



Science Review for the Scott Bar Salamander (*Plethodon asupak*) and the Siskiyou Mountains Salamander (*P. stormi*): Biology, Taxonomy, Habitat, and Detection Probabilities/Occupancy

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Introduction

The *Plethodon elongatus* Complex in the Klamath-Siskiyou Ecoregion of southern Oregon and northern California includes three species: the Del Norte salamander, *Plethodon elongatus*; the Siskiyou Mountains salamander, *P. stormi*; and the Scott Bar salamander, *P. asupak*. This review aims to summarize the current literature and information available on select topics for *P. stormi* and *P. asupak*. These are both terrestrial salamanders belonging to the Family Plethodontidae, which contains more species and has a wider geographic distribution than any other family of salamanders (Wake 1966, 2006; Pough 1989). The genera of this family have greatly diversified ecologically across North America, Central America, northern South America, Sardinia, southeastern France and northwestern Italy, and have recently been discovered on the Korean peninsula (Min *et al.* 2005). The genus *Plethodon* is found exclusively in North America and is split into three distinct clades, based upon morphology and phylogenetics (Highton and Larson 1979): eastern small *Plethodon*, eastern large *Plethodon*, and the western *Plethodon*. The western *Plethodon* are the greatest representation of Plethodontidae in the Pacific Northwest, with 8 species. The two species with the most restricted ranges of these regional congeners are the Siskiyou Mountains and Scott Bar salamanders.

These salamanders occupy the interior of the Klamath-Siskiyou Ecoregion which straddles the California and Oregon state lines, between Siskiyou County (CA) and Jackson and Josephine Counties (OR). The relatively recent discovery of *P. asupak* (Mead *et al.* 2005) and the limited range of both species have created an environment of uncertain conservation status for these species. This review will focus on four central topics of concern for land and resource managers: Biology; Taxonomy; Habitat; and Detection Probabilities/Occupancy.

Biology

Species of the genus *Plethodon* have fairly rigid physiological requirements. Some unifying characteristics of the salamanders in this genus are their fully terrestrial existence, direct development, relatively small size, and lack of functional lungs (Dunn 1926, Zug *et al.* 2001). Although a thorough physiological evaluation has not been conducted on either *P. stormi* or *P. asupak*, moist conditions are required by both forms. *Plethodon* salamanders, due to their lack of functional lungs, respire through their permeable skin. This process requires moisture to properly allow for cutaneous gas exchange (Feder 1983). This obligatory condition is attained by the salamanders actively seeking out moist microhabitats, including those found by retreating underground, in other animal burrows, or the interstitial spaces created by the rocky substrates.

Plethodon stormi and *P. asupak* can be found closest to the surface during the region's wet season, which starts with the first fall rains and runs through the spring, or when site specific conditions present equable conditions. The region has low humidity in summer or other dry spells (mostly late spring and early fall) when these organisms are driven into subterranean refugia for available moisture and to avoid high temperatures.

Water loss from dry conditions can be lethal to *Plethodon* salamanders, and evidence from the Del Norte salamander (*P. elongatus*) indicates sensitivity to these conditions (Ray 1958). This would infer limited utilization of habitats or microclimatic environments that occur outside their zone of tolerance (Welsh *et al.* 2007). If sites experience changes in these conditions, it may result in reduction of time spent for foraging and reproduction (Feder 1983). No current studies have attempted to examine the biological limits or conditions acceptable to either *P. stormi* or *P. asupak*, but changes in habitat and microclimate variables have been studied in their close relative *P. elongatus* (Biek *et al.* 2002, Major 2005, Karraker and Welsh 2006).

Mobility of *P. elongatus* appears to be extremely low (Welsh and Lind 1992). Due to the environmental extremes of the interior Klamath Siskiyou region with freezing winter temperatures and hot, dry summer conditions, most salamanders are found during a narrow sampling timeframe (D. DeGross, pers. observation). Further, seasonal movements across the landscape appear to be even more restricted for the two species found in the interior compared to other salamanders (e.g., *P. elongatus*) living closer to the coast and in less extreme conditions.

Large skin surface to body mass ratios have been correlated to greater water retention (Feder 1983). Mead *et al.* (2005) produced evidence that *P. stormi* and *P. asupak* appear to be larger in size, or more robust, than *P. elongatus*. If the interior animals are more robust, it likely reflects an evolutionary response to life in the more arid interior. Variable number of trunk vertebrae has been inferred as a possible temperature-dependent phenotypic response (Jockusch 1997) in the western Plethodontid genus, *Batrachoseps*. In the *Plethodon elongatus* Complex, fewer costal grooves (i.e., shorter trunk) and the larger forelimbs observed in *P. stormi* and *P. asupak* result in a more robust body form than what is found in *P. elongatus* (Mead *et al.* 2005). Thus, the higher elevations of the interior of the Klamath-Siskiyou Ecoregion, greater climatic extremes (hotter summers and colder winters), and the glacial history of the region could be the driving forces of the evolutionary patterns observed in the *Plethodon elongatus* Complex.

Taxonomy

The systematics of the *Plethodon elongatus* Complex has been an active area of study as two distinct and novel forms have been identified over the last 40 years. The first identified member of the Complex was *Plethodon elongatus* that was described from a coastal population in Del Norte County, California (Van Denburgh 1916). When *P. stormi* was described (Highton and Brame 1965), it was found inland of *P. elongatus* and geographically isolated from the nearest known population of *P. elongatus* by at least 9 miles (14.4 km) (Brodie 1971). However, as more field observations were made of these congeners, the gap in geographic separation continued to shrink, and regional observations of morphological similarities began to emerge in the interior of the region (Brodie 1970; Bury 1973, 1999). Inferences to inland populations of *P. elongatus* sharing morphological characters with nearby *P. stormi* led to the proposition of intergrades in the interior of the region (Bury 1973), as well as combination of both forms under one species with subspecies designations (Stebbins 2003). Morphological traits and color were used in these early analyses (Brodie 1970; Bury 1973, 1999) to designate systematic relationships or describe geographic variation in features. Most recently, *P. asupak* was described more interior to *P. elongatus* and south to southeast of *P. stormi* (Mead *et al.* 2005).

