

EVIDENCE OF A NEW NICHE FOR A NORTH AMERICAN SALAMANDER: *ANEIDES VAGRANS* RESIDING IN THE CANOPY OF OLD-GROWTH REDWOOD FOREST

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Abstract.—We investigated habitat use and movements of the wandering salamander, *Aneides vagrans*, in an old-growth forest canopy. We conducted a mark-recapture study of salamanders in the crowns of five large redwoods (*Sequoia sempervirens*) in Prairie Creek Redwoods State Park, California. This represented a first attempt to document the residency and behavior of *A. vagrans* in a canopy environment. We placed litter bags on 65 fern (*Polypodium scolieri*) mats, covering 10% of their total surface area in each tree. Also, we set cover boards on one fern mat in each of two trees. We checked cover objects 2–4 times per month during fall and winter seasons. We marked 40 individuals with elastomer tags and recaptured 13. Only one recaptured salamander moved (vertically 7 m) from its original point of capture. We compared habitats associated with salamander captures using correlation analysis and stepwise regression. At the tree-level, the best predictor of salamander abundance was water storage by fern mats. At the fern mat-level, the presence of cover boards accounted for 85% of the variability observed in captures. Population estimates indicated that individual trees had up to 29 salamanders. Large fern mats have high water-holding capacities, which likely enable year-round occupation of the canopy by *A. vagrans*. Other observations indicate that *A. vagrans* and its close relative *A. ferreus* also occupy additional habitats in forest canopies, especially moist cavities inside decaying wood.

Key Words.—*Aneides vagrans*, *A. ferreus*, *Sequoia sempervirens*, forest canopy, arboreal habitat use, salamander

INTRODUCTION

The temperate salamanders of North America are primarily terrestrial and fossorial, except some species in the family Plethodontidae that have been reported to occupy moist vertical rock faces (genus *Desmognathus*) and several species (genus *Aneides*) that climb into trees at least seasonally (Petranka 1998; Waldron and Humphries 2005). However, there has been no conclusive evidence of a temperate zone salamander species completing its entire life cycle in an arboreal environment. This report documents the year-round residency of the wandering salamander, *Aneides vagrans*, in the canopy of old-growth redwood forest in northwestern California.

Recent genetic evidence (Jackman 1998) indicated that the clouded salamander (*Aneides ferreus*) consisted of two separate species. A new species, the wandering salamander (*A. vagrans*), was proposed for populations south of the south fork of the Smith River in northwestern California. This species occurs primarily in northern California with disjunct populations that were introduced to Vancouver Island, British Columbia where they are abundant in terrestrial habitats (Jackman 1998; Davis 2002b). The name *A. ferreus* was retained for populations that occur primarily in western Oregon.

Aneides vagrans has a prehensile tail that it uses to assist in climbing vertical surfaces (Petranka 1998; Spickler and Sillett, pers. obs.) and long limbs with slender digits bearing sub-terminal toe pads (Petranka 1998). This species has previously been described as a primarily terrestrial salamander that is also found on logs, in trees, and on shrubs. It occupies moist terrestrial habitats, especially under exfoliating bark and in cracks and cavities of decomposing logs, stumps, snags, and talus (Davis 2002a; Stebbins 2003). Similarly, *A. ferreus* has climbing ability with individuals found as high as 6.5 m in trees

and, in the laboratory, will leap from the hand to nearby objects, clinging with great tenacity, even to vertical surfaces (Nussbaum et al. 1983). The arboreal salamander (*A. lugubris*) has been found in trees over 18 m above ground, and may deposit eggs in decay holes in live oak trees up to 9 m above ground (Staub and Wake 2005).

The first evidence that *A. vagrans* might reside in the temperate forest canopies of the redwood region was the discovery of a clutch of eggs (later hatched in the lab) inside a leatherleaf fern (*Polypodium scolieri* Hook. & Grev.) mat that had been dislodged from high in the crown of a redwood being felled for lumber (Welsh and Wilson 1995). Soon after the first *in situ* scientific investigations of old-growth redwood forest canopies began in 1996, we observed the arboreal presence of *A. vagrans* (Sillett 1999). All observations were made of individuals and pairs occupying tunnels and cavities in large epiphytic fern mats in trees, except one observation (SCS) of a mummified adult found in a shallow trunk cavity located 88 m above the ground in a large redwood tree.

Our objective was to study *A. vagrans* inhabiting an old-growth forest canopy in Prairie Creek Redwoods State Park, Humboldt County, California, including several trees whose crowns have been explored by two of us (JCS & SCS) since 1996. In particular, we investigated habitat use, activity patterns, and movements in the crowns of five large redwood trees to glean new information on the ecology of *A. vagrans* in trees.

The Redwood Forest Canopy Environment.—Old-growth forests dominated by *Sequoia sempervirens* (D. Don) Endl. (hereafter ‘redwood’) are home to some of the world’s tallest and largest trees.

