from nearby source populations and/or low survival of adult animals in young forests. We also found reduced body condition of *P. stormi* populations in young forests. Our results suggest that there are costs to populations occupying early seral forests, such as skewed age class structure and reduced body condition that are indicative of sink populations. Consideration of population-level metrics beyond occupancy and relative abundance can provide important insights when assessing a species' sustainability in managed forest landscapes.

Published by Elsevier Ltd.

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0006-3207/$ - see front matter Published by Elsevier Ltd.
doi:10.1016/j.biocon.2008.02.014

1. Introduction

To understand the true population status of species, it is necessary to determine population trends within the context of their known threats. While detailed long-term monitoring programs have been extremely successful for some species such as the Florida scrub jay (*Aphelocoma coerulescens*) (Root, 1998), there are insufficient population data for the vast majority of species, even in relatively well-studied North America (Morris et al., 2002). Researchers and resource managers attempting to collect population data on rare or secretive species encounter a range of difficulties from high expense and logistical constraints to regulatory permitting issues and statistical power problems due to low sample sizes. Often they end up relying on distribution and occupancy data which are used as surrogates for persistence across a landscape.

There is a large body of evidence showing that the mere presence of animals in a given location may not indicate self-sustaining populations or appropriate habitat conditions (e.g., Van Horne, 1983; Holt, 1997; Johnson, 2005). Animals may use sub-optimal habitats where their populations cannot persist without regular input from nearby source populations (Dias, 1996; Holt, 1997; Pulliam, 2000). The concept of sub-optimal habitats is consistent with the "source-sink" population theory where variation in habitat quality and defense of resources by residents generate differential population structures among habitats (Pulliam, 1988). In source populations births exceed deaths, often resulting in emigration of surplus individuals to adjacent, sometimes marginal habitats. Conversely, reproduction is lower than mortality in sink populations making them net importers of individuals and likely not self-sustaining. Survival of individuals in sub-optimal habitats may be greatly reduced compared to more optimal habitats but such reduced survival may go undetected when the signs of decline are obscured by immigration from nearby sources. (i.e., Tilman et al. 1994).

Optimally, the study of source-sink dynamics requires intensive demographic investigations where individuals are tracked throughout their lives using mark and re-capture techniques and births, survival between age classes, reproductive output, and mortality are tracked (e.g., Schmidt et al., 2005). Such studies are expensive and difficult to conduct (e.g., Jonzen et al., 2005), especially with species that are secretive or occur in inaccessible habitats. Terrestrial salamanders of the genus *Plethodon* are examples of such challenging species because they spend a large portion of their lives underground making it very hard to track individuals and population trends (Hyde and Simons, 2001). We often can only readily detect a small portion of the animals in a population (e.g., Welsh and Lind, 1992) so that the potential effects of low-quality habitat needs to be deduced indirectly by comparing metrics of population status such as relative abundance, site-specific population age structures, and the body condition of detected individuals. Such limited information, however, can be highly informative as to population status (e.g., Hairston, 1987; Graves, 1997; Ricklefs, 1997; Rohwer, 2004; Hossack et al., 2006). Patterns of low relative abundances, low proportions of adult animals, or low length-to-weight ratios of individuals associated with specific habitat conditions or disturbance regimes can be indications that these habitats support populations that are suboptimal (e.g., Stevenson and Woods, 2006) or not self-sustaining without immigration (e.g., Kreuzer and Huntly, 2003).

Shifts in population age structure can signify changes to the underlying rates of survivorship and fecundity that are difficult to see in count data alone (Doak and Morris, 1999). In animals that experience intraspecific competition for resources, including at least some plethodontid salamanders (Gabor and Jaeger, 1995), young inexperienced individuals may be forced to disperse from high-quality source habitats (Holt, 1997). This despotic dispersal creates age structure differences along habitat gradients that reflect habitat quality (Graves, 1997; Rohwer, 2004). A sub-population with low numbers of animals and an age class distribution skewed toward younger individuals can indicate a sink habitat, whereas a sub-population with high numbers of animals skewed towards adults may be indicative of source habitat (Van Horne, 1983). Information on the proportion of adults in a population also can be used to examine variation in adult survival across habitat gradients (Caughley, 1974; Ricklefs, 1997; Rohwer, 2004).

In addition, animals residing in low-quality habitats may incur physical stresses that reduce their ability to obtain food. The body condition (variation from the expected mass for a given length) of an animal may reflect its amount of energy reserves, health, and reproductive state, and can be related to environmental characteristics such as habitat quality and food availability (e.g., Pope and Matthews, 2002; Schulte-Hostedde et al., 2005; Stevenson and Woods, 2006). Poor body condition of individuals may eventually result in reduced population size due to lower survival and reproductive success (Johnson, 2005). Condition indices can be readily calculated from routinely collected length and weight data of individuals, and the use of this approach as an indication of the health of individuals within a population has received increased support (Jakob et al., 1996; Green, 2001; Schulte-Hostedde et al., 2005; Lowe et al., 2006; Stevenson and Woods, 2006).

We examined a combination of readily obtainable population metrics for two closely related exemplar species of plethodontid salamander to determine if the combined metrics can improve our understanding of how these secretive species respond to disturbance on a managed forest landscape. Plethodontid (lungless) salamanders are often the most common vertebrate in moist forests of North America (Hairston, 1987; Petranka and Murray, 2001) and their species richness and population status have been proposed as excellent indicators of forest ecosystem integrity (Welsh and Droege, 2001). Yet, usually just occupancy and/or abundance have been used to assess the status of plethodontids relative to habitat fragmentation (Wyman, 2003). Including information on population age structure and body condition can provide more informed insight as to true population status when assessing sustainability on managed forest landscapes.