Past studies and inferences of current studies on this complex have indicated the potential for additional taxonomic delineations or distinct population segments within the group (Bury 1973, Mahoney 2004, Mead *et al.* 2005, DeGross 2004, DeGross and Bury unpublished). However, none of these variants has been described in the literature. The systematic relationships of the group remain of high biological interest due to its marked geographic variation over relatively short geographic distances and the recent description of a new species.

Color and Morphology

Coloration differences between *P. elongatus* and *P. stormi* were originally the field diagnostic for their separation into different taxonomic units (Highton and Brame 1965, Brodie 1970). The ground color of *P. stormi* is usually black in juveniles and varies from light brown to purplish brown in subadults and adults (Highton and Brame 1965, Nussbaum *et al.* 1983). They lack a dorsal stripe, but may have many iridiphores (small spots) over the lateral surfaces and dorsum of the body. Juvenile *P. elongatus* in most interior locations have a distinct, dorsal red-brown stripe on a dark brown body color (Brodie 1971, Stebbins 2003, Bury 1999), however the adult stripe becomes lighter (olive-tan) or less distinct with age. Few localities were known at the time of the description of *P. stormi*, and Brodie (1971) reported that the two forms were allopatric (adjacent areas) in distribution. Past and present analyses and observations suggest that field identification based upon color alone can be problematic between the members of this complex, especially in western Siskiyou County, California.

Brodie (1970, 1971) reported that the number of trunk vertebrae in *P. stormi* (mode = 18) is one fewer than *P. elongatus* (mode = 19). Also, *P. stormi* has proportionally longer limbs than *P. elongatus* (Highton and Brame 1965, Bury 1999, Mead *et al.* 2005). Earlier, the variation observed by Brodie (1971) and Bury (1973) across the ranges of *P. elongatus* and *P. stormi* in coloration and morphological characters led Stebbins (2003) to consider a subspecies designation for inland *P. elongatus*, rather than full species status as *P. stormi*; however, this was a species account in a field guide and provided no specific rationale for the designation.

One locality of particular note and importance in the identification of these species was Seattle Creek, California, in the upper Klamath River basin. A fairly large series of specimens was first collected there by Bury (1973; specimens at Museum of Vertebrate Zoology), and reported on later by several authors (Brodie 1971; Bury 1973, 1999; Mead *et al.* 2005). A few samples taken from this locality would later be designated *P. stormi* from genetic analyses (Mahoney 2001, Pfrender and Titus unpublished, DeGross 2004, Mahoney 2004, Mead *et al.* 2005, Mead 2006, DeGross and Bury unpublished). Animals measured from this population and southward in the Klamath River drainage suggested clinal

variation in morphological traits between inland and coastal populations of *P. elongatus* (Bury 1973, 1999). Morphological analysis of both forms in the region demonstrated variation in vertebral counts between and within each form, consistent with prior findings (Bury 1999). Studies of variation in morphological traits (Brodie 1971; Bury 1973, 1999) reported a reduction of modal number of vertebrae (and, in turn, number of costal grooves) moving from coastal to inland *P. elongatus* (n = 19) and then to *P. stormi* (n = 18).

The most recent analysis of morphological traits (Mead *et al.* 2005) demonstrated variation and overlap between and within each of the three forms (*P. elongatus*, *P. stormi*, and *P. asupak*). However, they demonstrated a general trend of increased robustness with reduced number of costal folds and longer forelimbs of the inland forms compared to those closer to the coast. They also noted some subtle sexual dimorphism within each group.

Phylogenetics

The phylogenetic relationships among forms of this complex have been relatively well studied, especially in comparison to other western *Plethodons*. One of the driving forces to understand species' relationships among the complex is the protected status of these salamanders under federal or state species-management programs, including: Federal Survey and Manage list (USDA and USDI 1994), proposed listing as federal threatened and endangered species (Greenwald 2004), and the California State threatened species list (*P. stormi*) and Species of Special Concern List (*P. elongatus*). The designation or degree of protected status may rely, in part, upon how the forms are broken into discrete species units.

The first phylogenetic analysis to compare these salamanders utilized gene electrophoresis of more conservative gene-coding regions (Highton and Larson 1979). This original phylogenetic comparison of *P. stormi* and *P. elongatus* produced a Nei's genetic distance of $D = 0.33$, where D increases with decreasing relatedness. Further, Nei's normalized identity (I) of genes (decreases with decreasing relatedness) confirmed only two pairs of western *Plethodons* to be closely related, *P. elongatus* and *P. stormi* ($I = 0.72$), and *P. vandykei* and *P. idahoensis* ($I = 0.71$) which had a $D = 0.35$. The values observed for the Vandykei Complex infer slightly greater genetic divergence than those of the *P. elongatus* species Complex which seems intuitive with the disjunct distribution and large geographic distance between forms in the *P. vandykei* Complex (gap extending from the Washington Cascades to Idaho).