Individuals can exceed 112 m in height, 7 m in diameter, and have wood volumes over 1,000 m³ (Sawyer et al. 2000). Old-growth redwood forests contain some of the oldest and most structurally complex trees on the planet. These trees often live over 1000 years and develop highly individualized crowns shaped by natural forces

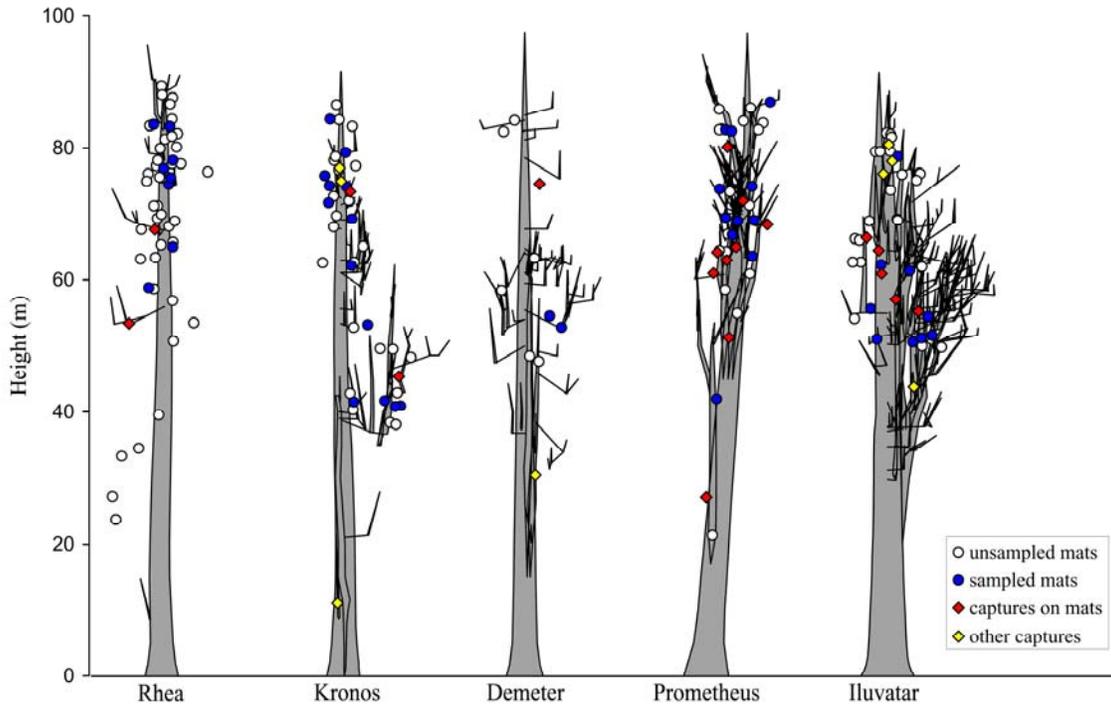


FIGURE 1. A two-dimensional display (view angle = 120°) of the three-dimensional crown structure of five redwood trees surveyed in this study. Main trunks and reiterated trunks are shaded gray. Limbs are indicated by thin, black lines. No branches are shown. Locations of *Polypodium scolieri* fern mats and *Aneides vagrans* captures are shown according to the legend. Note that “floating” symbols indicate locations on branches. “Sampled mats” are fern mats that were selected for placement of cover objects.

(Van Pelt 2001). Disturbances (e.g., windfall, crown fires) that increase light availability within tree crowns stimulate new growth from damaged trunks and branches. In redwood, this new growth can be in the form of either horizontal branches or vertical trunks (hereafter reiterated trunks), each with its own set of branches (Sillett 1999). Reiterated trunks can originate from other trunks or from branches. When a trunk arises from a branch, the branch thickens in response to the added weight and hydraulic demand of the trunk, creating a “limb.” Trunks, limbs, and branches also become fused with each other during crown development (Sillett and Van Pelt 2001). The highly individualized crowns of complex redwoods offer a myriad of substrates and habitats for epiphytic plants and other arboreal organisms (Williams 2006).

Crown-level complexity in redwoods promotes accumulation of organic material, including epiphytic plants, on tree surfaces (Sillett and Bailey 2003). Croches between the trunks, the upper surfaces of limbs and branches, and the tops of snapped trunks provide platforms for debris accumulation. Vertical and horizontal sections of dead wood also provide substrates for fungal decomposition. Over time, this debris develops into soil as organic materials decompose into humus, which provides a rooting medium for vascular plants. The most abundant vascular epiphyte in redwood rain forests is the evergreen fern, *P. scolieri* (Sillett 1999), with individual trees supporting up to 742 kg dry mass of these ferns and their associated soils (hereafter ‘fern mats,’ Sillett and Bailey 2003). As fern mats grow in size and number, their effects on within-crown microclimates become pronounced. Like a sponge, large fern mats store water within the crown, increasing the humidity (Ambrose 2004) and providing refuge for desiccation-sensitive species, including mollusks, earthworms, and a wide variety of

arthropods (Sillett 1999; Jones 2005). Large fern mats also tend to be internally complex, with tunnels and cavities between the rhizomes and dense roots as well as interstitial space around embedded sticks (Stephen Sillett, pers. obs.).

