Review

A Case for Using Plethodontid Salamanders for Monitoring Biodiversity and Ecosystem Integrity of North American Forests

HARTWELL H. WELSH JR.* AND SAM DROEGE†
*U.S. Forest Service, Pacific Southwest Research Station, Redwood Sciences Laboratory, 1700 Bayview Drive, Arcata, CA 95521, U.S.A., email hwelsh@fs.fed.us
†U.S. Geological Survey, Patuxent Wildlife Research Center, 12100 Beech Forest Drive, Laurel, MD 20708, U.S.A.

Abstract: *Terrestrial salamanders of the family* Plethodontidae *have unique attributes that make them excellent indicators of biodiversity and ecosystem integrity in forested habitats. Their longevity, small territory size, site fidelity, sensitivity to natural and anthropogenic perturbations, tendency to occur in high densities, and low sampling costs mean that counts of plethodontid salamanders provide numerous advantages over counts of other North American forest organisms for indicating environmental change. Furthermore, they are tightly linked physiologically to microclimatic and successional processes that influence the distribution and abundance of numerous other hydrophilic but difficult-to-study forest-dwelling plants and animals. Ecosystem processes such as moisture cycling, food-web dynamics, and succession, with their related structural and microclimatic variability, all affect forest biodiversity and have been shown to affect salamander populations as well. We determined the variability associated with sampling for plethodontid salamanders by estimating the coefficient of variation (CV) from available time-series data. The median coefficient of variation indicated that variation in counts of individuals among studies was much lower in plethodontids (27%) than in lepidoptera (93%), passerine birds (57%), small mammals (69%), or other amphibians (37-46%), which means plethodontid salamanders provide an important statistical advantage over other species for monitoring long-term forest health.*

Caso Sobre el Uso de Salamandras Plethodóntidas en el Monitoreo de la Biodiversidad y la Integridad del Ecosistema de Bosques de Nortéamerica

Resumen: *Las salamandras terrestres de la familia* Plethodontidae *tienen atributos únicos que las hacen excelentes indicadores de la biodiversidad y la integridad del ecosistema en hábitats forestales. Su longevidad, sus territorios de tamaño pequeño, su fidelidad de sitio, su sensibilidad a las perturbaciones naturales y antropogénicas, su tendencia a ocurrir en densidades altas y los bajos costos de muestreo indican que los conteos de salamandras plethodóntidas proveen numerosas ventajas sobre otros organismos de los bosques de Norteamérica para representar cambios ambientales. Además, estas salamandras están estrechamente ligadas fisiológicamente a procesos microclimiáticos y sucesionales que influencían las distribuciones y abundancias de otras especies de plantas y animales bidrofilicas que babitan los bosques, pero que son dificiles de estudiar. Los procesos de los ecosistemas tales como el ciclo de humedad, las dinámicas de la red alimenticia y la sucesión, con su variabilidad estructural y microclimática inherente, afectan la biodiversidad forestal y ba sido demostrado que afectan también a las poblaciones de salamandras. Determinamos la variabilidad asociada con el muestreo de salamandras plethodóntidas mediante la estimatión del coeficiente de variatión (CV) a partir de datos accesibles de series de tiempo. La mediana del CV indicó que la variatión en los conteos de individuos entre estudios fué mucbo menor en pletbodóntidos (27%) que en lepidópteros (93%), aves paserinas (57%), mamíferos pequeños (69%) y otros anfibios (37-46%), to cual significa que las salamandras plethodóntidas proveen una importante ventaja estadistica sobre las otras especies para el monitoreo a largo plazo de la salud del bosque.*

Paper submitted February 2, 2000; revised manuscript accepted August 30, 2000.

Conservation Biology, Pages 558-569
Volume 15, No. 3, June 2001

Introduction

Ecosystems are combinations of plants, animals, microbes, and the physical environment that coexist as interdependent, functional units within climatically, geologically, and geographically defined boundaries. If the naturally occurring sets of these species and their respective physical habitats are present and self-replicating within an area, then the components and processes that constitute a functioning ecosystem are present and the biological integrity (Karr 1991) of that ecosystem is being maintained. The introduction of stressors-physical, chemical, or biological entities that cause an adverse ecological effect (Lowrance & Vellidis 1995)-can disrupt this ecological integrity (Karr 1996) and threaten ecosystem processes and inherent stability (i.e., resistence and resilience; Waide 1995). Stressors act on organisms and/or their habitats by disrupting the ability of species (or assemblages) to survive and reproduce. Through such negative ecological effects or responses, ecosystem functions are disrupted and ecosystem stability is put at risk. The first signs of environmental stress usually occur at the population level, affecting especially sensitive species (Odum 1992). It follows, therefore, that an effective program designed to monitor ecosystem stability includes measures that assess the status of some putative sensitive species.

Although it is desirable to monitor all the plants and animals in a region (alpha richness), the number of species and the cost associated with developing a statistically appropriate sampling frame renders this impractical. Consequently, it makes sense to find surrogates whose changes in presence or abundance are likely to fluctuate with changes in the system, but that are reasonably easy, cost-effective, and statistically appropriate to monitor. Such surrogates should quickly reflect changes in the status of major aspects of the ecosystem (Simber-loff 1998; Caro & O'Doherty 1999).

In forest ecosystem monitoring, key habitat and vegetation features makes sense because of their importance to many medium- and large-sized wildlife species and their dominant role in structuring the ecosystem (e.g., large trees and downed logs in the late-seral forests of the Pacific Northwest). Such components are advantageous because they do not move and some can be remotely sensed. Nevertheless, in the case of smaller organisms and processes, which may operate somewhat independently of larger habitat elements, it may make more sense to look for other surrogates at a different spatial scale. Of particular interest are species, such as keystone species, whose life histories are tightly intertwined with other small life forms and fine-scale forest ecosystem processes (Power et al. 1996; Simberloff 1998).

Forest amphibians, particularly salamanders, have a number of characteristics that make them excellent candidates for monitoring forest ecosystems. They occur syntopically with many other small forest plants and animals, are often numerous (Fig. 1), can be easily and cheaply sampled, are functionally positioned at mid-levels in the food web, and are highly sensitive to stressor-induced perturbations of many sorts (Vitt et al. 1990; Olson 1991; Wake 1991; Blaustein et al. 1994; Welsh & Ollivier 1998). We present ecological, life-history, and statistical arguments for the inclusion of terrestrial salamanders in forest monitoring.

Advantages of Plethodontid Salamanders for Forest Monitoring

Wide Distribution and Lack of a Need for Aquatic Habitats

The plethodontid salamanders (family Plethodontidae) offer some unique attributes that make them good indicators of the status of forest ecosystems. This is the largest of the world's 10 salamander families, and one that is restricted primarily to the New World (Duelhnan 1999). The majority of its members are characterized by complete suppression of the aquatic larval stage, eggs laid in terrestrial nests, and hatchlings that resemble miniature adults (Wake & Hanken 1996). Freed from the necessity of breeding in water, many lineages of plethodontids have radiated over evolutionary time from their apparent origins in the streams of Appalachia to colonize moist forest habitats throughout the eastern and western United States and have dispersed into the New World tropics (Wake 1966, 1987; Wake & Lynch 1976). The large genus *Plethodon* (woodland salamanders) contains 21-40 species in the eastern and midwestern United States, 5-6 in the far west, and 1 in the southern

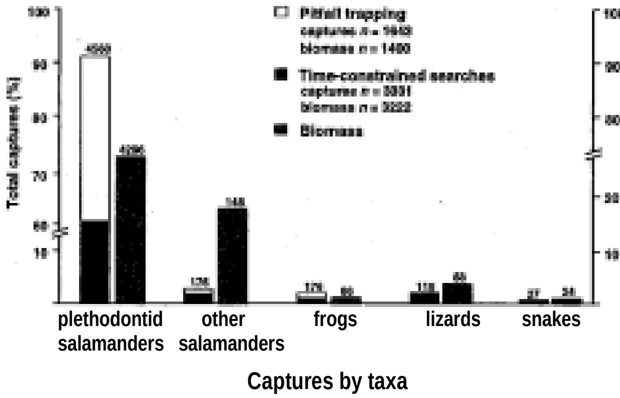

Figure 1. Relative numbers of plethodontid versus other salamanders, frogs, lizards, and snakes sampled over 3 years from 54 forest stands in the Klamath Mountains of northern California and southwestern Oregon (n = *4974). Numbers above bars are number of captures. For descriptions of sampling methods and the locations of the 54 stands sampled, see Welsh and Lind (1991).*

Rocky Mountains of New Mexico, depending on the taxonomic authority used (Stebbins 1985; Conant & Collins 1991; Highton 1995; Petranka 1998; Duellman & Sweet 1999; Highton 1999; Highton & Peabody 2000). The family contains other closely related terrestrial forest salamander genera comprised of species with life histories similar to those of the genus *Plethodon,* including *Aneides, Batrachoseps, Ensatina, Hydromantes,* and some of the *Desmognathus* group. Together *Plethodon* and these other genera constitute a large and diverse set of forest-dwelling salamanders with at least some species present in most North American forests.