The Siskiyou Mountains salamander (*Plethodon stormi*) and the Del Norte salamander (*Plethodon elongatus*) are endemic to the Pacific Northwestern USA (Jones et al., 2005) and are found in mixed conifer (primarily Douglas-fir [*Pseudotsuga menziesii*])/hardwood forests of northwestern California and southern Oregon. These sibling species (Mahoney, 2004) are allopatric in the Klamath–Siskiyou Bioregion (DeGross, 2004), with *P. elongatus* more widely distributed and found closer to the

coast, while *P. stormi* occupies a more restricted range in drier interior forests on both sides of the Siskiyou Crest that divides Oregon and California (Welsh et al., 2007). Previous research on *P. elongatus* documented higher relative abundances in old-growth forests compared to harvested forests (Raphael, 1988; Welsh, 1990; Welsh and Lind, 1991). Multi-scale analyses of habitat associations (Welsh and Lind, 1995; Welsh et al., 2006, 2007) have indicated that both species occur more frequently in naturally occurring mature (>100 years) to old-growth forests (>200 years old).

Both species have been considered Survey and Manage species (Molina et al., 2006), protected on US federal forestlands under the Northwest Forest Plan (USDA and USDI, 2004, 2006, 2007). The Survey and Manage provision has offered special protection to about 300 species on federal lands within the range of the northern spotted owl (*Strix occidentalis caurina*). To be considered under the provision, a species had to be a late-successional or old-growth forest associate. Most species met this criterion through studies comparing occupancy or relative abundance across forest age categories, although inclusion of some species has been hotly contended. One reason for debate was that occupancy or abundance did not provide an accurate representation of forest age association for rare or secretive species, where low abundances or low detectability precluded the finding of statistically significant results. Under the current political climate in North America, the Survey and Manage program has been challenged and may be eliminated entirely. None-the-less, there is much popular support for the protection of these species and their true status needs to be better understood in order to give land managers scientifically defensible management options for maintaining their populations (e.g., Suzuki et al., 2007; Welsh et al., 2007).

Despite the potential loss of Survey and Manage protection, *P. stormi* is currently a California State "threatened species" and under evaluation for listing on the US Endangered Species List (US District Court of Northern California, 2007). Because this species occurs in a drier region of the Klamath–Siskiyou province where it is climatically less favorable for plethodontid salamanders (Feder, 1983), it is likely more rare in general and may be more strongly affected by habitat disturbance than *P. elongatus*. For this reason, we examined both species-specific population metrics and also compared these metrics between the species. Conservation and management strategies for both species have recognized the need for additional research to better understand population level habitat relationships and the effects of timber harvest on long-term survival.

By considering relative detectability, relative abundance, population age structure, and body condition for these two species along the seral continuum, we may gain better insight into how these populations are associated with managed forest lands, how they are responding to changes on these landscapes, and what the implications may be for their long-term persistence.

2. Materials and methods

Due to the extensive subterranean habits of plethodontid salamanders (e.g., Taub, 1961) their detection can be highly variable (Hyde and Simons, 2001). In order to enhance our probability of encounters at sites with populations, we used survey protocols with sampling windows based on season and environmental conditions, specifically surface air temperature and ambient moisture, site attributes that coincided with known salamander surface activity (Clayton et al., 1999; Ollivier and Welsh, 1999). For all captures we measured snout-to-vent length (SVL), total length (±0.1 cm), and mass (±1 g), and documented reproductive status whenever possible (e.g., gravid females).

2.1. Datasets used to examine relationships with forest age

We used all or parts of four datasets, two for *P. stormi* and two for *P. elongatus*, collected between 1974 and 1998 (Table 1). Forest stand age was determined by using the mean of three tree cores from conifers of the dominant size class at each site. We used four forest age classes to analyze relationships with the seral continuum, defining these classes based on Franklin et al. (1986) and Franklin and Spies (1991) as pre-canopy (0–30 years),

Table 1 Datasets used for *Plethodon elongatus* (PLEL) and *P. stormi* (PLST) comparisons with sampling method and sample size

Comparisons	Species	Dataset	Method	No. of plots
Occurrence and relative abundance	PLEL	Welsh and Lind (1995)	49 m^2 area-constrained plots	57 (57)
	PLST	Welsh et al. (2007)	49 m^2 area-constrained plots	244 (244)
Age class distribution by forest age	PLEL	Welsh and Lind (1995)	49 m^2 area-constrained plots	57 (22)
		Welsh and Lind (1991)	Visual encounter surveys (4 h/year)	20 (9)
	PLST	Welsh et al. (2007)	49 m^2 area-constrained plots	244 (54)
		Nussbaum (1974)	Visual encounter surveys (7 h)	1 (1)
Proportion adults related to relative abundance; adult survival	PLEL	Welsh and Lind (1995)	49 m^2 plots	57 (10)
		Welsh and Lind (1991)	Visual encounter surveys and pitfall traps	20 (6)
Body condition	PLEL	Welsh and Lind (1995)	49 m^2 area-constrained plots	57 (22)
		Welsh and Lind (1991)	Visual encounter surveys (4 h/year)	20 (9)
	PLST	Welsh et al. (2007)	49 m^2 area-constrained plots	244 (54)

More detailed information on sampling design for each dataset can be found within the associated reference. Numbers in parentheses are the sample sizes used for each of the analyses listed.

young (31–99 years), mature (100–199 years), and old-growth (200 +years).

2.1.1. *Plethodon stormi*

We used data from a habitat relationship study that employed a random systematic design to sample across *P. stormi*'s entire range (Welsh et al., 2007). Salamander populations were sampled using area-constrained searches (Welsh, 1987; Bury and Corn, 1990) of the forest floor in 49-m^2 plots centered on rocky microhabitat (Welsh et al., 2007). We sampled 244 plots between 8 March 1995 and 27 June 1998 (43 pre-canopy stands, 69 young forest stands, 74 mature forest stands, and 58 old-growth stands) (Table 1).