MATERIALS AND METHODS

Study Area.—We studied *A. vagrans* in five redwood trees located in Prairie Creek Redwoods State Park (PCRSP), Humboldt County, California within an old-growth redwood forest. Mean annual rainfall in the study area was 1.67 m, with summer temperatures ranging from 7°–31° C and winter temperatures ranging from 1°–23° C during 2002–2004. Trees were selected from a 1-ha permanent reference stand that is 50 m elevation and 7 km from the Pacific Ocean. Within the reference stand, redwood accounts for 95.8% of the trunk basal area with the remainder consisting of Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco), hemlock (*Tsuga heterophylla* [Raf.] Sarg.), and a few hardwoods.

We selected study trees (Fig. 1) on the basis of size, structural complexity, and epiphyte abundance. Trees 1 (‘Kronos’) and 2 (‘Rhea’) have interdigitating sections of their crowns, where fern-covered branches and limbs allow the possibility of salamander movement from tree-to-tree without going to the ground. Tree 3 (‘Demeter’) stands 16 m from Kronos and Rhea. Its crown does not interact with these trees, so movement of a salamander between them would require ground contact. Trees 4 (‘Prometheus’) and 5 (‘Iluvatar’) stand over 50 m from each other and the other trees; they were selected because of their high crown-level structural complexity and epiphyte loads.

Tree access.—We achieved access to tree crowns by using a high-powered compound bow mounted to an open-face fishing reel. A rubber-tipped arrow trailing fishing filament was shot over branches



FIGURE 2. Left, a climber (Steve Sillett) ascends a large redwood in Prairie Creek Redwoods State Park, California, in search of *Aneides vagrans*. (Photograph by Marie Antoine, compliments of Steve Sillett). Right, Humboldt State University students Naomi Withers and Cameron Williams search a complex redwood crown for salamanders. This search area is 60 meters above the ground. (Photographed by James C. Spickler).

high in the crown, and a nylon cord was then reeled back over the branches and used to haul a 10 mm diameter static kernmantle climbing rope into the crown and back to the ground. One end of the climbing rope was then anchored at ground level, and the other end was climbed via single rope technique (Moffett and Lowman 1995). We had access to the rest of the crown via arborist-style rope techniques (Jepson 2000; Fig. 2). The climbing rope was threaded through a pulley hung from a sturdy branch near the treetop. The rope could be easily replaced with nylon cord when the tree was not being climbed.

Tree crown mapping.—We described tree crowns by measuring dimensions of the main trunk and all reiterated trunks with a basal diameter over 5 cm. We measured trunk diameters at 5 m height intervals. For reiterated trunks arising from the main trunk or other reiterated trunks, we recorded: top height, base height, basal diameter, and distance and azimuth (i.e., compass direction) of base and top from center of main trunk. For reiterated trunks arising from limbs we recorded the following additional measurements: limb basal diameter, diameter of limb at the base of the reiteration, and limb height of origin. Thus, the XYZ coordinates and architectural context of every measured diameter could be determined for use in 3-dimensional mapping. Total tree height was determined by dropping a tape from the uppermost foliage to average ground level.

We derived three structural variables and three fern mat variables from the mapping data, including total fern mat mass (kg), fern mat mass in crotches, proportion of fern mass in crotches, main trunk volume (m^3), reiterated trunk volume, and limb volume. Volumes of main trunks, reiterated trunks, and limbs were estimated by applying the equation for a regular conical frustum to the diameter data (Table 1) such as:

$$\text{Volume} = \text{Length} \times \pi/3 \times (\text{lower radius}^2 + \text{lower radius} \times \text{upper radius} + \text{upper radius}^2).$$

In each tree, we also determined the XYZ coordinates of all *P. scouleri* fern mats by measuring their heights above ground as well as their distances and azimuths from the main trunk. Fern mat size was quantified by the following measurements: mat length, mat width, average soil depth (calculated from multiple measurements with a metal probe), and maximum frond length. We calculated surface areas of fern mats by applying the equation for an ellipse:

$$\text{Area} = \pi \times 0.5(\text{mat length}) \times 0.5(\text{mat width}).$$

Surface area was multiplied by average soil depth to calculate fern mat volume. Dry masses of all mats were estimated by applying the following model equation ($n = 18$, $R^2 = 0.995$; unpubl. data of Sillett

TABLE 1. Summary of tree size, *Polypodium scolieri* fern mats, soil water storage, and salamander abundance in five redwood trees from Prairie Creek Redwoods State Park, California. Soil water storage values are whole-tree annual averages derived from a model (Sillett and Van Pelt unpublished). Salamander abundance is the number of *Aneides vagrans* captured on fern mats in each tree, excluding those captured with cover boards.