Abundant and Sensitive to Ecosystem Stresses

Extremely high densities of plethodontid salamanders have been recorded in temperate forests of North America. For example, Burton and Likens (1975a) estimated that the total biomass of the redback salamander (*Plethodon cinereus*) surpassed that of all other small vertebrates combined in a New Hampshire forest (for additional density estimates of eastern plethodontids, see Jaeger 1979; Hairston 1987). Welsh and Lind (1992) estimated a density of 3200-9000/ha for the Del Norte salamander (*Plethodon elongatus*) at a northern California site. Nussbaum (1974) and Ovaska and Gregory (1989) reported comparable densities for two other western plethodontids (*Plethodon stormi* and *Plethodon vehiculum*, respectively). Given their high numbers and unique physiological adaptations (Pough 1983), salamanders may play an important role in processing nutrients for forest growth and productivity (Burton & Likens 1975b). Such an important link has been established for small mammals in western conifer forests, where they are now known to be critical to the establishment of the root-mycorrhizae symbiosis and important prey for predators such as the Spotted Owl (*Strix occidentalis*) (Trappe & Maser 1977; Li et al. 1986). Despite their tremendous abundance, however, we have little real knowledge of the ecological roles of salamanders, the number of individuals required to fulfill those roles (cf. Conner 1988), and how salamander populations are linked to forest ecosystem processes. Wyman (1998) found that by reducing invertebrate numbers, *Plethodon cinereus* indirectly reduced the rate of decomposition of forest litter by between 11% and 17%, arguably altering forest carbon dynamics.

Although plethodontid salamander densities can be extremely high, with populations apparently quite stable where equable conditions persist (Hairston 1987; Hairston & Wiley 1993), recent evidence indicates that their numbers can decline dramatically in response to environmental stressors such as acidification (e.g., Frisbie & Wyman 1992; Wyman & Jancola 1992;) and timber harvesting (Ash 1997; Dupuis 1997; Waldick 1997; de Maynadier & Hunter 1998; Harpole & Haas 1999; Herbeck & Larsen 1999; for a review of the earlier literature, see deMaynadier & Hunter 1995). Although proximate reasons vary for changes in plethodontid salamander numbers in response to forest ecosystem stresses, the ultimate cause, and the best argument for the applicability of these organisms as indicators of forest ecosystems status, is their unique physiological restriction relative to litter and soil moisture and temperature (Feder 1983). Plethodontid salamanders have evolved to occupy a wide range of niches in the forest habitats of North America, overlapping broadly those microenvironmental and microclimatic conditions shared among a wide range of other small, more sessile forest organisms that are relatively easily perturbed by both natural and anthropogenic changes to the forest environment (e.g., Forest Ecosystem Management Assessment Team 1993).

Although the nature of any actual link between these organisms and plethodontid salamanders is mostly speculative or, at best, correlative (see Wyman 1998), most of these organisms are poorly described taxonomically, their natural history is poorly known, they are difficult to detect, and they cannot as yet be reliably sampled because we lack sufficient understanding of their life cycles. Thus, the fine-scale overlap with the forest micro-environment, shared with these poorly known organisms, make plethodontid salamanders excellent candidates for use in assessing fine-scale, soil-level processes within a forest-monitoring program. This approach is consistent with their use as "environmental monitoring indicators," or species that reflect environmental conditions (Fleishman 1997).

Plethodontid Salamanders and Forest Ecosystem Processes

Moisture

It is in the litter and upper soil layers that moisture is most important to terrestrial salamanders and many other hydrophilic forest-dwelling organisms. Because they must continuously maintain moist skin in order to respire, salamanders require constant contact with moist soil or litter. Surface activity, where the majority of feeding and mating occurs (Houck & Verrell 1993; Tilley & Bernardo 1993), requires high relative humidity. Even while out during high moisture conditions on the surface, salamanders are in a dehydrating situation and must return to litter and subterranean refugia for complete hydration (Jaeger 1978).

Changes in forests due to disturbance or climatic change that result in a drying of upper soil and litter layers decreases the capacity of the forest to support salamanders. A tall, multilayered canopy buffers weather extremes (i.e., wind, insolation, and fluctuations in temperature), providing stable, within-stand microclimates (Chen a al. 1999). The loss of canopy, or creation of large openings, reduces or removes this buffering element, and much of the evapotranspired moisture that maintains high relative humidity within the interior of the forest is lost. Increased wind effects, greater solar radiation reaching the forest floor, and temperature extremes reduce the available moisture on the forest floor (Chen et al. 1999). These factors shorten the period of suitable environmental conditions for surface activity by salamander and other moisture-dependent biota of the forest floor.

Vegetation uses large quantities of water, so its removal increases soil moisture and could therefore have a positive effect on salamander populations. The most critical habitat for salamander populations is not the soil layer, however, but the litter layer, where they feed and mate. Although soil moisture may increase when trees are cut (e.g., Keppler & Brown 1998), there is relatively little uptake of that moisture by the litter layer, and soil moisture is rarely physiologically limiting to salamanders. Consequently, although soil moisture may increase, this does not compensate for the drying of the litter layer that results from canopy removal.

Forest- Floor Microhabitats

Corn and Bury (1991) describe three important surface microhabitats available to and heavily used by terrestrial salamanders: rocky substrates, downed wood, and leaf litter (see also Welsh & Lind 1991). The latter two microhabitats generally occur in greater amounts in unmanaged, old-growth forests (Spies et al. 1988; Bingham & Sawyer 1991). Nonetheless, Bury et al. (1991) state that the occurrence and abundance of most species of woodland salamanders are more likely to be related to the presence of these microhabitats than to seral stage. For example, the unmanaged young stands of Douglas-fir that Aubry and Hall (1991) studied were naturally revegetating following a catastrophic wildfire. Despite the changes associated with the fire, many microhabitat features, usually more common in late-seral forests, were still present and providing habitat for amphibians.

This scenario is not likely to be the case for young, manage stands harvested under current rotation cycles favored by North American forest managers (Hansen et al. 1991). Managed forests tend to be depauperate in large woody material, both downed logs and snags (Aubry et al. 1988; Bury & Corn 1988; Spies & Cline 1988; Aubry & Hall 1991; Gilbert & Allwine 1991; Hansen et al. 1991), and in leaf litter (Covington 1981). Welsh and Lind (1991) found that salamander abundance was related to rock cover, groundcover-level vegetation, and the presence of large wood, in moderate decay classes (classes 3 and 4 on a scale of 1 to 5; Thomas 1979). Sites lacking one or more of these microhabitats contained a few generalist salamander species, but much of the species diversity was absent (Welsh & Lind 1991). Brooks (1999) found that *Plethodon cinereus* populations in Massachusetts forests varied with the density and abundance of woody debris and not with thinning practices or deer browsing.

Plethodontids use the burrows of other animals (e.g., small mammals), root channels, interstices, and rock fissures to move between the moister depths of the soil and talus and the surface. Salamanders do not dig burrows themselves (but see Jennings 1996). Compaction of soil and rock talus from heavy equipment appears to have lasting effects on these channels, crushing the pathways used for movement to the surface. Surface rock is often fragmented and rock orientation changed, resulting in fewer surface hiding and hunting places. If access to the surface is reduced drastically, reproduction and foraging access could decline. The importance of rocky substrates for some species is highlighted by the associations between high cobble density and salamanders such as the Siskiyou Mountains salamander (*Plethodon stormi*), Del Norte salamander (*Plethodon elongatus*), Shenandoah salamander (*Plethodon shenandoah*), and Cheat Mountain salamander (*Plethodon nettingi*) (Nussbaum 1974; Jaeger 1980; Herrington 1988; Diller & Wallace 1994; Welsh & Lind 1995).