We obtained a second *P. stormi* dataset from a single site with a known robust population to use as a reference site (Nussbaum, 1974). We compared stand age-specific demographic profiles from the first dataset to this robust population, one which we assumed based on its size to represent a population existing under optimum conditions. The reference site was in a 105-year-old (mature) forest near Hutton Guard Station, Rogue River National Forest, Oregon, that was sampled for salamanders between 12 April and 9 May 1974 (Nussbaum, 1974).

2.1.2. *Plethodon elongatus*

The largest *P. elongatus* dataset was collected using a random systematic design similar to the first dataset for *P. stormi* and consisted of 25 pre-canopy forest stands, 12 young forest stands, 4 mature forest stands, and 16 old-growth stands for a total of 57 sites (Table 1). All of the 49-m^2 plots were centered on rocky microhabitat and were sampled between 27 February 1989 and 6 June 1989 (Welsh and Lind, 1995).

For salamander age structure and body condition analyses, where occupancy rates and relative abundances across sites were not compared, we also used data from 20 sites (seven young, four mature, and nine old-growth stands) sampled during a study of forest seral stage relationships (Welsh and Lind, 1991). This study used time-constrained visual encounter surveys (Welsh, 1987; Bury and Corn, 1990) conducted between March and May of 1984–1986. A single old-growth site from this study was used as a reference site to derive population structure data from a robust population that appeared to be living under optimum conditions in order to make comparisons with our four forest-age-class-specific demographic profiles. This reference site, a 205-year-old (old growth) forest stand with the largest population of either species we have ever encountered, was located on the Six Rivers National Forest near Willow Creek, California (details in Welsh and Lind, 1992). Because this stand was a part of earlier datasets (Welsh and Lind 1991, 1995) it was removed from these datasets whenever comparisons were made with the reference site.

To calculate adult survival and to examine the relationship between the proportion of adults and relative abundance, we used the previously described datasets as well as pitfall trap data that were collected in October and November of 1984 and 1985 during the forest seral stage relationships study at the same 20 sites (Welsh and Lind, 1991). For these analyses, we used all individuals captured during visual encounter and pitfall trap arrays for each of the 20 sites.

2.2. *Detection probabilities, encounter rates and relative abundance*

Prior to assessing population metrics, we compared the detection probability (MacKenzie et al., 2002) of both species for the sampling techniques used in this study. Because our dataset for *P. stormi* did not consist of re-sampled sites, we used a 2006–2007 dataset from 34 sites collected by the US Fish and Wildlife Service (B. Woodbridge, unpublished data) that included 10 re-sampled sites using the same sampling protocol as our single sample datasets. For *P. elongatus* we used the 20 sites re-sampled for three consecutive years (Welsh and Lind, 1991).

We then compared relative rareness of *P. stormi* and *P. elongatus* in terms of both encounter rates (presence/not detected) and relative abundance when encountered. Using the 244 site dataset sampled for *P. stormi* and the 57 site dataset sampled for *P. elongatus*, both of which used the same area-constrained plot search methodology, we ran a Wilcoxon rank-sum test to determine if there were differences between species in the median number of salamanders encountered per plot. This was followed by a Kruskal–Wallis ANOVA to examine differences in the median number of animals encountered by forest age class for each species. For each species, we also ran binomial and Poisson linear regression models to compare presence and relative abundance data to forest ages. We log or square-root transformed abundances and forest age data to achieve normal distributions.

2.3. *Salamander life stage distributions*

Those sites with detections of salamanders were used in the population structure analyses (Table 1). Salamanders were assigned to life stages based on SVL, with juveniles <28.45 mm, sub-adults 28.45–46.74 mm, and adults $\geqslant$46.75 mm (Ollivier and Welsh, 2003). We compared population demographic profiles (i.e., life stage histograms) for the reference stands to histograms from each forest age class. The reference stands contained robust populations in which life stage distributions were a close match to those represented as stable populations by Hairston (1987), and presumed to represent salamander populations living under optimum conditions. We calculated 40% density trace lines for each reference histogram based on the relative concentration of animals of each size class (smoothed to a 40% interval). We used the reference density trace line to compare histograms from the four forest age to the general shape of the reference histogram for each species. To test for differences in life stage distributions among forest age classes and the reference sites, we used pair-wise Kolmogorov–Smirnov tests (Wheeler et al., 2003; Browne and Hecnar, 2007) with a Bonferroni correction.

Unfortunately, we lacked sufficient *P. stormi* detections per site (median = 2, max = 13) to accurately represent population structure by forest age class which also limited our ability to conduct additional demographic analyses. However, for *P. elongatus* we conducted further analyses based on the approaches of Ricklefs (1997) and Rohwer (2004). We combined the *P. elongatus* datasets for these analyses to maximize power but used only sites with >4 animals (n = 16) (Table 1). We compared proportions of adults, not abundances, across datasets.

We estimated the annual survival of adult *P. elongatus* in the different forest age classes using a survival equation derived by Ricklefs (1997). When populations are stable, the annual survival of adults is estimated as $A/(A + I)$, where A is the number of adults and I is the number of immatures in the sample. We computed standard errors for the estimates as $[(AI)/(A + I)^3]^{1/2}$ (Ricklefs, 1997). Important assumptions for the analysis included constant population size, discrete reproductive season, and unbiased collection of salamander life stages. Ricklefs (1997) assessed the errors in survival estimation resulting from relaxing these assumptions and found them to be small compared to the range of values for annual adult survival among populations. Furthermore, Welsh and Droege (2001) reviewed 35 studies of plethodontid salamanders where time-series data were obtained for more than 3 years and, using coefficients of variation, found evidence for stability of plethodontid salamander populations, with variation lower than those of anurans, ambystomatid salamanders, passerines, small mammals, and Lepidoptera (Gibbs et al., 1998).