Tree:	Rhea	Demeter	Kronos	Iluvatar	Prometheus
Height (m)	95.5	97.5	91.6	91.5	97.4
DBH (cm)	405	434	428	614	559
Main trunk volume (m ³)	359.3	389.7	335.4	874.0	598.5
Reiterated trunk volume (m ³)	1.2	20.2	30.5	162.5	63.1
Limb volume (m ³)	1.5	6.4	14.5	24.6	3.2
Fern mat dry mass (kg)	205	39	275	249	352
Fern mat dry mass in crotches (kg)	8	6	18	97	249
Soil water storage (l)	1003	437	1561	1908	4416
Fern mat salamander abundance	2	3	8	7	14

and Van Pelt):

Total mass (kg) = 32.912 × mat volume + 0.0250 × maximum frond length.

To better visualize individual tree crown complexity, we generated three-dimensional models of tree crowns using Microsoft Excel and the crown structure data (Sillett and Van Pelt, unpubl. data). We overlaid locations of fern mats and salamander captures on the crown models via their XYZ coordinates (Fig. 1). We used this information to quantify movements of salamanders captured more than once during the study.

Capturing salamanders.—To locate *A. vagrans* without destructive sampling, we placed cover objects on fern mats within each tree crown. We constructed cover objects from gray fiberglass screening. We cut and folded materials to produce flat envelope-like bags (hereafter ‘litter bags’) that were filled with decomposing leaf litter and soil, producing both small (25 × 20 cm) and large (25 × 40 cm) bags. To limit introduction of foreign materials to the canopy, only litter and soil from each selected site were used to fill the bags.

Placement of litter bags was determined randomly. The total surface area of a tree’s fern mats was calculated by summing the surface areas of all the mats on the tree. Ten percent of the mat area on each tree was covered such that half was covered by each type of litter bag. The probability of an individual fern mat being randomly selected for a given litter bag was proportional to its surface area. Thus, some fern mats, especially large ones, received multiple litter bags while others, especially small ones, received none. The placement of individual litter bags on selected fern mats was not done randomly. Instead, we spaced the bags across the mats in an attempt to minimize the likelihood of their being blown from the crown during storms. This involved nestling the bags into relatively flat regions of the mats. Wooden sticks were placed underneath each litter bag to maintain crawl spaces for salamanders.

Besides litter bags we deployed cover boards, which were crafted from pairs of 2-cm-thick boards cut into 25 x 25 cm sections (Davis 1991). We placed boards together but separated by parallel 1-cm-thick strips of wood that created a crawl space for salamanders. Our cover boards were designed to simulate preferred terrestrial habitats of *A. vagrans*: 6 mm spaces between bark and heartwood with a smooth firm surface (Davis 1991). This species is often found under the splintered wood of recently fallen trees or exfoliating bark (Davis 2002b; Stebbins 2003). We limited use of cover boards for fear of causing injury to climbers and tourists visiting the grove if the boards happened to fall from the trees. However, we left two cover boards on a large fern mat in Prometheus

and one on a large fern mat in Iluvatar. These locations seemed stable enough to prevent loss of the boards during storms. As an extra precaution we equipped the boards with small lengths of cord anchored to the tree.

Access restrictions.—Summer and spring observations were not possible due to climbing restrictions to protect the nesting habitat of two threatened species in the area: the Marbled Murrelet (*Brachyramphus marmoratus*) and Northern Spotted Owl (*Strix occidentalis caurina*). Thus, our field season was limited to the fall (late September) through winter (end of January), during three field seasons from 2000 to 2002. During these periods, we checked our cover objects 2-4 times per month, weather permitting. We also made weekly checks of litter bags and cover boards in Prometheus during the 2002-2003 field season, and made one visit to Iluvatar during this time. During each visit, all cover objects were checked. A description of any salamander activity, time and location of each capture were recorded.

Marking salamanders.—We anesthetized captured *A. vagrans* using a pH neutral solution of MS-222 (3-aminobenzoic acid ethyl ester) achieved by combining 1.0 g MS-222 + 2.4 g sodium bicarbonate dissolved in 500 ml distilled water. Once salamanders were immobile, they were permanently and uniquely marked under anesthesia with 1 x 2 mm fluorescent alpha-numeric tags (Northwest Marine Technologies, Inc., Seattle, Washington, USA) injected subcutaneously on the ventral side of the tail immediately posterior to the vent. Photographs of dorsal patterns were taken of salamanders too small to be injected with tags. Marked animals were returned to their point of capture once fully recovered from the MS 222. We recorded snout to vent length (i.e., from tip of snout to anterior margin of vent), total length, number of costal folds between adpressed limbs, weight (to the nearest 0.1 g), sex if recognizable by secondary sexual characteristics (e.g., shape of head, presence of mental glands, cirri, eggs in oviducts), and any injuries or other identifying marks.