By the late 1990s, mitochondrial DNA (mtDNA) sequence analysis had become the most widely utilized technique for evaluating population designations. The first mtDNA phylogenetic analysis to assess the relationship of these closely related forms supported a sister species designation between *P. stormi* and *P. elongatus* (Mahoney 2001). However, the scale of inference of this first study for interior populations

was somewhat small due to only one population of *P. stormi* being used in the analysis.

A more focused phylogenetic analysis of *P. stormi* sampled populations from the Applegate River drainage (along the Oregon and California state line) south to the Klamath River, California (Pfrender and Titus unpublished). This report found a lack of genetic diversity in *P. stormi* within the Applegate River drainage, likely due to a recent range expansion and genetic bottleneck as individuals dispersed into the lower reaches of the watershed. However, salamanders sampled further south over the Siskiyou Mountain crest displayed significant divergence. Overall for *P. stormi*, three strongly supported mtDNA clades were recognized (Pfrender and Titus unpublished), and later published (Mead *et al.* 2005): (1) the Applegate drainage samples (North clade); (2) the adjacent populations on the southside of the Siskiyou crest, which formed a monophyletic group with the Applegate populations (South clade); and (3) a more deeply divergent clade from south of the Klamath River and east of Grider Creek, California.

A parallel study of mtDNA diversity across the range of *P. elongatus* (Mahoney 2004) sampled the lower two-thirds of the *P. elongatus* range (*i.e.*, primarily in California), as well as across the range of *P. stormi*. Mahoney (2004) identified three distinct clades within her samples of *P. elongatus* and confirmed the two clades of *P. stormi* on either side of the Siskiyou Mountains reported by Pfrender and Titus (unpublished). Additionally, one sample from south of the Klamath River and east of Grider Creek Ridge formed its own discrete clade in analyses, further supporting the findings of Pfrender and Titus (unpublished). Inferences were made as to the origin of phylogenetic patterns observed in *P. stormi* and the relationship it has with its sister taxa, *P. elongatus*. It was deduced that glaciation and changes in climate in the Klamath-Siskiyou Ecoregion seem to be the most plausible explanation of the complex patterns and species distribution seen in this group of salamanders.

A fourth, more extensive study utilized both mtDNA and morphological analyses to assess, with greater sampling, the form found south of the Klamath River, and led to designation of the third discrete form of the complex, *P. asupak* (Mead *et al.* 2005). The study added additional support for the two clades within the range of *P. stormi* (North and South), and demonstrated that *P. asupak* was a more basal lineage than the group formed by *P. elongatus* and *P. stormi*.

Time frames of divergence can be estimated from results of MtDNA analyses. If one were to adopt the conservative time frame (slow mtDNA clock) of speciation for poikilotherms set forth by Avise *et al.* (1998) with approximately 0.5% sequence divergence per million years, there is a long history of separation in the Elongatus Complex that precedes the most recent glacial periods of the region. An average of 2.22% sequence divergence between the two clades of *P. stormi* (North and South) translates to over 4 million years of separation (Mead *et al.* 2005). Values of sequence divergence between *P. elongatus* and both clades (North and South) of *P. stormi* are 8.62% and 7.59%, respectively, which relate to 17

and 15 million years of separation. The amount of sequence divergence between *P. asupak* and the North clade of *P. stormi*, the South clade of *P. stormi*, and *P. elongatus* are 11.5%, 11.68%, and 12.85% respectively, and these correspond to 23–26 million years of separation. These values are estimates, but the time elapsed since divergence for each form in the Elongatus Complex precedes the region's Pleistocene and Holocene glaciations as well as the warming trends associated with each.

Limited levels of gene flow are reported from these analyses, with only 2 of 63 individuals of *P. stormi* tested from the contact zones (one from West Grider and the other from Horse Creek) demonstrating truly mixed ancestry (*i.e.*, demonstrating more 'inheritance' of its genome from the opposite form). These findings support the reproductive isolation of *P. stormi* and *P. elongatus*, a classical criterion used to designate species. Past confusion that stemmed from morphological similarities near Happy Camp, California, have been clarified with substantial molecular evidence delineating *P. stormi* exclusively north of the Klamath River and west of Seiad Valley to Happy Camp, California. The one population (Seattle Creek population) that previously had been defined as *P. elongatus* or intergrades (Brodie 1970; Bury 1973, 1999) has produced only *P. stormi* mtDNA haplotypes (DeGross 2004, Mahoney 2004, Mead *et al.* 2005, Mead 2006). Still, relatively few samples have been analyzed for genetic identification in this area. Besides no *P. elongatus* mtDNA haplotypes in samples from this locality, only one specimen out of nine analyzed from the microsatellite analysis demonstrated a limited admixed (<13% *P. elongatus*; > 87% *P. stormi*) genome (DeGross 2004, DeGross *et al.* unpublished).

The evidence of sympatry (occurring in same area) and a narrow zone of contact between *P. elongatus* and *P. stormi* in the Indian Creek drainage of western Siskiyou County, California, further confirms the distinct taxonomy between these two forms. The current region of contact between *P. stormi* and *P. asupak* north of the Klamath River and south of Horse Creek appears complicated. Further sampling and nuclear analyses are needed to define where each species occurs. Comparatively, there are deep levels of divergence between these three species of salamanders and are most likely reflective of the extremely complex geologic and climatic history of the Klamath-Siskiyou Ecoregion.

Habitat

To date, only one peer-reviewed scientific study has rigorously analyzed the habitat correlates for these salamander species (Welsh *et al.* 2007). Anecdotal and observational reports of habitat use are relatively well documented, especially for *Plethodon stormi* (Nussbaum 1974, Nussbaum *et al.* 1983, Clayton and Nauman 2005, Nauman 2005, Bull *et al.* 2006, Farber 2007). Many *P. asupak* sites on private lands (Farber 2007) as well as several on managed public lands (Bull *et al.* 2006) had past timber harvesting and other ground

disturbances. However, these studies are all retrospective. The habitat correlates study of Welsh *et al.* (2007) included study sites that would later be identified through molecular techniques as inhabited by *P. asupak*.