It is difficult, however, to distinguish between regional variations in age ratios, which probably signify despotic dispersal, from range-wide differences in age ratios, which probably reflect differential survival (Rohwer, 2004). Despotism generally forces young animals into marginal habitats, and thus may affect local age ratios in ways that do not reflect differences in survival (Graves, 1997; Rohwer, 2004). The distance over which despotism affects age ratios depends on how far subordinate animals move after a despotic interaction. Assuming despotism may occur at our sampling scales, we also examined the relationship between the proportion of adults and relative abundance of all life stages. We achieved normal distributions in the data by using arcsine square-root or log transformations. Despotic movement is implicated when the proportion of adults in local samples increases with population density and/or habitat quality. We used Spearman rank correlation coefficients (R_s, two-tailed) to quantify the relationship between the proportion of adults and relative abundance of salamanders encountered. Alpha was set at $P = 0.1$ (Schrader-Frechette and McCoy, 1993).

2.4. Body condition index

Using the sites with salamander detections (Table 1), we compared salamander body condition (body mass associated with energy reserves after correcting for body size) among forest age classes. We compared the residuals from ordinary least squared regressions of salamander weight to total length as an index of body condition (Schulte-Hostedde et al., 2005) with the equation

$$\log(\text{body mass}) = \beta_0 + \beta_1 \log(\text{body length}) + \delta$$

where β_0 and β_1 are constants representing the intercept and slope of the regression line and δ is the residual with median equal to zero. The index of body condition (predicted energy reserves) is δ. A positive residual represents better body condition than a negative residual (Jakob et al., 1996). Gravid females were eliminated from this analysis because of their potential to bias the regression equation. For both species, we ran a Kruskal–Wallis one-way ANOVA on ranks, corrected for ties, to test for differences in salamander body condition among forest age classes.

3. Results

3.1. Detection probabilities, encounter rates and relative abundance

Overall we found *P. elongatus* at a higher proportion of sites than *P. stormi* (53% versus 27%; Table 2), even though detection probabilities were similar ($P = 0.80 \pm 0.11$ S.E. for *P. stormi* and $P = 0.75 \pm 0.08$ S.E. for *P. elongatus*). We also found a higher number of individuals of *P. elongatus* at sites where salamanders were detected (mean = 4.87, S.E. = 1.07) compared to *P. stormi* (mean = 2.72, S.E. = 0.30; Table 2). However, the non-normality of the count data required we test for differences in the median rather than mean number captured per site ($Z = 1.79$, $P = 0.07$). In relation to forest age class, we captured a higher number of *P. elongatus* compared to *P. stormi* per site in young ($Z = 1.87$, $P = 0.06$) and old-growth ($Z = 2.25$, $P = 0.02$), but found no difference in captures between species in pre-canopy and mature sites.

Looking at each species separately, we encountered *P. elongatus* at 28% of pre-canopy sites surveyed compared to 72% of the other forest age classes combined (Table 2). For *P. stormi*, we found at least one salamander at 19% of pre-canopy sites surveyed compared to 28% of the other forest age classes combined (Table 2). Where salamanders were detected, we found fewer total salamanders at pre-canopy sites

Table 2 Capture summaries for *P. elongatus* (PLEL) and *P. stormi* (PLST) by forest age class

Forest age class	Species	No. of sites	No. sites with captures (%)	Total captures	Mean no. captures per site (S.E.)
Precanopy	PLEL	25	7 (28)	8	1.14 (0.14)
	PLST	43	8 (19)	11	1.38 (0.18)
Young	PLEL	12	7 (58)	42	6.00 (1.38)
	PLST	69	19 (28)	58	3.05 (0.54)
Mature	PLEL	4	2 (50)	7	3.50 (2.50)
	PLST	74	22 (30)	67	3.05 (0.63)
Old-growth	PLEL	16	14 (88)	89	6.36 (2.05)
	PLST	58	16 (28)	41	2.56 (0.58)
All	PLEL	57	30 (53)	146	4.87 (1.07)
	PLST	244	65 (27)	177	2.72 (0.30)

Mean numbers of captures per site are for sites with captures only (with standard error in parentheses). Data for PLEL are from Welsh and Lind (1995) and for PLST are from Welsh et al. (2007).

for both *P. elongatus* (mean = 1.14, S.E. = 0.14) and *P. stormi* (mean = 1.38, S.E. = 0.18) compared to all other forest age classes (Table 2). Regression results showed that both the probability of finding *P. elongatus* at a site, and the counts of salamanders at sites, were positively related to forest age ($T = 4.79$, $P = 0.00001$ and $F = 27.41$, $P = 0.00003$, respectively). Results of similar regressions were not significant for *P. stormi* (binomial: $T = 1.1$, $P = 0.27$ and Poisson: $F = 1.2$, $P = 0.27$).

3.2. *Life stage distributions*

Due to the low number of salamanders found in pre-canopy sites (a total of 8 *P. elongatus* and 11 *P. stormi*), we were unable to construct meaningful demographic profiles for pre-canopy stands and thus were not able to make demographic comparisons between pre-canopy and the other forest age classes. Despite the low detections, all salamander life stages of both species were found in pre-canopy stands.

3.2.1. *Plethodon elongatus*

Adult *P. elongatus* accounted for more of the individuals at the reference site (60%), old-growth (47%) and mature (46%) stands than they did in young (20%) stands (Fig. 1). A greater proportion of adults were found at the reference, old-growth, and mature sites compared to young forests (Kolmogorov–Smirnov tests: reference, $D = 0.50$, $P < 0.0001$; old-growth, $D = 0.35$, $P = 0.0002$; mature, $D = 0.43$; $P = 0.003$). We also found a significantly greater proportion of adults at the reference site compared to the old-growth sites (Kolmogorov–Smirnov test: $D = 0.19$; $P = 0.02$).