Data analyses.—We used stepwise multiple regression analysis to evaluate potential effects of individual fern mat characteristics on

TABLE 2. Estimated sizes of *Aneides vagrans* populations on large redwood trees over two years derived from mark-recapture data using the Chapman (1951) method (see Chao and Huggins 2005). Numbers in parentheses are one standard error. Estimates are only for the portion of the arboreal population using fern mats.

Tree	Salamander Abundance	
	January 2002	January 2003
Prometheus	11 (0)	29 (8)
Iluvatar	11 (2)	20 (11)
Kronos	8 (4)	–
Five trees combined	54 (15)	–

salamander abundance in those mats with cover objects ($n = 65$). The following independent variables were included: percentage of surface covered by litter bags, total area covered by litter bags, total surface area, dry mass, and height above ground. The number of cover boards on each fern mat (0, 1, or 2) was also used as an independent variable to account for the potential effects of this sampling technique. The dependent variable was the number of salamander captures per mat.

We evaluated potential effects of fern mats and tree structure on *A. vagrans* abundance using correlation analysis. Tree-level independent variables ($n = 5$) included total fern mat mass (kg), mass of fern mats in crotches, and the average amount of water stored (l) in each tree's fern mats throughout the year. This last variable was derived from a canopy soil hydrology model developed for the permanent reference stand that includes all of the trees in this study (Sillett and Van Pelt, unpubl. data). Structure variables included volumes (m^3) of each tree's main trunk, reiterated trunks, and limbs. The dependent variable was the number of marked animals per tree. We corrected for sampling effort by dividing the actual number of visitations per tree ($n = 27$ – 33) by the highest number of visitations for any tree. We eliminated the potentially confounding effects of cover boards by removing those two mats from the data set prior to the analysis.

Tree-level salamander abundance was estimated with the Chapman (1951) method (see Chao and Huggins 2005). We used the unbiased estimator for population size (N):

$$N = \frac{(M+1)(C+1)}{R+1} - 1$$

where M = number of individuals marked in the first sample, C = total number of individuals captured in the second sample, and R = number of marked individuals recaptured in the second sample. For this analysis, we made the following assumptions: 1) sampling was random; 2) the population was closed (i.e., no immigration, emigration, birth, or death) within each field season; 3) all animals had the same chance of being caught in the first sample; 4) marking individuals did not affect their catchability; 5) animals did not lose marks between sampling intervals; and 6) all marks were reported on discovery in the second sample. We recognize that there are limitations to this method (see Pollack et al. 1990) but our small samples did not permit a more sophisticated approach. As a consequence we consider these estimations only as first approximations of salamander abundance in fern mats.

Other salamander observations.—The inaccessibility of study trees during the spring and summer greatly limited our ability to make year-around observations of arboreal *A. vagrans* activity. However, several relevant observations were made by forest activists participating in “tree-sits” at other nearby locations, and by scientists working in the canopy on research unrelated to this study. We include a summary of these anecdotal observations with our results because these accounts fill gaps in our temporal record and provide documentation of salamander presence in the canopy throughout the entire year.

RESULTS

Tree-level population estimates.—A total of 55 captures were made of 42 individual *A. vagrans*, including 13 recaptures. One individual was captured five times, two individuals were

captured four times, three individuals were captured twice, and 36 individuals were captured only once. Captured individuals ranged from 1.3–7.1 cm in SVL, 2.4–14.7 cm in total length, and 0.1–5.9 g in mass. Salamanders were found in all five study trees with the most captures in Prometheus ($n = 28$) and the least in Rhea ($n = 2$). Small sample sizes forced us to use entire field seasons as sampling intervals to make population estimates for each tree. Thus, *A. vagrans* abundance was estimated once for three trees (Prometheus, Iluvatar, Kronos) in January 2002 for animals marked in the first field season and marked or recaptured in the second field season (8–11 individuals per tree), and again for two trees (Prometheus and Iluvatar) in January 2003 for animals marked in the second field season and marked or recaptured in the third field season (20–29 individuals per tree, Table 2). There were insufficient data to make any tree-level population estimates for two of the trees (Demeter and Rhea). However, we combined data from all five trees to calculate an estimate of 54 salamanders for these five tree crowns collectively in January 2002 based on animals marked in the first field season and marked or recaptured in the second field season (Table 2).