Overall, available moisture and rocky talus appear to be the two most important habitat conditions for these two species. The reduced annual precipitation and climatic extremes of the inland portion of the Klamath-Siskiyou Ecoregion, in comparison to more coastal environments, likely has a major influence on habitats that support populations of *P. stormi* or *P. asupak*. Average daily temperatures of the Klamath Mountain Province in the summer, when solar insolation is the greatest in the mid-latitudes of the northern hemisphere, are about 32° C (90° F). The winter average daily temperature is 0° C (32° F) and winter is the season receiving the greatest percentage of the region's annual precipitation 50–190 cm (20–75 in). This seasonal precipitation generally falls as rain below 1219 m (4000 ft) and snow above (USDA Forest Service 1994b). Besides influencing suitable habitat, these environmental variables will drive seasonal surface activity of salamanders such as mate selection and reproduction, and therefore genetic exchange.

The first identification of *P. stormi* from the upper reaches of the Applegate River Valley in Jackson County, Oregon, was from one or two talus slopes (Storm 1966). This species was reported as being associated with talus slopes for several decades (Highton and Brame 1965, Nussbaum 1974, Herrington 1988, Blaustein *et al.* 1995). The first in-depth distributional analysis (Nussbaum 1974) of the species described differences in habitat correlates for this species as well as interior populations of the closely related *P. elongatus* compared to coastal habitats of *P. elongatus*. He reported the interior populations at elevations of 488–1078 m (1340–3540 ft), with the densest populations occupying talus deposits or fissured rock outcrops on heavily-wooded, north-facing slopes. Early on, many of the populations of *P. stormi* occurred in talus slopes along road cuts, which exposed the underlying rock substrate and created accessible habitat for biologists to search for salamanders. Talus environments provide interstitial spaces where organisms, like *Plethodon* salamanders, can move with relative ease to find cool, moist subterranean retreats. Additionally, the immediate forest habitat observed at occupied sites was conifer-hardwood, mixed canopy (Highton and Brame 1965). Surface activity in the more arid interior was restricted to the wet season of late fall through spring, and only on very wet days could individuals be found in or under downed wood and leaf litter (Nussbaum *et al.* 1983).

The most recent reports of habitat conditions for both *P. stormi* and *P. asupak* have been addressed by: (1) observational studies recording conditions found at previously occupied sites (Bull *et al.* 2006, Farber 2007); (2) a Federal report which used a stratified random design to select survey sites (Nauman and Olson 2004b); and (3) a scientific publication (Welsh *et al.* 2007). Additionally, three other documents will soon be available to better understand the requirements and habitat conditions of these species (Nauman and Olson

in press, Reilly *et al.* in press, Suzuki and Olson in press). Of these, the study by Welsh *et al.* (2007) has the greatest spatial inference because they used a rigorous experimental design that randomly selected sites across the range of both species. In contrast, the least inference is provided by Farber (2007), which was a retrospective study of 36 known populations. Still, findings of each study are informative about the conditions at sites occupied by salamanders.

Welsh *et al.* (2007; published version of the interim report of Ollivier *et al.* 2001) is the most statistically rigorous evaluation of habitat correlates as well as additional habitat variables for parent geology and GIS-based climate models. Welsh *et al.* (2007) had site selection criteria at three different spatial scales. The coarsest scale was “biogeographical” and assessed possible sites across the entire range of the species based upon underlying geology and forest type. The second was “possible habitats” and was based upon the USGS Township and Range system. Within each township, 4 of the 36 sections (each 1-mile²) were randomly selected. Further, they had to have the requirement of available rock substrate. The final scale was the seral stage of forest types within each section, and they selected four to represent each classification in each of the selected townships: pre-canopy (0-30 yrs), young (31-99 yrs), mature (100-199 yrs), and old-growth (200+ yrs).

They sampled 239 sites within the range of both *P. stormi* and *P. asupak* from March 1995 to June 1998 and recorded associated habitat correlates from 120 continuous and 8 categorical independent habitat variables. These variables were broken into three spatial scales: landscape; macrohabitat; and, microhabitat. Further, data from the north and south slopes of the Siskiyou crest were assayed for inherent differences. They sampled 163 sites from the northern slope of the crest and species range of *P. stormi*, and 76 from the south slope or southern portion of the range of *P. stormi* and the northern portion of *P. asupak*. Of the 163 sites surveyed on the northern slope, only 46 (28%) produced *P. stormi*. Of the 76 south slope sites, only 15 (20%) produced *P. stormi* or *P. asupak*. They found climate variables (annual precipitation, solar incidence, and soil temperature) were present in the most informative multi-scaled models. Precipitation patterns observed across the landscape and across temporal scales were more consistent on the northern slope in the Applegate Valley, Oregon, than on the southern slope in California. Models for habitat on the south slope had consistently higher predictive capabilities than the northern slope models. Across all spatial scales, the models that either represented or acted as surrogates for climatic conditions were the best predictors of salamander presence. These models indicated an emphasis for forest stands that have the ability to sustain moist microclimates, and therefore meet the physiological and biological requirements of these salamanders. Thus, those requirements are different for the northern and southern slopes, and the availability of habitats meeting those requirements are not equally distributed across both landscapes. Use of these data to prioritize unsurveyed habitats has great utility.