In addition to a positive relationship between the proportion of *P. elongatus* adults and forest age, the proportion of adults in individual forest stands where >4 salamanders were found was positively correlated with the total number of salamanders captured at a site ($R_s = 0.32$, $P = 0.07$, Fig. 2). Using Ricklefs' (1997) estimated annual adult survival equation, expected adult survival was almost twice as high in old-growth forest (0.47 ± 0.03) compared to young forest stands (0.25 ± 0.06; Fig. 3).

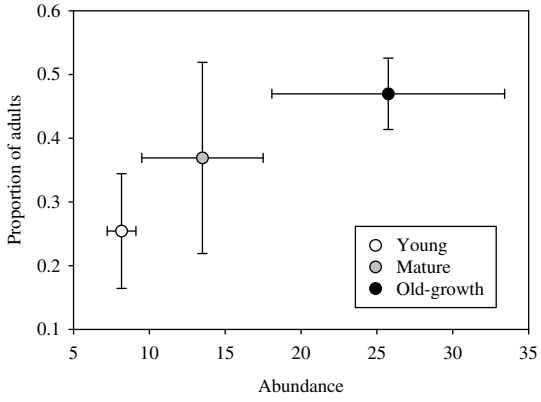

Fig. 2 – Relationship between the proportions of adult *P. elongatus* and relative abundance of animals by forest age category. Error bars represent ±S.E. Data used were those from plots with >4 salamanders.

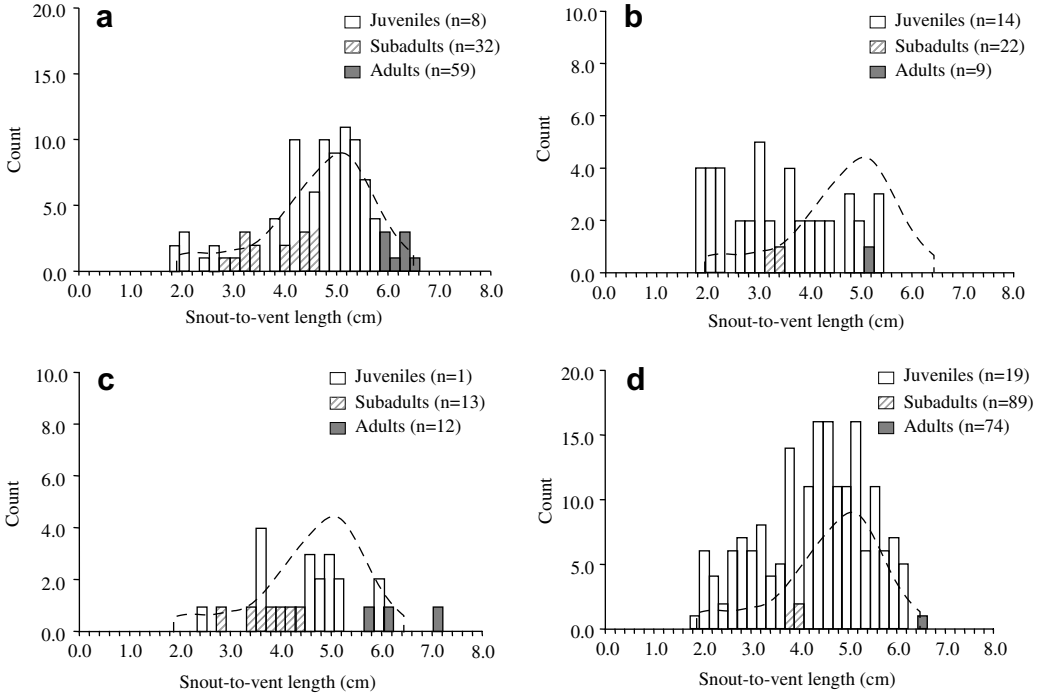

Fig. 1 – *Plethodon elongatus* size frequency distribution for the (a) old-growth reference site (b) young forest stands ($n = 8$), (c) mature forest stands ($n = 3$), and (d) old-growth forest stands ($n = 19$). The dotted line in all graphs represents the 40% density trace for the reference site. The 40% density trace line was calculated as the relative frequency (concentration) of data points along the 40% data range.

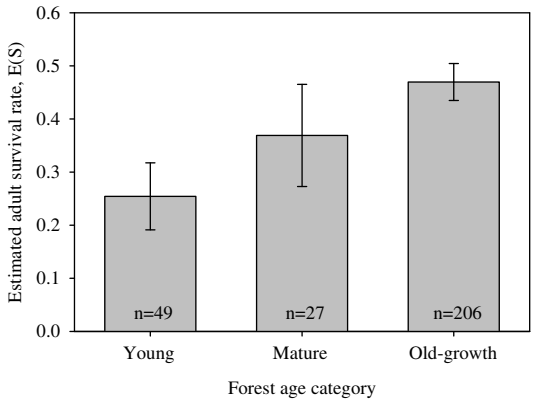

Fig. 3 – Relationship between estimated adult *P. elongatus* annual survival rate and forest age (±S.E.). *n* = number of salamanders used in the analysis for each forest age class. We included only salamanders from sites with >4 animals. Analysis was based on Ricklefs, 1997.

3.2.2. *Plethodon stormi*

Adult *P. stormi* comprised the largest age class on the reference site (46%) (Fig. 4). The numbers of adult *P. stormi* on the reference, old-growth (43%), mature (41%) and young sites (33%) were not significantly different from one another (Fig. 4). In fact we found no significant differences in life stage distributions between any of the forest age classes for *P. stormi*.

3.3. *Body condition index*

For *P. elongatus*, we found differences in body condition between the reference site and the other forest age classes ($H = 22.11$, df = 3, $P < 0.001$; Fig. 5a); salamanders at pre-canopy, young and old-growth sites had a higher median body condition than those captured in either mature or reference forests.

For *P. stormi*, when we compared salamander body condition by forest age class we found significant differences ($H = 8.90$, df = 2, $P = 0.01$; Fig. 5b), with individuals in mature forests having a higher median body condition than those captured in young forests.