Forest Canopy

The openness of the canopy in a forest stand can have profound effects on temperature and moisture regimes on the forest floor (Chen et al. 1999), which in turn affects salamander populations (e.g., Harpole & Haas 1999). For example, the Del Norte salamander is the southernmost occurring *Plethodon* in the far west (California), existing in drier and hotter climates than other species. Although Diller and Wallace (1994) found no relationship between canopy closure and the presence of this species on the coast (in redwood forest), Welsh and Lind (1995) found an important relationship with canopy closure for Del Norte salamanders on interior sites. Data from their Douglas fir-mixed hardwood sites indicate a canopy closure of between 62% and 83% (95% C.I.) for sites supporting salamanders (Welsh & Lind 1995). In fact, of the 43 environmental features measured, percent canopy closure was the single best variable for predicting the occurrence of Del Norte salamanders (Welsh & Lind 1995: Table 1).

Harpole and Haas (1999) found that following the first year of several different gap-creating forestry treatments, counts of salamanders declined under even the lightest cuts, whereas understory removal with herbicides had no apparent short-term effect. In a study of forest gaps in upstate New York, Messere and Ducey (1998) could detect no effect on populations of *Plethodon cinereus*, but their study was conducted for only 1 year after har-

Table 1. Summary of coefficients of variation (CV) for 35 studies of plethodontid salamanders.*

Species	*CY*	*Mean*	*Years*	*Technique*	*Citation*
Aneides vagrans	28	-	3	AC	Davis 1996
A. hardii	0.21	41.75	8	TC	Ramotnik 1997
A. hardii	30	75.29	7	TC	Ramotnik 1997
A. hardii	29	40.00	7	TC	Ramotnik 1997
A. hardii	41	4.67	6	TC	Ramotnik 1997
A. hardii	27	14.60	5	TC	Ramotnik 1997
A. hardii	15	31.4	5	TC	Ramotnik 1997
Desmognathus aeneus	48	7.13	15	TC	Hairston & Wiley 1993
D. monticola	02	219.65	3	MR	Bruce 1995
D. monticola	36	91.96	5	MR	Bruce 1995
D. monticola	22	37.88	5	MR	Bruce 1995
D. monticola	23	31.10	5	MR	Bruce 1995
D. monticola	27	26.60	15	TC	Hairston & Wiley 1993
D. ocrophaeus	27	17.53	15	TC	Hairston & Wiley 1993
D. ocrophaeus	26	31.39	3	NS	Hairston 1986
D. ocrophaeus	52	18.4	6	AC	T. Pauley, unpublished data
D. quadramaculatus	65	7.20	15	TC	Hairston & Wiley 1993
Ensatina eschscholtzii	42	14.60	5	NCO	Stebbins 1954
E. eschscholtzii	23	32.40	5	NCO	Stebbins 1954
E. eschscholtzii	27	4.80	5	NCO	Stebbins 1954
E. eschscholtzii	15	6.00	5	NCO	Stebbins 1954
E. eschscholtzii	109	26.7	6	PF	D. Wake, unpublished data
Eurycea quadridigitata	50	33.25	4	PT	Dodd 1992
E. quadridigitata	270	484.38	16	PT	Semlitsch et al. 1996
Plethodon cinereus	22	35.67	12	NCO	Jaeger 1980
P. cinereus	24	31.88	8	NCO	Jaeger 1980
P. cinereus	17	7.00	4	NCO	Taub 1961
P. cinereus	26	1.01	4	NC	J. Gibbs, unpublished data
P. cinereus	28	34.9	8	AC	J. Witham, L. Monti, & M. Hunter Jr., unpublished data
P. cinereus	55	20.8	6	AC	T. Pauley, unpublished data
P. elongatus	37	26.25	13	TC	H. Welsh, A. Lind, & L. Ollivier, unpublished, data
P. glutinosus (complex)	46	11.07	15	TC	Hairston & Wiley 1993
P. jordani	10	32.25	8	AC	Hairston 1983
P. jordani	20	55.00	15	TC	Hairston & Wiley 1993
P. vehiculum	30	-	3	AC	Davis 1996

**Data include the CV, mean count or capture (mean), number* of *years studied (year), type* of *survey technique (technique: ACO, artificial cover object; NCO, natural cover object; MR, mark recapture; PT pitfall trap; TC, time-constrained search; AC, area-constrained search).*

vest, which may not have been enough time to detect effects (Harpole & Haas 1999). In Massachusetts forests that underwent 40-50% reductions in the stocking class 12-21 years prior to being studied, Brooks (1999) found no difference in counts of *P. cinereus* among those sites that presumably had returned to full canopy closure. deMaynadier and Hunter (1998) documented the importance of high canopy closure for *P. cinereus* in Maine.

Forest Succession and Microclimate

Several studies have indicated that plethodontid salamander abundances in the Pacific Northwest are associated more with forest structure than stand age or successional stage per se (Aubry et al. 1988; Bury & Corn 1988; Aubry & Hall 1991; Bury et al. 1991; Corn & Bury 1991; and Gilbert & Allwine 1991). These structural elements consisted primarily of downed woody materials, often in the form of large decaying logs and associated debris. Nonetheless, because amounts and sizes of decaying logs are not independent of forest succession (e.g., Spies et al. 1988; Bingham & Sawyer 1991), forest age and salamander population sizes are probably indirectly linked.

Species are described as late-successional or old-growth associates if they are significantly more abundant in that stage or almost exclusively found in that stage (Ruggiero et al. 1991). Most species of woodland salamanders studied appear to reach their peak abundance in late seral stage or old-growth forests and yield depressed population counts following cutting of forests or in earlier successional habitats (Nussbaum 1974; Blymer & McGinnes 1977; Bury 1983; Raphael 1988; Welsh & Lind 1988, 1991, 1995; DeGraaf & Yamasaki 1992; Forest Ecosystem Management Assessment Team 1993; Mitchell et al. 1997; Dupuis et al. 1995; Ash 1997; Petranka et al. 1994; deMaynadier & Hunter 1998; Harper & Guynn 1999; Herbeck & Larsen 1999; but see Diller & Wallace 1994).

Although timber harvesting sets the successional sequence back to an earlier stage, dead and downed wood is sometimes left in place after harvest. In particular, cuts of old-growth forests in the West can result in unusually large quantities of these materials remaining. Consequently, unlike most of the eastern research, many western forestry impact studies demonstrate little change in terrestrial salamander population counts (Aubry et al. 1988; Bury & Corn 1988; Herrington 1988; Aubry & Hall 1991; Bury et al. 1991; Corn & Bury 1991; Gilbert & Allwine 1991). These results may give a misleading impression of the ability of these forests to continue to support large salamander populations (Hansen et al. 1991). Over time, and especially on industrial forestry lands, this downed woody material will decompose and not be replaced because of short cutting rotations. Climate may be an additional ameliorating factor; studies that showed no effect were all conducted in the wetter and cooler parts of the Pacific Northwest, where climate provides more of a buffer from the effects of canopy removal than in the more southern coastal ranges of the West (e.g., Bury 1983; Raphael 1988; Welsh & Lind 1988, 1991) and throughout the East (deMaynadier & Hunter 1995; Harpole & Haas 1999).