Recently, two landscape-scale habitat models for *P. stormi* in the Applegate watershed were developed from mapped habitat variables from an earlier study (Ollivier *et al.* 2001). The model developed by Reilly *et al.* (in press) included rocky soil types with adequate interstitial spaces, forest canopy closures above 70%, and conifer forest types with average tree size > 43 cm (17 in) Diameter Breast Height. An additional GIS-based variable “illumination index” was used, which incorporated seasonal hillside shading with aspect. Using a different modeling approach, Suzuki and Olson (in press) used the same variables as Reilly *et al.* (in press) and added distribution of three tree species: Douglas-fir, Oregon white oak, and white fir. They found the occurrence of salamanders was associated ($p < 0.05$) positively with rocky soils and negatively with Oregon white oak and white fir; 84% of occupied sites were correctly classified by their model. Additionally, this model incorporated variables for risk to and persistence of salamanders (see section “Combined Risk Model”).

Another study (Nauman and Olson in press) randomly sampled sites on federal lands south of the Siskiyou crest for *P. stormi* and *P. asupak*. Their objective was to investigate patterns of occupancy with federal land allocation termed matrix or reserve. They found *Plethodons* at 26% of their sampled points, with higher detection rates in lower elevation lands where matrix lands dominated and higher precipitation occurred.

Two reports (Farber *et al.* 2001, Farber 2007) focus on salamanders and habitat at sites with previous disturbance and, in several cases, multiple disturbances: 94% of the 36 sites from the 2007 report had one or more disturbances recorded on site. Of the 36 sites with salamanders, 31 (86%) of the sites had northerly facing aspects, and canopy closure ranged from 0% to 100%. A mean of 68% canopy closure was reported at the original 18 occupied sites (Farber *et al.* 2001), but no mean is provided for canopy closure at the 36 sites (Farber 2007).

Finally, Bull *et al.* (2006) reported field surveys conducted on 92 known sites for the two salamander species (*P. stormi*, *P. asupak*) to document habitat elements, substrate, and disturbance. The majority of the sites (87%) were on private lands stewarded by Timber Products Company and Fruit Grower Supply Company, and the remaining sites were on federal lands. Of their 92 sites, their subsequent habitat data analyses were reported for the 68 sites where *P. stormi* were detected. Conifers dominated the basal area, but hardwoods were present and provided cover at 37 (54%) of the sites with detections. Percent of rock > 2.54 cm (1 in) covering > 50% of the plot was found at 35 sites (51.5%). Evidence of timber harvest (stumps) was observed at 31 sites (46%) and reported moderate (10-50%) and high (>50%) basal removal at 54% and 26% of these sites, respectively (Bull *et al.* 2006). Further, at 30 (44%) sites with animal detections there was at least 50% soil disturbance.

The historically accepted view of these animals being tied to talus slopes in forested areas has been somewhat substantiated in several studies, but it remains unclear as to the obligatory reliance of salamanders on these habitats. The amount of

over-story canopy and its shade on the forest floor seem intuitive with the requirement of moisture and moisture retention by salamanders. However, there are reports that these organisms can exist at sites lacking over-story canopy and, in lieu of past disturbances, both manmade and naturally occurring. Collectively, a better understanding has developed that these species require moist habitat and adequate access to subterranean refugia. Climate, topography, and canopy therefore can act as surrogates for and affect microhabitat moisture. These characters in combination with talus and fissured substrate seem to provide optimal habitat for these species of salamanders.

In summary, several studies have found these salamanders to be associated with diverse habitat variables, including those indicative of older forest conditions, wet climatic conditions, rocky substrates, tree species (*e.g.*, conifers or mixed forest), and topographic conditions (*e.g.*, slopes). The relative importance of these various features appears complex and may not be easily resolved in a single set of factors to classify all sites across their ranges. If key site conditions favoring these salamanders include rocky substrates and cool, moist conditions, then salamanders may live at some sites with less influence from forest canopy conditions. For example, north-facing aspects, darker-illumination indices, and precipitation patterns are three additional factors that can play dominant roles in microsite conditions for salamanders (see discussions in Nauman and Olson 2004b, Nauman 2005, Welsh *et al.* 2007, Reilly *et al.* in press, Suzuki and Olson in press).

Impacts to Habitat

The ranges of both *P. stormi* and *P. asupak* fall in the interior of the Klamath-Siskiyou Ecoregion where rocky substrates abound and cool, moist environmental conditions are found in the late fall and early spring (Clayton and Nauman 2005, Mead *et al.* 2005, Welsh *et al.* 2007). Several disturbances may have effects on the habitats of both *P. stormi* and *P. asupak*. In particular, the region has a long history of mining (Orr and Orr 2000), timber harvesting (Jules *et al.* 1999), recreation, and road building that provides access for these activities to remote areas. Additionally, natural phenomena like wildfires (Frost and Sweeney 2000, Major 2005, Bury 2005) alter habitat conditions and play a role in dictating biotic assemblages throughout the region. Here, we synthesize the limited body of literature on the effects various disturbances have on these species and their habitats.

Timber Harvest and Silvicultural Practices

The most widespread ground-disturbing activity in the region is timber harvest (Bury and Pearl 1999). Due to the loss of overhead canopy from removal of trees and consequent

increased exposure of occupied sites to altered microclimate regimes, timber harvesting has been implicated as the single greatest threat to these species (Nussbaum 1974, Blaustein *et al.* 1995, Petranka 1998, Bury and Welsh 2005). No study to date has experimentally addressed the effects of any timber harvest practices on *P. stormi* and *P. asupak*. However, field research on the related *P. elongatus* suggests more salamanders in older than younger forests (Welsh 1990, Welsh and Lind 1992). Our understanding of the relationships of these animals to timber harvest now relies on retrospective studies of the species' habitat relationships and occupancy of sites with various disturbance histories.