4. Discussion

Using a combination of population metrics readily obtained from existing datasets including detection rates, relative abundance, age structure and body condition, we were able to gain insight into the distributions and population structures of two secretive salamander species on managed forest landscapes in the US Pacific Northwest. In addition to occupancy rates and counts being lower in younger forest stands, proportions of adult *P. elongatus* were also lower compared to old-growth forests. Given that we found a negative relationship between the proportion of immature animals and overall relative abundance at a site, the high proportion of young animals in young forest stands is more likely due to dispersal of immature salamanders from nearby source populations and/or low survival of adult animals in young forests than due to rapid population growth in young forests. Optimally, the study of survival and recruitment requires intensive demographic investigations where individuals are tracked throughout their lives using mark and re-capture techniques (Conn et al., 2005). However, for species such as *P. stormi* and *P. elongatus* that are difficult and expensive to track over large areas

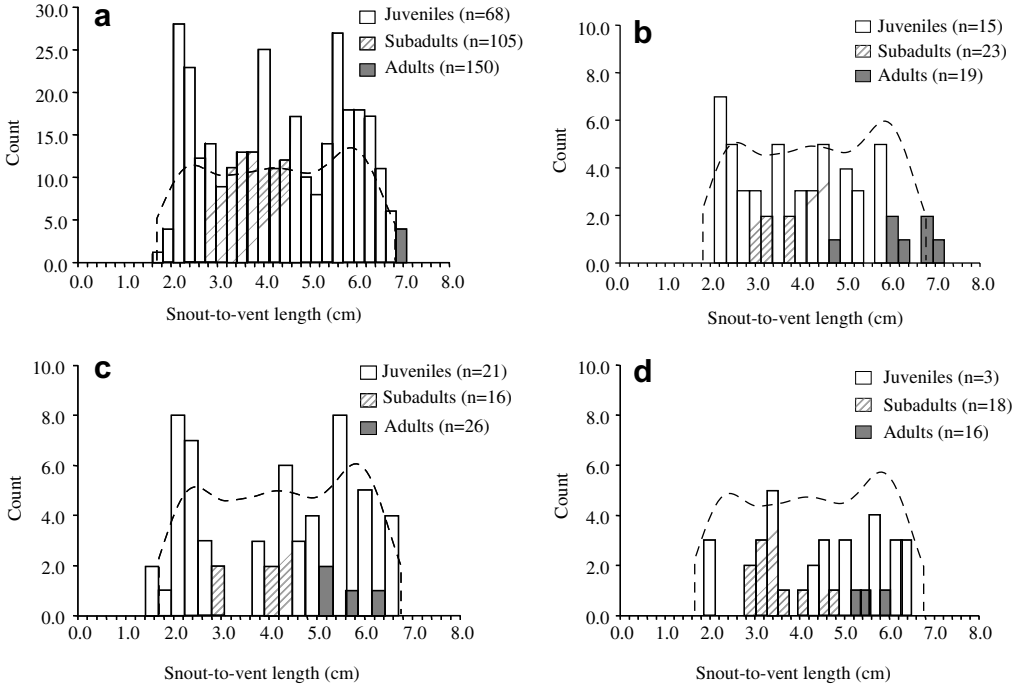

Fig. 4 – *Plethodon stormi* size frequency distribution for the (a) mature forest reference site (Nussbaum, 1974), (b) young (*n* = 19), (c) mature (*n* = 21), and (d) old-growth (*n* = 14) forest sites. The dotted line in all graphs represents the 40% density trace for the reference site. The 40% density trace line was calculated as the relative frequency (concentration) of data points along the 40% data range.

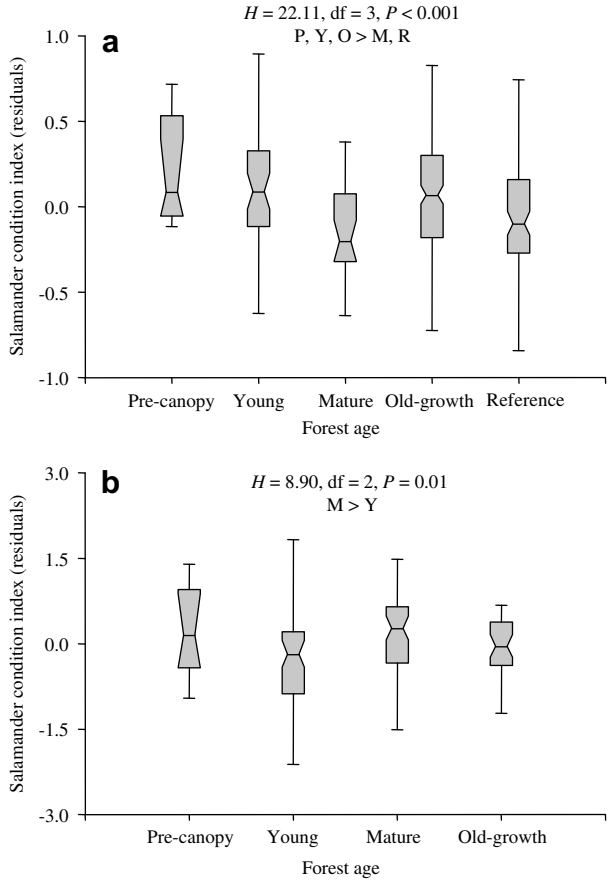

Fig. 5 – Salamander body condition index by forest age class for (a) *P. elongatus* and (b) *P. stormi*, and Kruskal–Wallis analysis of variance test results. Body index was calculated by regressing salamander body mass to length and using the residuals of the regression as the index. Animals with positive residuals can be considered to be in better condition than animals with negative residuals.

such as the managed forest landscapes of the Klamath-Siskiyou region, indices such as age ratios may provide sufficiently good and more cost-effective tools for elucidating regional-scale patterns.