Salamander abundances can vary greatly with particular stand attributes that change as succession proceeds (Fig. 2). The varying role played by seral stage with geographic location and disturbance history illustrates how this ecological parameter influences the lives of these animals. The primary role of succession lies in the changing nature of forest stand structure, which becomes more heterogeneous with age (e.g., more large logs and snags in various stages of decay [Welsh & Lind 1991: their Table 8 & Fig. 4]). Closely related to structural change, and even more important for plethodontids, however, is the fact that seral stage strongly influences microclimate. Microclimates tend to be cooler and moister, with lower variability, in late seral forest than in harvested sites, road cuts, and heavily altered stands (Chen et al. 1993, 1999). The importance of narrow, stable, and equable ranges of temperature and moisture for salamanders is well estab-

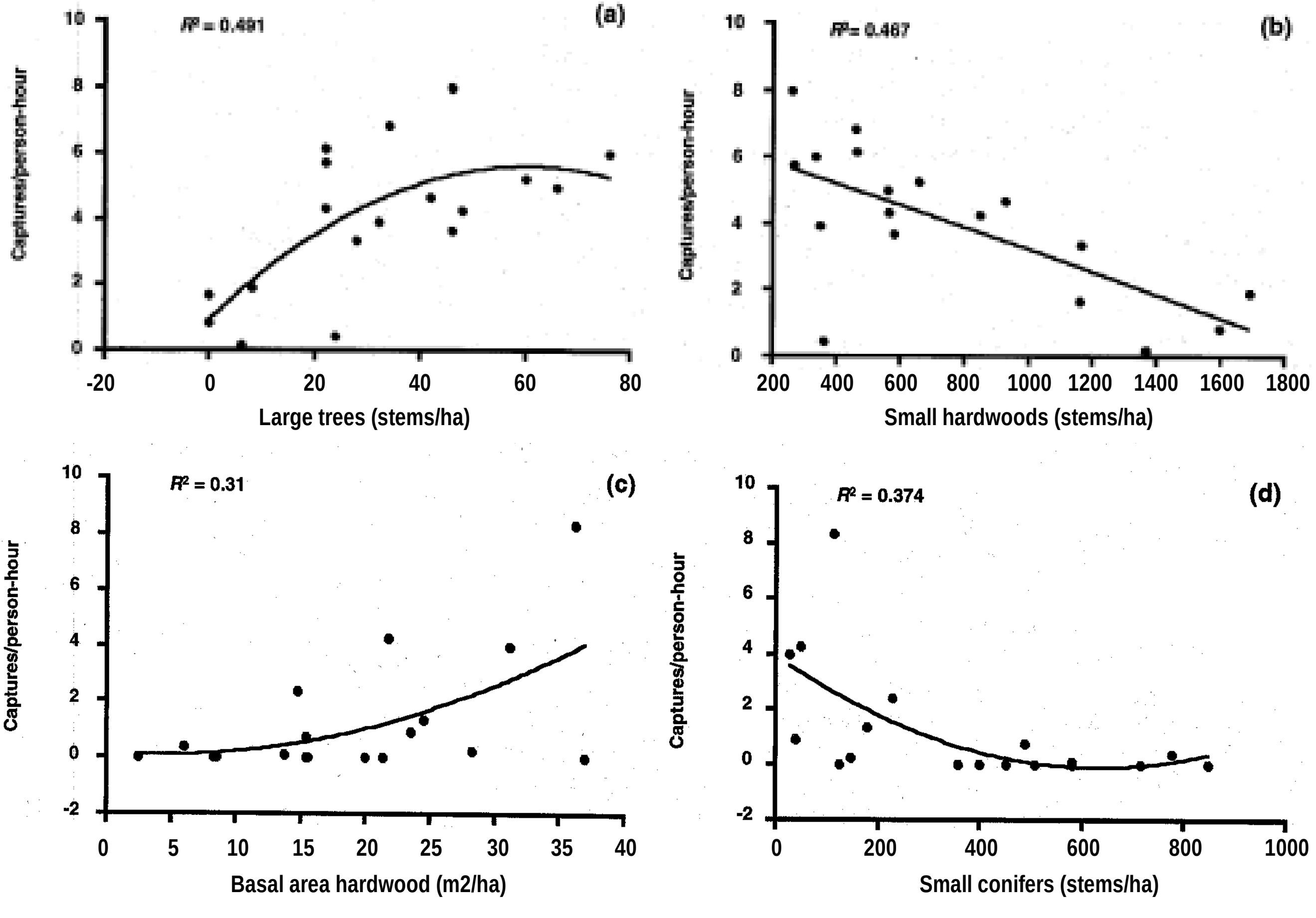

Figure 2. Bivariate scatterplots and regressions of (a) California slender salamander (Batrachoseps attenuatus) *abundance and large trees; (b) California slender salamander* (Batrachoseps attenuatus) *abundance and small hardwoods; (c) Del Norte salamander* (Plethodon elongatus) *abundance and basal area of hardwoods; and (d) Del Norte salamander* (Plethodon elongatus) *abundance and small conifers. Data are from H. Welsh (unpublished), but for descriptions of sampling methods and the locations of stands sampled for each of these species, see Welsh and Lind (1991).*

lished (Spotila 1972; Feder 1983), and many critical aspects of their natural history depend on such conditions (Tilley & Bernardo 1993). Older forests can better maintain the high moisture and low temperatures required by these heat- and dessication-sensitive species (Welsh 1990), a role that is clearly more important southward and toward the warmer interior portions of the ranges of western plethodontids. Consequently, it appears from both the ecological and evolutionary perspectives that many plethodontids are ecologically dependent (sensu Ruggiero et al. 1988) on conditions most often found in late seral forests.

Differences in forest structure associated with succession provide essential microclimates for a taxonomically diverse array of forest organisms endemic to late seral stages, including fungi, moss, lichens, ferns, and many understory trees, shrubs, and herbs (Bingham & Sawyer 1991, 1992; Spies 1991; Frost 1997; Chen et al. 1999; Jules & Rathcke 1999) and even some endotherms such as the Spotted Owl (Burrows 1981). Modification of forest structure (e.g., canopy removal) has a profound effect on interior microclimates (Chen et al. 1993, 1999; Brosofske et al. 1997; Harpole & Haas 1999) and ground-level vegetation (Chen et al. 1992; Frost 1997; Jules & Rathcke 1999). Such effects can quickly restrict or eliminate the ability of plethodontid salamanders to perform critical life-history functions such as foraging and reproduction (e.g., Fraser 1976; Lynch & Wallace 1987; Gergits & Jaeger 1990). The presence of and changes in salamander populations can thus provide independent feedback as to whether forests are being managed in ways that both sustain salamander populations and provide an adequate range of essential microhabitats and stable microclimatic characteristics for associated plant and animal- species (i.e., that maintain potential biodiversity). Using plethodontid salamanders in this way would be consistent with their use as "management effectiveness indicators" (Fleishman 1997).

Five plethodontid salamanders are among the late-seral-stage species included in the list of species to survey and manage in the Pacific Northwest Forest Plan (U.S. Forest Service et al. 1994: Table C-3). In the East all of the terrestrial salamanders reach their peak abundances in mature and old-growth forests (Petranka 1998), with the exception of the federally endangered *Plethodon shenandoah* (restricted to three remnant populations on talus slopes) and possibly the federally listed (as threatened) *Plethodon nettingi* (now restricted to scattered rocky outcrops and narrow ravines, but formerly thought to inhabit groves of mature red spruce [*Picea rubra*], all of which have been cut).

Metapopulation Considerations

Each species of plethodontid salamander is associated with particular habitats and microclimatic conditions; consequently, none is uniformly distributed in the forest. For example, in one of the more extreme cases of patchiness, Nussbaum (1974) estimated that approximately 3% of the known range of the Siskiyou Mountains salamander is suitable habitat for this species. This species is associated with rocky forested substrates that are distributed patchily. Even within apparently suitable habitat, sites are not occupied equally; some, such as rock outcrops and talus slopes, can support large concentrations of salamanders, whereas others have few or no animals.

Patchiness of habitats, combined with low fecundity, small home ranges, short dispersal distances (Mathis et al. 1995), and a propensity for geographic isolation, make some salamander populations highly vulnerable to forest fragmentation. Species complexes within the unglaciated regions of the United States which have undergone a high degree of genetic radiation in mountainous landscapes (e.g., Highton & Peabody 2000) are particularly vulnerable to loss of local gene pools through alteration and fragmentation of habitats. At the other end of the spectrum, red-backed salamander populations are nearly ubiquitous in the formerly glaciated regions of northeastern forests and appear relatively unaffected by even severe fragmentation (Gibbs 1998). Most species have distributions that lay between these extremes, so special consideration needs to be given to issues of fragmentation and land management for this group (Saunders et al. 1991; Fahrig & Merriam 1994). Using the presence and relative abundance of populations of some species as an indication of ecosystem functionality may require integrating a landscape perspective of metapopulation dynamics. Such knowledge of the entire plethodontid assemblage of a given region, based on objective criteria such as mtDNA or allozyme analysis (e.g., Larsen et al. 1984), can help reveal underlying phylogeographic relationships that indicate which species might be expected in healthy forests of a given locality.