There are unpublished reports (Farber *et al.* 2001, Bull *et al.* 2006, Farber 2007) that document both *P. stormi* and *P. asupak* at areas with little natural canopy cover, or pre-canopy sites where past disturbance has removed the majority of or all of the overhead forest structure. These observational studies primarily represent habitats found on private and matrix lands in the Klamath River drainages. These habitats may not be representative of or are the most optimal for the species, and inferences should not be made about habitat use across the range of either salamander. There is unpublished evidence that *P. stormi* living in early seral stages of harvested forests have reduced body condition and skewed age distributions with higher proportions of animals as juveniles and sub-adults (Welsh *et al.* pers. comm., unpubl. data). They also report this to be a population structure to be indicative of sink (declining) populations.

Occupancy (*e.g.*, presence of few animals) at sites and the proportion of all life stages may be providing only a coarse estimator of influence of timber harvest effects on these animals. Effects of these disturbances may not be lethal to all members of a population, but may be seen in terms of their densities, survivorship, reproduction, or altered demographics. While demographic data for some retrospective case study sites are becoming known, they do not address the effect of the disturbance on the animals at the site. Related to this, detectability of salamanders can change with demography and survey method used across studies. Among available studies (cited above), survey methods were not similar. In particular, Ollivier *et al.* (2001) surveyed small plots, 7 x 7 m. It is possible that their effort most often resulted in detections at sites only with abundant salamander populations, and hence, their findings may reflect more optimal habitat associations. It is likely that *P. stormi* and *P. asupak* are relatively rare salamanders with patchy distributions across the landscape and therefore, relatively low detection rates should be expected. For example, Welsh *et al.* (pers. comm., unpublished data) compared *P. stormi* and *P. elongatus* and found the latter to be 3.5 times more readily detected across all forest age classes than was *P. stormi*.

There are currently only two anecdotal studies that monitor sites for *P. stormi* in areas with timber harvest. Both were on north-facing slopes of Siskiyou Mountain ridges. Both produced very different observations of salamanders post-harvest. One was a paired-plot survey, conducted by the U.S.

Forest Service (D. Clayton pers. comm.) where they surveyed for salamanders in spring 1992 immediately following a forest clear cut in fall 1991. They found 40 salamanders in the first spring post-harvest (10 salamanders per person hour), one juvenile the following year, and then no animals for another eight years. In spring 2001, a juvenile was again found after a search by two field crews (D. Degross, personal experience). In the immediate vicinity, another timber harvest operation used helicopter yarding instead of cable yarding (employed at the previous harvest site) and activities were monitored by Fruit Growers Supply Company (Taylor 2007). As a condition of the California Endangered Species Act Biological Opinion, the project area was surveyed for *P. stormi*. They surveyed salamanders on 39 plots (35 harvested and 4 controls) prior to harvest, one year post-harvest, and again 10 years post-harvest. Counts of salamanders did not change significantly over each of three observation periods (Taylor 2007). While persistence of salamanders is documented for this study site, no detection probabilities for each plot were quantified, making conclusions about there being stable salamander populations uncertain.

A variety of published studies are available that examine various management impacts on the closely related *P. elongatus*. However, the range of *P. elongatus* covers a greater geographical area, diversity of habitats, and closer proximity to the Pacific Ocean than either *P. asupak* or *P. stormi*. Therefore, before making any inferences to *P. stormi* and *P. asupak*, one must consider that the effects of land-use practices may not be strongly correlated unless the study is from the more interior portion of the range of *P. elongatus*. With existing information on plethodontid salamander physiology, it is reasonable to believe that anthropogenic alterations to forest habitats in the drier interior of the Klamath-Siskiyou region would have more of a negative impact on *P. stormi* and *P. asupak* than it would have on *P. elongatus* closer to the Pacific Ocean that has milder conditions overall.

Evidence of *P. elongatus* across forest conditions and forest edges has been reported by several authors, but with variable results that are influenced by proximity of sites to the coast (Diller and Wallace 1994, Welsh and Lind 1995, Biek *et al.* 2002, Karraker and Welsh 2006). However, results from at least one of these studies indicated there were effects to individual's body conditions (Karraker and Welsh 2006). Furthermore, Welsh and Lind (1995) demonstrated a significant relationship with high forest canopy (>80%) and numbers of *Plethodons*. Welsh and Lind (1995) show a habitat model where *P. elongatus* were highly correlated with conditions prevalent in old-growth forests that have the pre-requisite microclimates required by these salamanders. Other inferences suggest that site-specific microclimates would have the greatest influence on occupancy of salamanders, particularly in the interior of the species' range (Diller and Wallace 1994, Welsh and Lind 1995, Biek *et al.* 2002).

In the Pacific Northwest, examination of microclimate modification of Douglas-fir forests after silvicultural practices suggests less optimal environmental conditions

for both species of salamanders (Chen *et al.* 1993, Chen *et al.* 1995, Rykken *et al.* 2007). The relevance of these studies stems from the region-wide representation of this forest type, and it is a dominant forest component in lower elevation habitat zones of the Klamath-Siskiyou Ecoregion (Staus 2002) where many private timber lands reside. The effects on microclimate conditions are variable depending on the characteristic and the distance from the edge into the forested habitat (Chen *et al.* 1995). Landscape-scale characters play a pivotal role on the impacts that loss of canopy or a silvicultural edge may have on forested habitats. Latitude, aspect, and local weather patterns are all considerations when assessing the impact of edges on microclimates (Chen *et al.* 1995).