4.1. *Detection probabilities, encounter rates and relative abundance*

Encounter rates and numbers of salamanders found per site were both much higher for *P. elongatus* compared to *P. stormi*. Our finding that detection probabilities were both high and similar between species, confirmed the validity of our sampling protocols based on established patterns of surface activity (Clayton et al., 1999; Ollivier and Welsh, 1999), and supports the conclusion that differences are real in both frequency of occupied sites (53% for *P. elongatus* versus 26% for *P. stormi*) and mean number of individuals per site (4.9 for *P. elongatus* versus 2.7 for *P. stormi*). These differences likely resulted from the fact that the range of *P. stormi* lies east of the range of *P. elongatus* in a drier region of the Klamath–Siskiyou province where it is climatically less favorable for plethodontid salamanders (see Feder, 1983). The prevailing west-to-east storm track and the topographic relief of the Klamath–Siskiyou region cause much of the precipitation to drop before reaching the range of *P. stormi* (see Froehlich et al., 1982). Welsh et al. (2007) made a compelling case for a similar effect from north-to-south within the range of *P. stormi*, where the Siskiyou Mountains that form the border between Oregon and California influence the moisture regime by reducing precipitation southward. The longitudinal difference in climate also results in hotter and drier summers and colder winters in the range of *P. stormi* with much of the precipitation coming in the form of snow (Froehlich et al., 1982). On the ground, these climatic differences appear to manifest in a narrower range of suitable habitat conditions for *P. stormi*, likely contributing to a more spotty distribution of salamander populations southward (Welsh et al., 2007). These findings indicate that given the relative distribution of populations across the landscape, and relative numbers of individuals where animals do occur, *P. stormi* populations are both fewer, and smaller (as is its entire range), and thus this species is more susceptible than *P. elongatus* to range fragmentation and loss of isolated populations. It would follow that *P. stormi* requires more active management of the landscape matrix to assure environmental conditions are maintained that allow the species to remain self-sustaining.

Forest age was a strong positive predictor of salamander occurrence and relative abundance with salamanders encountered more often and in greater numbers in older forest age categories. For *P. elongatus*, we were approximately twice as likely to encounter salamanders in young and mature forest compared to pre-canopy stands, and three times more likely in old-growth compared to pre-canopy. For *P. stormi*, differences among forest age classes were found only between pre-canopy sites and the other three forest age classes. We were 1.5 times more likely to encounter these salamanders in young, mature or old-growth stands compared to pre-canopy stands, and we found 2.5 times as many salamanders in young, mature or old-growth stands compared to pre-canopy stands. The pattern of strong differences in salamander presence at sites at the extremes of the seral continuum is similar to previous studies in North American forests assessing distributions of terrestrial salamanders along the forest chronosequence (reviewed in deMaynadier and Hunter, 1995; Cushman, 2006). More recently, Karraker and Welsh (2006) found *P. elongatus* and *Ensatina eschscholtzii* more often and in higher numbers in late-seral forest than in pre-canopy. Other Pacific Northwest studies including Dupuis et al. (1995) and Bury and Martin (1973) also reported fewer terrestrial amphibians in pre-canopy versus old-growth forests.

4.2. *Life stage distributions*

We found a higher proportion of adult salamanders in older forest age classes for *P. elongatus*. A similar pattern was observed for *P. stormi* but the differences were not significant, likely due to the small sample sizes. Although variation in age ratios by forest age class may reflect differences in adult survival, it also could be caused by differential local productivity and recruitment. Higher recruitment in young forest stands would yield a higher proportion of young animals on these sites. Another possibility is that younger stands have

a higher proportion of low quality breeding or foraging sites compared to older stands, and thus operate as sinks for dispersing young animals from nearby source populations (Graves, 1997; Rohwer, 2004). The first alternative, differences in local productivity and recruitment, contradicts our findings of a positive relationship between the proportion of adult animals and total number of animals found at a site. If higher reproductive output was responsible for the higher proportion of young animals in young forests, then we would also expect to see higher numbers of salamanders in young forests. Given that we found relatively low counts of salamanders in young forests, the only way the first hypothesis could be supported is if the young forest stands were all sampled during periods of rapid population growth. Young forest ages ranged between 30 and 99 years old. It seems highly unlikely that we would, by chance, sample several of the young stands during periods of rapid salamander population growth over 30 years post-disturbance.

The second alternative, despotic dispersal of immature salamanders to young forest stands from nearby source populations, is harder to distinguish from differential survival of adults. Because adult survival estimates are based on the proportion of adults in a sample $A/(A + I)$ and despotism between adults and subordinate animals may affect age ratios, both differential adult survival and despotic movements may cause the variation in age ratios we observed across forest age classes (Rohwer, 2004). At scales within the low dispersal capabilities of plethodontid salamanders (Welsh and Lind, 1992; Marsh et al., 2004; Karraker and Welsh, 2006), despotic interactions between adults and subordinates is more likely to create the differences in age ratios, while at large scales beyond the dispersal distances of the animals, differences in age ratios would be better explained by differential survival. Our datasets here encompass a large portion of the range of *P. elongatus* and extend well beyond the dispersal capabilities of the animals; however, due to a long history of logging and forest fires, the Klamath–Siskiyou region consists of a patchwork of forest stands of varying ages and varying stages of recovery. Rohwer (2004) concluded that when samples are collected from contiguously distributed localities across the environmental gradient, differences in age ratios likely infer despotically driven dispersal. There is evidence of territoriality in terrestrial salamanders (Mathis, 1990, 1991), which likely results in younger individuals being forced to disperse. Regardless of whether the pattern is driven by despotic movement from source to marginal habitats or reduced adult survival in younger forests, we can conclude that, in general, younger forest stands provide reduced habitat quality for *P. elongatus* compared to mature and old-growth forest stands.