Tree-level effects on salamander abundance.—Based on correlation analyses at the tree-level, there were two significant predictors of salamander abundance per tree: average water storage by fern mats ($r = 0.930$, $P = 0.022$) and mass of fern mats in crotches ($r = 0.885$, $P = 0.046$). Our small sample size ($n = 5$ trees) prohibited further analyses of tree-level effects for other fern mat variables (total fern mat mass, proportion of total fern mat mass in crotches), and three structural variables (main trunk volume, reiterated trunk volume, and limb volume).

Effects of fern mat characteristics on salamander captures.—Fern mat-level effects on *A. vagrans* captures and recaptures were evaluated separately for a total of 65 fern mats (i.e., only those with cover objects) in five trees using regression analysis. Total number of *A. vagrans* captured, including recaptures, was positively associated with number of cover boards ($R^2 = 0.85$, $P < 0.0001$), area covered by litter bags ($R^2 = 0.38$, $P < 0.0001$), fern mat mass ($R^2 = 0.28$, $P < 0.0001$), and fern mat area ($R^2 = 0.22$, $P < 0.0001$). No associations were found between captures and either the percentage of fern mat surface area covered by litter bags ($R^2 = 0.002$, $P = 0.70$) or height ($R^2 = 0.004$, $P = 0.62$). Stepwise multiple regression analysis revealed that number of cover boards (adjusted $R^2 = 0.85$, $P < 0.00001$), fern mat mass (cumulative $R^2 = 0.90$, $P < 0.00001$), and height of fern mat (cumulative $R^2 = 0.91$, $P < 0.03$) all accounted for significant amounts of variation in the number of salamander captures.

The strongest variable affecting the number of *A. vagrans* captured was not a physical characteristic of the fern mats, but was an artifact of our sampling technique. Significantly more salamanders were captured on fern mats with cover boards than on mats with only litter bags. In Prometheus, the total number of captures on one fern mat was 15, representing 5 individuals. All of the captures were made in two cover boards, although 8 litter bags occurred in close proximity to the cover boards. Nine of the 15 captures were recaptures, including four of a single large male who had apparently taken up residence in an area that included both of the cover boards, which were located < 0.5 m apart. He was captured during all 3 years of the study, and on several occasions he was found with other salamanders. On one fern mat in Iluvatar, there were 9 captures representing seven individuals. Seven of these were made in a cover board, while the remaining two were made under a litter bag located 75 cm away.

Movement of recaptured salamanders.—We found no evidence of among-tree movements of marked salamanders, via interacting crowns

or the ground. Of the 13 recaptures, 12 were of individuals found in the same locations as their initial captures. The single exception was a juvenile *A. vagrans* (1.2 g, SVL= 4.35 cm) found under a litter bag (first capture) and then recaptured a week later on the surface of a fern mat 7.5 m higher in the tree.

Seasonal activity.—Our limited field season precluded observations of seasonal differences in movement and habitat use, but based on our findings and several anecdotal observations made outside of our field seasons (see below), it appears that at least some individual *A. vagrans* occupy the forest canopy throughout the year.

Other observations.—The few spring and summer observations were often made while canopy researchers were conducting surveys for protected species (Marbled Murrelet and Spotted Owl). Also, salamander observations were made by non-scientists illegally occupying trees to protect them from logging. It is understandable that the protection of threatened species takes priority over new research dealing with a salamander that appears to be abundant, at least in terrestrial habitats, but the lack of data for these seasons left us with several unknowns concerning the life history and ecology of *A. vagrans* in redwood forests. The following observations may help us to understand *A. vagrans* behavior during these periods.

The willingness of tree sitters to stay aloft for extended periods enables them to make observations that scientists working under research permits cannot afford to do. In the spring of 2002, an activist designated as Remedy began a tree-sit on private timber lands. Remedy, along with other activists, established sleeping platforms in several large redwoods near Freshwater, in coastal Humboldt County, California. Remedy remained aloft for nearly a year before being forcibly removed and arrested for trespassing. In that time period she made numerous observations of a pair of wandering salamanders.

On seven occasions from April to September, Remedy observed the “same pair” of wandering salamanders moving within an area around a small cavity located 3 m from her living platform. The original leader of the tree had broken at an approximate height of 40 m; the living platform was located a few meters below the break. The loss of the leader occurred at least 100 years before, and two reiterated trunks had replaced it. A zone of decaying wood that had formed around the break created the cavity that the salamanders occupied. The same cavity was also shared by a small “tree squirrel,” probably a Douglas’ Tree Squirrel (*Tamiasciurus douglasii*) or a Northern Flying Squirrel (*Glaucomys sabrinus*). A *P. scouleri* fern mat occupied the top of the broken trunk.