Species of the genus *Plethodon* rely on a specific set of environmental conditions in which they can be surface active to acquire greater food resources and find potential mates (Feder 1983). In direct correlation with the surface activity of these terrestrial salamanders, microclimate variables are temporally and spatially variable (Chen *et al.* 1999). South-facing slopes that are inhabited by *P. stormi* and *P. asupak* may only provide a limited period per year of suitable moist and thermally equable conditions for these species to carry out biological functions. Multivariate factors should be evaluated on a site-specific basis. For example, Welsh and Lind (1992) reported extremely high densities of *P. elongatus* on a south-facing slope of old-growth Douglas-fir forest, but on an adjacent clear-cut that has been continuously sampled 20 years post-harvest (since 1987), no animals have been detected since 2002, and the few that were previously found were mostly juveniles. Detections in the old-growth stand continue to remain high and represent all age classes of salamanders (Welsh, unpublished data).

Fire

Fire regimes throughout the Klamath-Siskiyou Ecoregion are as variable as topography, species assemblages, and the climates present in the region. Wildfires in the region tend to burn in the late summer and early fall (Pilliod *et al.* 2003). This timeframe does not correspond with the surface activity of the terrestrial salamanders of the region, and therefore is assumed to not have direct impacts on salamander populations (Bury 2004). However, these events may have indirect effects on the salamanders. Large-scale wildfires and prescribed burning projects affect available wood resources and leaf litter for seasonal cover on the forest floor for salamanders. Further, removal of overhead canopy will decrease the ability of the forest to retain moisture until vegetation is re-established on site. Fire suppression practices of the past decades exacerbate the issue by allowing the accumulation of fuels on the forest floors (Bury *et al.* 2002, Major 2005). No study has been conducted to examine the effects of prescribed burning on these species, but the seasonal choice for these fuel management operations is the spring when there is remnant moisture still available in leaf litter and understory vegetation, helping con-

trol the rate and behavior of the burn. The springtime practice of broadcast burning and even pile burning could have a direct effect on the salamander species based upon seasonal use of cover objects on the surface by these salamanders. However, no evidence is currently available to support this hypothesis.

Mining and Other Ground Disturbing Practices

The terrane stratigraphy of the Klamath Siskiyou exposes abundant mineral resources (Orr and Orr 2000). Evidence of abandoned mines near sites with *P. stormi* and *P. asupak* may suggest that mining activities have little adverse effect on salamanders. However, much of the Klamath River drainage in the vicinity of Seiad Valley and Happy Camp, California has been hydraulically mined, as evidence of tailings that now make up the majority of the banks of the river (D. Degross, personal observation). Much like road building or road cuts, mining removes and undermines the integrity of salamander habitat and then exposes the remaining underlying rock and talus of an area, creating exposure of the remaining substrate to the surface and reducing the complexity of the habitat (Nussbaum 1974, Diller and Wallace 1994). Several known sites of both of these salamanders are adjacent to mine or quarry sites, and many sites across both ranges lie in road cuts, but this is most likely a remnant of surveyor bias.

Combined Risk Model

Recently, the USDA Forest Service, USDI Bureau of Land Management, and the USDI Fish and Wildlife Service signed a conservation strategy for the northern populations of *P. stormi*. This strategy incorporated a risk assessment (Suzuki and Olson in press) to provide for conservation of this species within the Applegate River drainage, Oregon. This model used a habitat suitability model (Reilly *et al.* in press) as well as incorporation of 4 factors quantifying risk and 2 factor quantifying species persistence. Occurrence of *P. stormi* was positively correlated with the distribution of rocky substrates and negatively associated with June solar illumination, Oregon white oak and white fir trees. This model assisted in the location of key conservation areas for the salamander, and it will aid managers to delineate suitable sites to maintain the species across the landscape.

Detection Probabilities/Occupancy

The majority of studies on *P. stormi* and *P. asupak* have utilized either time constrained and/or area constrained survey techniques (Farber *et al.* 2001, Bull *et al.* 2006, Welsh *et al.* 2007, Nauman and Olson in press). These methods produce relative abundance estimates calculated from catch per unit effort (*i.e.*, salamanders/ person hours or area). From these estimates, researchers calculate the proportion of an area occu-

pied by the species based upon the proportion of sites with observations (Bailey *et al.* 2004). However, when comparing these results to those of other studies, or even the same study over different years, an assumption is made that the probability of detection is the same temporally and spatially. Understanding detection probabilities for each site, method, and year is needed to make more valid comparisons.

Importantly, detection probability (*i.e.*, animals are present) has been shown to vary with local habitat conditions (Bailey *et al.* 2004, Dodd and Dorazio 2004) to the extent that it can lead to flawed conclusions. It should be calculated in field studies of western Plethodontid salamanders (N. Chelgren *et al.* unpublished data). Further, within the range of *P. stormi* and *P. asupak*, the time window for optimal site conditions allowing for salamander surface activity and, therefore detection, is small and highly variable across their respective ranges. Aspect, forest type and seral stage, amount of available cover, and seasonal precipitation all influence site microhabitat conditions and the window of opportunity for detecting these terrestrial salamanders. As these characters change across the landscape, so do respective detection probabilities for sites. It is imperative from this point forth to account for differences in detection probabilities between areas when making comparisons of salamander occupancy and abundance.