Statistical Advantages of Using Plethodontids as Indicators for Forest Monitoring

To use salamanders as bioindicators requires appropriate and cost-effective counting techniques that are precise and replicable (i.e., exhibit low count variances) and accurate (i.e., unbiased). From the literature it is possible to determine the variability associated with sampling amphibian species by estimating the coefficient of variation (CV) from time-series studies of >3 years duration (Table 1). From the Amphibian Count Database (Eagle 1988), the median CV (with the effects of trend removed) for all amphibians in North America was 42% (*n* = 204); for anurans, 46% (*n* = 125); for salamanders of the genus Ambystoma, 37% (*n* = 34), and for plethodontids, 27% (*n* = 26). Although these studies do not represent a random sample of, species or geographic regions, thus rendering statistical evaluations not entirely appropriate, they are a reflection of techniques commonly used by herpetologists. From these results it is clear that variation in counts appears to be lower in plethodontids than other groups of amphibians. This is likely a reflection of the relatively stable forest environments they inhabit compared with amphibians that migrate to wetlands and vernal-pool breeding sites. The highest CVs are associated with counts from pitfall traps, a technique that differentially captures dispersing animals and is often used for reasons other than developing a standardized capture probability for salamanders. In our study, the pitfalls were run continuously through weather and seasons that both promoted and prevented salamander movements, which likely caused the high CV (Table 1). In addition, CVs for many of these populations could be further improved (i.e., by reducing the variance components of the counts) by limiting the counts to appropriate weather and time-of-year conditions and by using variance-reducing analysis techniques to account for the effects of observers and other environmental factors.

The practical result of low variation in -counts is high power to determine relative abundance across plots (or trends over time) compared with other amphibians and other groups of animals (e.g., mean CV for passerines, 57%; small mammals, 69%; lepidoptera, 93% [Gibbs et al. 1998]). Low variation also means that smaller sample sizes are necessary to achieve a given level of power.

Although the benefits in terms of sample sizes are clear for the low count variances exhibited by plethodontids, low variances cannot counter factors that may bias those counts. Bias here refers to departures of the population index (e.g., counts under boards or night transects) from some linear relationship with the true population. Only a small fraction of the total number of salamanders present at a site are counted at any given time because of their diel and seasonal patterns of vertical movement through the soil column (Taub 1961; Scott & Ramotnik 1992). Welsh and Lind (1992) and S. Droege, L. Bailey, R. Jung, and L. Weir (personal communication) indicated that for ground searches of salamanders during the daytime, capture probabilities are almost never >10% (1 in 30 estimates) and often are <5% (21 of 30); they used mark-recapture estimates from program JOLLY (Pollock et al. 1990) and Capture program, model *h* (White et al. 1982), respectively. These estimates come from populations in the Great Smoky Mountains of Tennessee, the Blue Ridge Mountains of Virginia, the coastal plain of Maryland, and the Klamath Mountains of California and varied greatly in estimated population size, habitat, moisture regime, plant communities, and species composition. Although these capture probabilities are extremely low, they are relatively uniform. Such uniformity in probabilities across such a diversity of potentially biasing factors (including the involvement of over 15 different observers) and circumstances is a good sign that indices for these salamanders may be directly comparable across landscapes and time. Further investigations are being conducted by a number of groups to test for differences in detectability through direct experimental manipulation, particularly of natural and artificial cover, which would appear to have the greatest potential to increase detectability of plethodontids. Although low capture probabilities themselves are not biasing, the low probability of detecting individual salamanders means that when population densities in the field are low; search rates need to be increased or the presence of these salamanders could be overlooked.

Disadvantages of Plethodontids as Indicators

There are some disadvantages to using woodland salamanders as subjects for monitoring. For example, these salamanders do not occur across all forests types in North America and are often absent from, drier forest types and heavily disturbed forests. Consequently, it would be wise to run pilot surveys to determine which, if any, species are present and whether they are sufficiently abundant and well distributed to be used effectively in a monitoring program. Another concern involves potential problems, with identification. In most regions identification of species is straightforward and requires little training. In the southern Appalachians, however, the number of species is high and their correct identification is often challenging. Consequently, the required skills and the costs of training observers will be higher in these areas.

Conclusions

Measures of forest health must accommodate all the communities of plants and animals (alpha biodiversity) that exist under the defining umbrella of large, woody plants. The process of tracking changes in salamanders (declines and increases) provides ecological insights into the community of hydrophilic organisms that dominates the soil-litter zone of many forests. These indices of change may also contribute to a more realistic assessment of forest ecosystem integrity than those based on the classical forestry measures of stocking and growth rates. Changes in the numbers of salamanders reflect the forest's balance of invertebrates, leaf litter, moisture, pH, debris, burrows, and other habitat features. Given their high sensitivity, detecting plethodontid declines may provide lead time to search for the root causes of such declines and prompt and appropriate actions to reverse habitat damage before the loss of other associated biota can occur. Given the longevity; site fidelity, small territory size, and low fecundity of plethodontid salamanders and the stability of a forest's soil environment (all features that also contribute to the low variances and high power of salamander counts), changes in salamander counts are more likely to represent significant environmental changes than counts of most other forest species.

The long-term tenure of woodland salamanders in the forested ecosystems of North America also suggest that these species have become well integrated if not integral to many moist-forest ecosystems of North America. The naturally high densities and biomass of plethodontid salamanders dictate that changes in their populations would have lasting and cascading effects throughout a forest as their invertebrate prey and vertebrate predators adjust. The rationale for monitoring terrestrial salamanders rests on their key role and high densities in many forests, the stability in their counts and populations, their vulnerability to air and water pollution, their sensitivity as a measure of change, and the threatened and endangered status of several salamander species. The measurement of plethodontid salamander abundance and species diversity offers a logical, cost-effective metric for monitoring the ecosystem integrity and related biodiversity of North American forest lands.

Acknowledgments

We thank N. Karraker and B. Zielinski for reviewing earlier versions of this manuscript and N. Karraker for help with the figures.

Literature Cited

Ash, A. N. 1997. Disappearance and return of plethodontid salamanders to clearcut plots in the Southern Blue Ridge Mountains. Conservation Biology **11**:983-989.

Aubry, K. B., and P. A. Hall. 1991. Terrestrial amphibian communities in the southern Washington Cascade range. Pages 327-340 in L. F. Ruggiero, K. B. Aubry, A. B. Carey, and M. H. Huff, technical coordinators. Wildlife and vegetation of unmanaged Douglas-fir forests. General technical report PNW-GTR-285. U.S. Forest Service, Pacific Northwest Research Station, Portland, Oregon.

Aubry, K. B., L. L. C. Jones, and P. A. Hall. 1988. Use of woody debris by plethodontid salamanders in Douglas-fir in Washington. Pages 32-37 in R. C. Szaro, K. E. Severson, and D. R. Patton, technical coordinators. Management of amphibians, reptiles and small mammals in North America. General technical report RM-166. U.S. Forest Service, Rocky Mountain Research Station, Fort Collins, Colorado.

Bingham, B. B., and J. O. Sawyer Jr. 1991. Distinctive features and definitions of young, mature, and old-growth Douglas-fir/hardwood forest. Pages 363-377 in L. F. Ruggiero, K. B. Aubry, A. B. Carey, and M. H. Huff, technical coordinators. Wildlife and vegetation of unmanaged Douglas-fir forests. General technical report PNW-GTR-285. U.S. Forest Service, Pacific Northwest Research Station, Portland, Oregon.

Bingham, B. B., and J. O. Sawyer Jr. 1992. Canopy structure and tree condition of young, mature, and old-growth Douglas-fir/hardwood forests. Pages 141-149 in R. Harris and D. Erman, editors. Symposium on biodiversity of northwestern California. Wildland Resources Center, University of California, Berkeley.

Blaustein, A. R., D. B. Wake, and W. P. Sousa. 1994. Amphibian declines: judging stability, persistence, and susceptibility of populations to local arid global extinctions. Conservation Biology **8:** 60-71.