Remedy often observed the salamanders moving in close proximity to each other, but they appeared to be “moving independently as if unaware of each other.” Most of the salamander activity was limited to the area on and around the fern mat, but on two occasions a salamander moved out along branches and continued to the outer crown where it could no longer be seen. All observations were made during early evening and under similar microclimatic conditions: dry substrate with elevated air humidity. Conditions were described as “warm and muggy, perfect weather for flying insects.” One stated impression was that the salamanders were more affected by temperature than by moisture as no animals were observed moving during the rain or immediately thereafter. There was limited flying insect activity during and immediately after rain storms. Observations were always made during calm conditions with little or no wind. The two salamanders were

observed throughout the spring and summer with the last observation occurring on 21 September 2002, when “evenings became too cold for foraging.”

Remedy reported an *A. vagrans* eating while in the canopy. One evening, she noted an insect, a “winged termite,” alight on a small branch approximately 30 cm from the salamander. The salamander then rapidly moved to the insect, which it ate without hesitation. After a moment, the salamander continued moving along the branch to the outer crown.

Similar observations were made by another activist, Raven, participating in a tree-sit in the Van Duzen watershed in Humboldt County. Raven made several observations of a pair of *A. vagrans* foraging near his sleeping platform. He also described how *A. vagrans* activity decreased along with decreasing nighttime temperatures as autumn and winter approached. On 2 February 2003, he observed a pair of *A. vagrans* move on to his platform. He watched them for several minutes before they continued off into the darkness.

On 17 September 2002 at 0800 hrs, one of us (Stephen Sillett) and his graduate student (A. Ambrose) observed an adult *A. vagrans* while crown-mapping a large redwood in Humboldt Redwoods State Park. The observation was made during warm conditions with high air humidity and low cloud cover; the tree’s bark was dry. We observed a single adult *A. vagrans* moving vertically along the trunk at a height of 93 m above ground. The salamander’s path was exposed with no soil or obvious cover nearby. The nearest area of apparent cover was in a cavity of dead wood located 100.6 m above the ground, but the surface of this site was also exposed and dry. Obvious fissures and crevices in the decaying wood, however, likely allow such animals to enter and retire within damp cavities.

We also have made incidental observations of *A. ferreus*, a close relative of *A. vagrans*. On three separate occasions in 2002, one of us (James Spickler) and N. Bowman observed adult *A. ferreus* while studying the nesting behavior of the red-tree vole (*Arborimus pomo*) in old-growth Douglas-fir forests of coastal Oregon (BLM forest lands, Salem and Eugene Districts). Observations were made in the summer (July-August), midday during periods with high humidity and on moist substrates. In all cases, salamanders were inactive and hidden within the stick nests of a western grey squirrel (*Sciurus griseus*). Two of these salamanders were found in an active nest containing fresh feces and elevated temperatures from the recently departed rodent’s body.

In 1993, Stephen Sillett observed an *A. ferreus* while conducting canopy research in a 700-year-old Douglas-fir forest (Middle Santiam Wilderness Area, Willamette National Forest, Willamette County, Oregon; see Sillett 1995). While climbing in a large Douglas-fir tree adjacent to a 30-year-old clearcut, he found an adult salamander under moss (*Antitrichia curtipendula*) on a large branch approximately 30 m above the ground. After being disturbed, the salamander moved horizontally across the branch and retreated under a bark flake on the tree trunk. The observation was made midday during the dry season (early autumn), and the moss mat was “merely damp.”

DISCUSSION

Plethodontid salamanders are unique in that they are the only salamander family to have invaded the tropics, where many species occupy arboreal niches (Lynch and Wake 1996). However, in spite of the high number of species displaying arboreal habits in tropical forests, little is known about this phenomenon beyond a few anecdotal accounts (e.g., Good and Wake 1993; McCranie and Wilson 1993). Our results here provide information on a new niche dimension for a North American temperate zone plethodontid salamander, the resident use of arboreal habitats in redwood forest canopies by *Aneides vagrans*.

Like other plethodontid salamanders, *A. vagrans* is lungless and respire exclusively through its skin and buccopharynx. Presumably,

this requires the maintenance of skin moisture to facilitate respiratory gas exchange (Shoemaker et al. 1992). The skin of most amphibians is highly permeable to liquid and gas, allowing for moisture exchange rates similar to those of standing water (Spotila and Berman 1976). To avoid fatal desiccation, amphibians have developed a variety of behavioral and physiological means by which to control water loss (Shoemaker et al. 1992). Plethodontid salamanders select habitats with suitable microsites that retain relatively high moisture contents as the macrosite begins to dry (Thorson 1955; Cunningham 1969; Ovaska 1988; Cree 1989; Shoemaker et al. 1992). This desiccation-avoidance behavior has been observed in terrestrial *A. vagrans* (Davis 2002b).