Compounding these probabilities is the patchy distribution of these species across the landscape and their variable densities at sites where they are found. The range-wide habitat correlate assessments for these species (Ollivier *et al.* 2001, Welsh *et al.* 2007) are the only studies that randomly selected sites, and therefore can infer range wide patterns. These studies incorporated single-site visits using area-constrained searches to produce relative abundance estimates, and therefore were not able to produce detection probabilities. Mounting evidence demonstrates that single site visits grossly underestimate relative abundance values (Bailey *et al.* 2004). Hence, earlier findings (*e.g.*, Ollivier *et al.* 2001, Welsh *et al.* 2007) are likely to be conservative perspectives of habitat conditions, perhaps where the more abundant populations of salamanders occur. Repeat sampling visits within a season alleviate the underestimates, but may be a challenge for both of these species due to their rare and patchy distribution across the landscape as well as the small window of optimal seasonal conditions for detection.

Conclusions

Systematics

The utilization of combined phylogenetic and morphometric analyses has produced substantial evidence for differentiating species in the *Plethodon elongatus* group. The limited degree of contact and consistent phylogenetic breaks observed from multiple analyses supports designation of at least three

species. Still, the evolutionary processes acting upon these salamanders remain poorly understood and, therefore, more rigorous biogeographic analyses should help our understanding of these processes and may alter our interpretations. The conservation status of *P. stormi* and recent discovery of *P. asupak* have been instrumental in increasing the sampling and analyses across the range of both, but gaps in knowledge persist. Assessment of gene flow between *P. asupak* and the two other species, now that populations of each have been found adjacent to one another, seems integral in better understanding the evolutionary history and trajectory of the *Plethodon elongatus* Complex.

Habitat

Rocky talus substrates with interstitial space appear to be an integral habitat characteristic for the presence of *P. stormi* and *P. asupak* in the interior of the Klamath Siskiyou Ecoregion. The ability for these salamanders to move vertically from the surface to subterranean refugia to avoid desiccation appears to be provided by talus and fissured rock environments. The seasonally limited conditions for these organisms to be surface active can be enhanced by microhabitat, macrohabitat, and landscape conditions that act as surrogates or extend the period for moist climate. The development of models to predict occupancy of salamanders (Welsh *et al.* 2007, Reilly *et al.* in press, Suzuki and Olson in press) has greatly improved the ability to assess potential habitat and conservation strategies for *P. stormi*. The major variables of the models were based upon conditions found in late-seral forests and habitats which do not receive a lot of solar insolation throughout the year. These conditions invariably include aspect, solar incidence, closed canopies, larger DBH categories, and vegetative species (indicative of mesic conditions). Although in-depth physiological studies have yet to be conducted for *P. stormi* and *P. asupak*, the requirements of the species in the genus *Plethodon* are fairly restrictive, and rely primarily on available moisture. Habitat components of sites where these species occur may be variable, but the ability of a site to sustain population appears correlated to more mesic conditions.

The role of specific forest types and seral stages as elements of salamander habitat may vary with local site conditions. The only analysis of habitat associations with presence-absence data across both species ranges (primarily *P. stormi*) alluded to the strong role that landscape-level attributes, such as precipitation patterns and aspect, play in predicting habitat occupancy (Welsh *et al.* 2007). However, it is the microclimate conditions at occupied sites that appear to allow these species to spend more time on the surface seasonally, and likely persist as a thriving population. Some evidence suggests that these species are able to occupy a variety of habitats, forest types, and can withstand habitat disturbance (Farber *et al.* 2001, Bull *et al.* 2006, Farber 2007). However, these unpublished studies did not produce any gauge for changes in individual body con-

dition, site specific population structure, or provide any baseline population data to compare their results. In many of these sites the disturbance footprint has been from tree harvesting, and no experimental study has rigorously inspected cause and effect responses of the practices to *P. stormi* or *P. asupak* across their range. The amount of land allocated within the range of each species for timber practices is 24% (14% federal matrix lands and 10% private lands), but these allocations currently provide 36% of all known sites for these species (Bull *et al.* 2006). In general, these lands present better conditions for persistence of salamanders because they reside at lower elevations that receive more wet precipitation than higher elevation habitats (Nauman and Olson 2004b).

The combination of variable habitats and greater occupancy of salamanders observed on these historically disturbed low-elevation habitats in private and matrix land allocations warrants further inspection south of the Siskiyou crest (in the ranges of *P. asupak* and southern populations of *P. stormi*). Risk analysis much like that of Suzuki and Olson (in press), for northern populations of *P. stormi*, would be useful to designate areas for conservation purposes. Further, we need more information to assess demographics and critically evaluate persistence of populations at sites and across the landscape. It will be a challenge to accomplish these goals because these species have secretive habits, and fossorial existence for much of the year. This leads to our current inability to quantify robust population estimates, and estimation of genetically effective population (N_e) size. The majority of known sites for these species in California, are on private lands and in Northwest Forest Plan non-withdrawn federal lands (*i.e.*, subject to timber harvest). If the goal is to conserve these species of salamanders, then identifying and protecting habitats known to support healthy populations of these animals across the region is needed.

Modeling Salamander Populations and Habitat

Development of accepted conservation of these species and their habitat management is difficult due to these salamanders' secretive habits, our inability to rigorously quantify population size, and their patchy distribution across the landscape. Models have recently been developed to aid in both these arduous tasks. The habitat suitability model by Reilly *et al.* (in press), and the combined risk model of Suzuki and Olson (in press) have provided useful tools for focusing conservation efforts of *P. stormi* and its potential habitat in the Applegate River drainage, Oregon. A similar model would greatly improve efforts for southern populations of *P. stormi* and *P. asupak*. Additionally, detection probabilities and occupancy models have been developed for terrestrial salamanders to assess spatial and temporal variation in sampled populations. These calculations will be critical in assessing land management practices effects on populations, due to site complexity, population differences across the landscape, seasonal climatic differences, and many other variables researchers are

unable to control when rigorously evaluating population level changes and effects.

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