Blymer, J. M., and B. S. McGinnes. 1977. Observations on possible detrimental effects of clearcutting on terrestrial amphibians. Bulletin of the Maryland Herpetological Society **13**:79-83.

Brooks, R. T. 1999. Residual effects of thinning and high white-tailed deer densities on northern redback salamanders in Southern New England oak forests. Journal of Wildlife Management **63**:1172-1180.

Brosofske, K. D., J. Chen, R. J. Naiman, and J. F. Franklin. 1997. Harvesting effects on microclimatic gradients from small streams to uplands in western Washington. Ecological Applications **7**:1188-1200.

Bruce, R. C. 1995. The use of temporary removal sampling in a study of population dynamics of the salamander *Desmognathus monticola*. Australian Journal of Ecology **20**:403-412.

Burrows, C. W. 1981. Roost selection by spotted owls: an adaptation to heat stress. Condor 83:302-309.

Burton, T. M., and G. E. Likens. 1975a. Salamander populations and biomass in the Hubbard Brook Experimental Forest, New Hampshire. Copeia **1975**:541-546.

Burton, T. M., and G. E. Likens. 1975b. Energy flow and nutrient cycling in salamander populations in the Hubbard Brook Experimental Forest, New Hampshire. Ecology **56**:1068-1080.

Bury, R. B. 1983. Differences in amphibian populations in logged and old-growth redwood forest. Northwest Science **57**:167-178.

Bury, R. B., and P. S. Corn. 1988. Douglas-fir forests in the Oregon and Washington Cascades: relation of the herpetofauna to stand age and moisture. Pages 11-22 in R. C. Szaro, K. E. Severson, and D. R. Patton, technical coordinators. Management of amphibians, reptiles and small mammals in North America. General technical report RM-166. U.S. Forest Service, Rocky Mountain Research Station, Fort Collins, Colorado.

Bury, R. B., P. S. Corn, K. B. Aubry, F. F. Gllbert, and L. C. Jones. 1991. Regional patterns of terrestrial amphibian communities in Washington and Oregon. Pages 353-362 in L. F. Ruggiero, K. B. Aubry, A. B. Carey, and M. H. Huff, technical coordinators. Wildlife and vegetation of unmanaged Douglas-fir forests. General technical report PNW-GTR-285. U.S. Forest Service, Pacific Northwest Research Station, Portland, Oregon.

Caro, T. M., and G. O'Doherty. 1999. On the use of surrogate species in conservation biology. Conservation Biology **13**:805-814.

Chen, J., J. F. Franklin, and T. A. Spies. 1992. Vegetation responses to edge environments in old-growth Douglas-fir forests. Ecological Applications **2**:387-396.

Chen, J., J. F. Franklin, and T. A. Spies. 1993. Contrasting microclimates among clearcut, edge, and interior old-growth Douglas-fir forest. Agricultural and Forest Meteorology **63**:219-237.

Chen, J., S. C. Saunders, T. R. Crow, R. J. Naiman, K. D. Brosofske, G. D. Morz, B. L. Brookshire, and J. F. Franklin. 1999. Microclimate in forest ecosystem and landscape ecology. Bioscience **49**:288-297.

Conant, R., and J. T. Collins. 1991. A field guide to reptiles and amphibians: eastern and central North America. Houghton Mifflin, Boston.

Conner, R. N. 1988. Wildlife populations: minimally viable or ecologically functional. Wildlife Society Bulletin **16**:80-84.

Corn, P. S., and R. B. Bury. 1991. Terrestrial amphibian communities in the Oregon coast range. Pages 305-318 in L. F. Ruggiero, K. B. Aubry, A. B. Carey, and M. H. Huff, technical coordinators. Wildlife and vegetation of unmanaged Douglas-fir forests. General technical report PNW-GTR-285. US. Forest Service, Pacific Northwest Research Station, Portland, Oregon.

Covington, W. W. 1981. Changes in forest floor organic matter and nutrient content following clear cuttings in northern hardwoods. Ecology **62**:41-48.

Davis, T. M. 1996. Distribution, abundance, microhabitat use and interspecific relationships among terrestrial, salamanders on Vancouver Island, British Columbia. Ph.D. dissertation. University of Victoria, Victoria, British Columbia, Canada.

DeGraaf, R. M., and M. Yamasaki. 1992. A nondestructive technique to monitor the relative abundance of terrestrial salamanders. Wildlife Society Bulletin **20**:260-264.

deMaynadier, P. G., and M. L. Hunter Jr. 1995. The relationship between forest management and amphibian ecology: a review of the North American literature. Environmental Review **3**:230-261.

deMaynadier, P. G., and M. L. Hunter Jr. 1998. Effects of silvicultural edges on the distribution and abundance of amphibians in Maine. Conservation Biology **12**:340-352.

Differ, L. V., and R. L. Wallace. 1994. Distribution and habitat of *Plethodon elongatus* on managed, young growth forests in north coastal California. Journal of Herpetology **28**:310-318.

Dodd, C. K., Jr. 1992. Biological diversity of a temporary pond herpetofauna in north Florida sandhills. Biodiversity and Conservation **1**:125-142.

Duellman, W. E., editor. 1999. Patterns of distribution of amphibians. Johns Hopkins University Press, Baltimore, Maryland.

Duellman, W. E., and S. S. Sweet. 1999. Distribution patterns of amphibians in the nearctic region of North America. Pages 31-109 in W. E. Duellman, editor. Patterns of distribution of amphibians. Johns Hopkins University Press, Baltimore, Maryland.

Dupuis, L. 1997. Effects of logging on terrestrial amphibians of coastal British Columbia. Pages 185-190 in D. M. Green, editor. Amphibians in decline: Canadian studies of a global problem. Herpetological conservation 1. Society for the Study of Amphibians and Reptiles, Saint Louis, Missouri.

Dupuis, L., J. N. M. Smith, and F. Bunnell. 1995. Relation of terrestrial-breeding amphibian abundance to tree-stand age. Conservation Biology **9**:645-653.

Eagle, P. 1988. Power analysis of monitoring programs: how many samples? Patuxent Wildlife Research Center, Laurel, Maryland. Available from http://www.mpl-pwrc.usgs.gov/powcase/powcase.html (accessed 21 August 2000):

Fahrig, L., and G. Merriam. 1994. Conservation of fragmented populations. Conservation Biology **8**:50-59.

Feder, M. E. 1983. Integrating the ecology and physiology of plethodontid salamanders. Herpetologica **39**:291-310.

Fleishman, E. A. 1997. Mesoscale patterns in butterfly communities of the central Great Basin and their implications for conservation. Ph.D. dissertation. University of Nevada, Reno.

Forest Ecosystem Management Assessment Team. 1993. Forest ecosystem management: an ecological, economic, and social assessment. Report 1993-793-071. U.S. Government Printing Office, Washington, D.C.

Fraser, D. F. 1976. Empirical evaluation of the hypothesis of food competition in salamanders of the genus *Plethodon.* Ecology **57**:459-471.

Frisbie, M. P., and R. L. Wyman. 1992. The effect of soil chemistry on sodium balance in the red-backed salamander: a comparison of two forest types. Journal of Herpetology **26**:434-442.

Frost, E. J. 1997. Edge effects in old-growth forests of the Klamath mountains: evidence from the understory flora. Pages 23-36 in J. K. Beigel, E. S. Jules, and B. Snitkin, editors. Proceedings of the first conference on Siskiyou ecology. The Siskiyou Regional Education Project, Cave Junction, Oregon.

Gergits, W. F., and R. G. Jaeger. 1990. Field observations of the behavfor of the red-backed salamander (*Plethodon cinereus*): courtship and agonistic interactions. Journal of Herpetology **24**:93-95.

Gibbs, J. P. 1998. Distribution of woodland amphibians along a forest fragmentation gradient. Landscape Ecology **13**:263-268.

Gibbs, J. P., S. Droege, and P. Eagle. 1998. Monitoring populations of plants and animals. BioScience **48**:935-940.