The increased presence of juveniles and adults in young forests compared to pre-canopy, and the lack of a difference between mature and old-growth forests, suggests that population recovery occurs between 30 and 100 years (during the young forest age class). Ash (1997) found that *P. jordani* were not detected in clear-cuts within 2 years of logging, but were detected after 4–6 years following cutting in the southern Appalachian region. He predicted that salamander numbers in clear-cut stands would attain the same numbers as on forest plots by 20–24 years after cutting. Petranka (1999) countered with projections that suggested a much longer turnaround time. We had very low captures in pre-canopy forests (0–30 years), which indicated relatively extreme detrimental effects of clear-cut harvesting on both *P. stormi* and *P. elongatus* populations. deMaynadier and Hunter (1995) determined that plethodontid populations in the eastern United States require 30–60 years to recover from clear-cutting, an estimate within the range of our young forest stands of 30–99 years.

4.3. *Body condition index*

Body condition patterns related to forest age differed between *P. stormi* and *P. elongatus,* with body condition lower for *P. stormi* in the young stands, and lower for *P. elongatus* in the mature and reference stands. The results for *P. elongatus* are contradictory to our hypothesis that we would find low body conditions in poor quality habitats. These results suggest that despite the recognized associations of both species with habitat conditions found in late-seral forests (Welsh and Lind, 1995; Welsh et al., 2007), some fundamental ecological differences may exist between these two salamander species and forest succession. Low body condition of *P. elongatus* in older forests with larger population sizes may reflect intraspecific competition that leads to despotic movement into peripheral habitats where there is less competition. The relatively wet and warm spring and fall seasons within the range of *P. elongatus* may facilitate successful short-distance dispersals compared to the apparently harsher conditions within the range of *P. stormi*. We never found large populations of *P. stormi* similar to *P. elongatus,* suggesting that *P. stormi* may not reach population numbers where intraspecific competition has an effect. Thus, body condition indices for *P. stormi* may provide a better metric of actual habitat quality for resident salamanders compared with *P. elongatus*. Conditions suitable for salamander surface activity may be available for shorter annual durations in young forests, reducing the critical period for foraging and reproducing (Huey and Kingsolver, 1989). This decrease in foraging activity time may explain the lower body conditions of *P. stormi* in these forests.

4.4. *Forest age and habitat quality*

A main focus of this paper was to compare salamander age structure and condition by forest stand age without reference to particulars of habitat quality. We wanted to see if patterns existed with forest age alone. We understood at the outset that the distribution of both species is closely tied to and limited by habitat and climatic features that may or may not be affected by forest age (e.g., Welsh and Lind, 1995; Welsh et al., 2007). Forest stands recover from disturbance differently depending on the severity, size, and type of disturbance and on the general environment in which the disturbance occurred (Franklin et al., 2002). These differences result in widely contrasting starting conditions for stand development. Timing of stand regeneration varies greatly as well and is dependent on the proximity of a seed source, soil quality, and environmental conditions such as drought (Franklin et al., 2002). It is likely that we sampled in a range of forest disturbance regimes and recovery trajectories that influence the suitability of the habitats for salamanders at different rates. Understanding the underlying complexity of forest

recovery is imperative to properly interpret the variability within our results. Even with this heterogeneity, we found some distinct patterns of demography that suggest a positive association of salamander numbers and increased life stage structural complexity with characteristics of later-succession forest stands.

While much of the evidence for distinct differences in habitat quality for plethodontid salamanders along the forest chronoseqence is indirect, clearly the preponderance of that evidence (e.g., deMaynadier and Hunter, 1995; Wyman, 2003; this paper) indicates that later-successional forests support more salamander populations with more individuals representing mature life stages, and with individuals often in better condition. Davic and Welsh (2004) reviewed the evidence that older forests support higher numbers of salamanders and higher species diversity as well. Because habitat quality is at the core of source-sink dynamics in that high quality habitats function as sources in which birth exceeds deaths, and emigration outweighs immigration; while low quality habitat functions as a sink in which deaths exceed births, and immigration out-weighs emigration (Pulliam, 1988), it follows that these populations in later-seral forests have a much higher probability of sustained viability and persistence on the landscape (Schooley and Branch, 2007).

4.5. *Management implications*

Our results support the contention that finding salamanders in pre-canopy or clear-cut forest stands does not inherently mean that healthy or self-sustaining populations are present. Looking beyond presence/not detected data should be considered when determining the status of any population. Metrics such as population age structure and body condition indices are valuable for providing clues to the true status of secretive animals. Although some of our results are inconclusive (e.g., *P. stormi* demographic profiles), we do provide evidence that at least some of the salamander populations we examined in clear-cut and young forest stands are likely sink populations requiring recruitment from nearby sources to be sustained.

Our studies were not comprehensive enough to propose standard thresholds for relative abundance levels, age distributions, or body conditions for *P. elongatus* or *P. stormi*. However, we believe that developing standards and thresholds should be a goal of amphibian monitoring programs. With little additional effort in using standardized protocols and taking consistent weight and length measurements, population metrics could be monitored so that population dynamics could be better understood and tracked over time. Furthermore, managers should consider landscape design approaches to maintain connectivity between potential sink and source habitats (e.g., Olson et al., 2007).

Lastly, the limited distributions and old-growth forest associations of these two species may reflect niche conservatism similar to that demonstrated for eastern plethodontids (Kozak and Wiens, 2006). Species with strong niche conservatism have a poor ability to adapt to altered environmental conditions such as climate change or successional re-setting because they lack the behavioral or physiological plasticity to adjust to such changes. Environmental change can thus modify and fragment their distributions, which may lead to speciation where possible (Kozak et al., 2005), or result in an extinction trajectory (e.g., Bernardo and Spotila, 2006). Addressing this problem will be a supreme challenge for managers who want to preserve these conservative species on the landscapes of the future (e.g., Bulman et al., 2007).

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