Gilbert, F. F., and R. Allwine. 1991. Terrestrial amphibian communities in the Oregon Cascade range. Pages 319-326 in L. F. Ruggiero, K. B. Aubry, A. B. Carey, and M. H. Huff, technical coordinators. Wildlife and vegetation of unmanaged Douglas-fir forests. General technical report PNW-GTR-285. U.S. Forest Service, Pacific Northwest Research Station, Portland, Oregon.

Hairston, N. G. 1983. Growth, survival and reproduction of *Plethodon jordani:* trade-offs between selective pressures. Copeia **1983:** 1024-1035.

Hairston, N. G. 1986. Species packing in *Desmognathus* salamanders: experimental demonstration of- predation and competition. The American Naturalist **127**:266-291.

Hairston, N. G., Sr. 1987. Community ecology and salamander guilds. Cambridge University Press, Cambridge, United Kingdom.

Hairston, N. G., Sr., and R. H. Wiley. 1993. No decline in salamander (Amphibia: Caudata) populations: a twenty year study in the southern Appalachians. Brimleyana **18**:59-64.

Hansen, A. J., T. A. Spies, F. J. Swanson, and J. L. Ohmann. 1991. Conserving biodiversity in managed forests. Bioscience **41**:382-392.

Harper, C. A., and D. C. Guynn Jr. 1999. Factors affecting salamander density and distribution within forest types in the Southern Appalachian Mountains. Forest Ecology and Management **114**:245-252.

Harpole, D. N., and C. A. Haas. 1999. Effects of seven silvicultural treatments on terrestrial salamanders. Forest Ecology and Management **114**:349-356.

Herbeck, L., and D. R. Larsen. 1999. Plethodontid salamander responses to silvicultural practices in Missouri Ozark forests. Conservation Biology **13**:623-632.

Herrington, R. E. 1988. Talus use by amphibians and reptiles in the Pacific Northwest. Pages 216-221 in R. C. Szaro, K. E. Severson, and D. R. Patton, technical coordinators. Management of amphibians, reptiles and small mammals in North America. General technical report RM-166. U.S. Forest Service, Rocky Mountain Research Station, Fort Collins, Colorado.

Highton, R. 1995. Speciation in eastern North American salamanders of the genus *Plethodon.* Annual Review of Ecology and Systematics **26**:579-600.

Highton, R. 1999. Geographic protein variation and speciation in the salamanders of the *Plethodon cinereus* group with descriptions of two new species. Herpetologica **55**:43-90.

Highton, R., and R. B. Peabody. 2000. Geographic protein variation and speciation in salamanders of the *Plethodon jordani* and *Plethodon glutinosus* complexes in the southern Appalachian mountains with the description of four new species. Pages 31-94 in R. C. Bruce, R. G. Jaeger, and L. D. Houck, editors. The biology of the plethodontid salamanders. Plenum Publishers, New York.

Houck, L., and P. Verrell. 1993. Studies of courtship behavior in plethodontid salamanders: a review. Herpetologica **49**:175-184.

Jaeger, R. G. 1978. Plant climbing by salamanders: periodic availability of plant-dwelling prey. Copeia **1978**:686-691.

Jaeger, R. G. 1979. Seasonal spatial distributions of the terrestrial salamander *Plethodon cinereus.* Herpetologica **35:**90-93.

Jaeger, R. G. 1980. Density-dependent and density-independent causes of extinction of a salamander population. Evolution **34**:617-621.

Jennings, M. R. 1996. *Ambystoma californiense* (California tiger salamander). Burrowing ability. Herpetological Review **27**:194.

Jules, E. S., and B. J. Rathcke. 1999. Mechanisms of reduced *Trillium* recruitment along edges of old-growth forest fragments. Conservation Biology 13:784-793.

Karr, J. R. 1991. Biological integrity: a long neglected aspect of water resources management. Ecological Applications **1**:66-84.

Karr, J. R. 1996. Ecological integrity and ecological health are not the same. Pages 97-109 in P. C. Shultz, editor. Engineering within ecological constraints. National Academy Press, Washington, D.C.

Keppler, E. T., and D. Brown, 1998. Subsurface drainage processes and management impacts. Pages 25-34 in R. Ziemer, technical coordinator. Proceedings of the conference on coastal watersheds: the Caspar Creek story. General technical report PSW GTR-168. U.S. Forest Service, Albany, California.

Larsen, A., D. B. Wake, and K. P. Yanev. 1984. Measuring gene flow among populations having high levels of genetic fragmentation. Genetics **106**:293-308.

Li, C. Y., C. Maser, Z. Maser, and B. A. Caldwell. 1986. Role of three rodents in forest nitrogen fixation in western Oregon: another aspect of mammal-mycorrhizal fungus-tree mutualism. Great Basin Naturalist **46:**411-414.

Lowrance, R., and G. Vellidis. 1995. A conceptual model for assessing ecological risk to water quality function of bottomland hardwood forests. Environmental Management **19:**239-258.

Lynch, J. E., and R. L. Wallace. 1987. Field observations of courtship behavior of Rocky Mountain populations of Van Dyke's salamander *(Plethodon vandykei)* with a description of its spermatophore. Journal of Herpetology **21**:337-340.

Mathis, A., R. G. Jaeger, W. H. Keen, P. K. Ducey, S. C. Walls, and B. W. Buchanan. 1995. Aggression and territoriality by salamanders and a comparison with the territorial behavior of frogs. Pages 633-676 in H. Heatwole and B. K. Sullivan, editors. Amphibian biology. 2. Social behavior. Surrey Beatty and Sons, Chipping Norton, New South Wales, Australia.

Messere, M., and P. K. Ducey. 1998. Forest floor distribution of northern redback salamanders, *Plethodon cinereus,* in relation to canopy gaps: first year following selective logging. Forest Ecology and Management **107**:319-324.

Mitchell, J. C., S. C. Rinehart, J. F. Pagels, K. A. Buhlmann, and C. A. Pague. 1997. Factors influencing amphibian and small mammal assemblages in central Appalachian forests. Forest Ecology and Management **96**:65-76.

Nussbaum, R. A. 1974. A report on the distributional ecology and life history of the Siskiyou Mountain salamander, *Plethodon stormi,* in relation to the potential impact of the proposed Applegate Reservoir on this species. U.S. Army Corps of Engineers, Portland, Oregon.

Odum, E. P. 1992. Great ideas in ecology for the 1990's. Bioscience **42**:542-545.

Olson, D. H. 1991. Ecological susceptibility of amphibians to population declines. Pages 55-62 in R. R. Harris, and D. C. Erman, technical coordinators. Symposium on biodiversity of northwestern California. Report 29. Wildland Research Center, University of California, Berkeley.

Ovaska, K., and P. T. Gregory. 1989. Population structure, growth, and reproduction in a Vancouver Island population of the salamander *Pletbodon vehiculum.* Herpetologica **45**:133-143.

Petranka, J. W. 1998. Salamanders of the United States and Canada. Smithsonian Institute Press, Washington, D.C.

Petranka, J. W., M. P. Brannon, M. P. Hopey, and C. K. Smith. 1994. Effects of timber harvesting on low elevation populations of southern Appalachian salamanders. Forest Ecology and Management **67**: 135-147.

Pollock, K. H., J. D. Nichols, C. Brownie, and J. E. Hines. 1990. Statistical inference for capture-recapture experiments. Wildlife Monographs 107.

Pough, F. H. 1983. Amphibians and reptiles as low energy systems. Pages 141-188 in W. P. Aspey and S. I. Lustick, editors. Behavioral energetics the cost of survival in vertebrates. Ohio State University Press, Columbus.

Power, M. E., D. Tilman, J. A. Estes, B. A. Menge, W. J. Bond, L. S. Mills, G. Daily, J. C. Castilla, J. Lubchenco, and R. T. Paine. 1996. Challenges in the quest for keystones. Bioscience **46**:609-620.

Ramomik, C. A. 1997. Conservation assessment of the Sacramento Mountain salamander. General technical report RM-GTR-293. U.S. Forest Service, Rocky Mountain Forest and Range Experiment Station, Port Collins, Colorado.

Raphael, M. G. 1988. Long-term trends in abundance of amphibians, reptiles, and small mammals in Douglas-fir forests of northwestern California. Pages 23-31 in R. C. Szaro, K. E. Severson, and D. R. Patton, technical coordinators. Management of amphibians, reptiles, and small mammals in North America. General technical report RM-166. U.S. Forest Service, Rocky Mountain Research Station, Fort Collins, Colorado.

Ruggiero, L. F., R. S. Holthausen, B. G. Marcot, K. B. Aubry, J. W. Thomas, and E. C. Meslow. 1988. Ecological dependency: the concept and its implications for research and management. Transactions of the North America Wildlife and Natural Resource Conference **53**: 115-126.

Ruggiero, L. F., L. C. Jones, and K. B. Aubry. 1991. Plant and animal habitat associations in Douglas-fir forests of the Pacific Northwest: an overview. Pages 447-462 in L. F. Ruggiero, K. B. Aubry, A. B. Carey, and M. H. Huff, technical coordinators. Wildlife and vegetation of unmanaged Douglas-fir forests: General technical report PNW-GTR-285. U.S. Forest Service, Pacific Northwest Research Station, Portland, Oregon.

Saunders, D. A., R. J. Hobbs, and C. R. Margules. 1991. Biological consequences of ecosystem fragmentation: a review. Conservation Biology **5**:18-32.

Scott, N. J., Jr., and C. A. Ramomik. 1992. Does the Sacramento Mountain salamander require old-growth forest? Pages 170-178 in M. R. Kaufmann, W. H. Moir, and R. L Bassett, technical coordinators. Old-growth forests in the Southwest and Rocky Mountain Regions. Proceedings of a workshop. General technical report RM-213. U.S. Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado.

Semlitsch, R. D., D. E. Scott, J. H. K. Pechmann, and J. W. Gibbons. 1996. Structure and dynamics of an amphibian community. Pages 217-250 in M. L. Cody and J. A. Smallwood, editors. Long-term studies of vertebrate communities. Academic Press, San Diego, California.

Simberloff, D. 1998. Flagships, umbrellas, and keystones: is single-species management passe in the landscape era? Biological Conservation **83**:247-257.

Spies, T. A. 1991. Plant species diversity and occurrence in young, mature, and old-growth Douglas-fir stands in western Oregon and Washington. Pages 111-121 in L. F. Ruggiero, K. B. Aubry, A. B. Carey, and M. H. Huff, technical coordinators. Wildlife and vegetation of unmanaged Douglas-fir forests. General technical report PNW-GTR-285. U.S. Forest Service, Pacific Northwest Research Station, Portland, Oregon.

Spies, T. A., and S. P. Cline. 1988. Coarse woody debris in forests and plantations of coastal Oregon. Pages 5-24 in, C. Maser, R. F. Tarrant, J. M. Trappe, and J. F. Franklin, technical coordinators. From the forest to the sea: a story of fallen trees. General technical report PNW-GTR-229. U.S. Forest Service, Pacific Northwest Research Station, Portland, Oregon.

Spies, T. A., J. F. Franklin, and T. B. Thomas. 1988. Coarse woody debris in Douglas-fir forests of western Oregon and Washington. Ecology **69**:1689-1702.

Spotila, J. R. 1972. Role of temperature and water in the ecology of lungless salamanders. Ecological Monographs **42**:95-125.

Stebbins, R. C. 1954. Natural history of the salamanders of the plethodontid genus *Ensatina.* Pages 47-124 in A. H. Miller, F. A. Pitelka, and K. Stern, editors. University of California publications in zoology. University of California Press, Berkeley.

Stebbins, R. C. 1985. A field guide to western reptiles and amphibians. Houghton Mifflin, Boston.

Taub, F. B. 1961. The distribution of the red-backed salamander, *Plethodon c. cinereus,* within the soil. Ecology **42**:681-698.

Thomas, J. W., editor. 1979. Wildlife habitats in managed forests of the Blue Mountains of Oregon and Washington. Agriculture Handbook 553. U.S. Forest Service, Washington, D.C.

Tilley, S. G., and J. Bernardo. 1993. Life history evolution in plethodontid salamanders. Herpetologica **49**:154-163.

Trapper J. M., and C. Maser. 1977. Ectomycorrhizal fungi: interactions of mushrooms and truffles with beasts and trees. Pages 165-178 in T. Walters, editor. Mushrooms and man: an interdisciplinary ap proach to mycology. Linn Benton Community College, Albany, Oregon.

U.S. Forest Service, Department of the Interior, and Bureau of Land Management. 1994. Record of decision on management of habitat for late-successional and old-growth forest related species within the range of the Northern Spotted Owl. Northwest forest plan, Oregon.

Vitt, L. J., J. P. Caldwell, H. M. Wilbur, and D. C. Smith. 1990. Amphibians as harbingers of decay. Bioscience **40**:418.

Waide, J. B. 1995. Ecosystem stability: revision of the resistance-resilience model. Pages 372-396 in B. C. Patten and S. E. Jorgenson, editors. Complex ecology, the part-whole relation in ecosystems. Prentice Hall, Englewood Cliffs, New Jersey.

Wake, D. B. 1966. Comparative osteology and evolution of the lungless salamanders, family Plethodontidae. Memoirs of the Southern California Academy of Science **4**:1-111.

Wake, D. B. 1987. Adaptive radiation of salamanders in Middle American cloud forests. Annals of the Missouri Botanical Garden **74**:242-262.

Wake, D. B. 1991. Declining amphibian populations. Science **253**:860.

Wake, D. B., and J. Hanken. 1996. Direct development in the lungless salamanders: what are the consequences for developmental biology, evolution and phylogenesis? International Journal of Developmental Biology **40**:859-869.

Wake, D. B., and J. F. Lynch. 1976. The distribution, ecology, and evolutionary history of plethodontid salamanders in tropical America. Science Bulletin 25. Natural History Museum of Los Angeles County, Los Angeles.

Waldick, R. 1997. Effects of forestry practices on amphibian populations in eastern North America. Pages 191-205 in D. M. Green, editor. Amphibians in decline: Canadian studies of a global problem. Herpetological conservation 1. Society for the Study of Amphibians and Reptiles, Saint Louis, Missouri.

Welsh, H. H., Jr. 1990. Relictual amphibians and old-growth forests. Conservation Biology **4**:309-319.

Welsh, H. H., Jr., and A. J. Lind. 1988. Old-growth forests and the distribution of the terrestrial herpetofauna. Pages 439-458 in R. C. Szaro, K. E. Severson, and D. R. Patton, technical coordinators. Management of amphibians, reptiles, and small mammals in North America. General technical report RM-166. U.S. Forest Service, Rocky Mountain Experiment Station, Fort Collins, Colorado.

Welsh, H. H., Jr., and A. J. Lind. 1991. The structure of the herpetofaunal assemblage of the Douglas-fir forests of northwestern California and southwestern Oregon. Pages 394-413 in L. F. Ruggiero, K: B. Aubry, A. B. Carey, and M. H. Huff, technical coordinators. Wildlife and vegetation of unmanaged Douglas-fir forests. General technical report PNW-GTR-285. U.S. Forest Service, Pacific Northwest Research Station, Portland, Oregon.

Welsh, H. H., Jr., and A. J. Lind. 1992. Population ecology of two relictual salamanders from the Klamath Mountains of northwestern California. Pages 419-437 in D. R. McCulloch, and R. H. Barrett, editors. Wildlife 2001: populations. Elsevier Science, London.

Welsh, H. H., Jr., and A. J. Lind. 1995. Habitat correlates of the Del Norte salamander, *Plethodon elongatus,* (Caudata: Plethodontidae), in northwestern California. Journal of Herpetology **29**:198-210.

Welsh, H. H., Jr., and L. M. Ollivier. 1998. Stream amphibians as indicators of ecosystem stress: a case study from California's redwoods. Ecological Applications **8**:1118-1132.

White, G. C., D. R. Anderson, K. P. Burnham, and others. 1982. Capture-recapture and removal methods for sampling closed populations: LA-8787-NERP. Los Alamos National Laboratory, Los Alamos, New Mexico.

Wyman, R. L. 1998. Experimental assessment of salamanders as predators of detrital food webs: effects on invertebrates, decomposition and the carbon cycle. Biodiversity and Conservation **7**:641-650.

Wyman, R. L., and J. Jancola. 1992. Degree and scale of terrestrial acidification and amphibian community structure. Journal of Herpetology **26:**392-401.