Our correlation analysis of tree-level effects on salamander abundance highlights the importance of water storage in soils beneath epiphytes and location of this material within the crown (e.g., in crotches). Soils on limbs drain faster than those in crotches (Ambrose 2004; Enloe et al. 2006) and thus may become too dry for perennial occupancy by salamanders. Microclimate data from fern mats show that crotches have more stable moisture and temperature regimes than branches or limbs (Ambrose 2004; Sillett and Van Pelt, unpubl. data). Compared to those on branches or limbs, fern mats in crotches hold more water per unit mass and store water longer (Sillett and Van Pelt, unpubl. data). Furthermore, soils in crotches have higher bulk densities and lower hydraulic conductances than soils on branches or limbs (Enloe et al. 2006), providing relatively stable refugia from desiccation during the dry season. Trees with soil in deep crotches likely provide suitably moist arboreal habitats for the year-round occupancy of old-growth redwood forest canopies by *A. vagrans*, enabling this salamander to breed and potentially live its entire life within tree crowns.

The effects of fern mat size and height on salamander captures are ecologically interpretable. The positive correlation between fern mat size and *A. vagrans* abundance can be attributed to the larger surface area available for foraging, higher water-holding capacity, and greater internal complexity of larger fern mats. Although the arboreal feeding habits of *A. vagrans* have not been studied, the salamanders probably take prey from fern mats. Fern mat surfaces (at least seasonally) have more invertebrate biomass than other surfaces (e.g., bark and foliage) in redwood crowns (Jones 2005). In fact, the mites and collembolans inhabiting fern mats experience population explosions during the wet season, and have densities similar to those observed in terrestrial habitats under similar conditions (Jones 2005).

Larger, deeper fern mats have greater water storage and slower rates of desiccation than smaller mats (Ambrose 2004), thus providing more stable, moist microclimates conducive to *A. vagrans* habitation. As a fern mat increases in size, new roots and rhizomes grow to replace the old ones, which subsequently decay. Although debris from litter fall, especially tree foliage, is a major component of the *P. scouleri* fern mats, the majority of organic material in these mats comes from *P. scouleri* itself, especially humus derived from decaying roots and rhizomes (Sillett and Bailey 2003). Dead, decomposing rhizomes leave behind "tunnels" in the soil. Larger debris (e.g., branches) that falls onto fern mats can also create tunnels and internal cavities as it is covered by other debris and begins to decompose. On three occasions, Sillett and Bailey (2003) found *A. vagrans* occupying interstitial spaces in *P. scouleri* mats (mats were being harvested for the development of equations to predict fern mass). Also, an egg cluster of *A. vagrans* was found within a *P.*

scouleri mat on a freshly fallen old-growth redwood (Welsh and Wilson 1995). These observations suggest that the tunnels and cavities in fern mats are used by *A. vagrans*, and it is likely that they are important refugia, but the fragile nature of the substrate makes searching the tunnels nearly impossible without permanently altering the habitat.

The negative effect of fern mat height on salamander captures can be attributed to the varying microclimates at different heights within a forest canopy. During periods with no precipitation, the upper canopy receives more light and wind, and the air is less humid compared to the lower canopy (Parker 1995, Sillett and Van Pelt, unpubl. data). Therefore, fern mats in the upper canopy, regardless of size, are subjected to more frequent and severe periods of desiccation than those in the lower canopy. In redwood forest canopies this effect can be seen in *P. scouleri* itself. Although fern mat size is not correlated with height, the size and shape of fronds become progressively smaller with increasing height in the forest (Sillett and Bailey 2003). The negative effect of height on number of *A. vagrans* captured can be attributed to the less stable microclimate of upper canopy fern mats compared to those in the lower canopy. Fern mats higher in a tree may be important for salamanders foraging during wet periods, but the prolonged occupation of these sites may be risky during dry periods. This idea is supported by our discovery of two mummified individuals near the tops of two trees over 90 m tall (see also Maiorana 1977).

Dead wood may represent another important habitat for arboreal salamanders in redwood forests. At the forest level, the average water storage in dead wood (16,500 l ha⁻¹) rivals the amount stored in canopy soil (19,700 l ha⁻¹), and seasonal variation in dead wood water storage is less than that in soils on branches and limbs (Sillett and Van Pelt, unpubl. data). Even though we did not quantify salamander abundance in dead wood habitats, a number of anecdotal observations suggest that *A. vagrans* use dead wood and hollow cavities. The highest observation of this species ever made (93 m) was of a salamander climbing upwards on a late summer morning towards the dead, broken top of a large redwood nearly lacking vascular epiphytes and soil. It is likely that large populations of *A. vagrans* reside within hollow trunks of standing redwoods in old-growth forests.

Movement and territoriality.—If a salamander finds a habitat that has a favorable moisture regime and sufficient prey availability, it would be advantageous for the animal to stay in that habitat or return to it frequently (Jaeger 1980). Terrestrial *A. vagrans* move only short distances, are site-tenacious, and return periodically to particular habitats within their home range (Davis 2002a). Our canopy findings parallel these terrestrial observations.

On 6 occasions we captured more than one salamander on a fern mat. Twice we found two males in a cover board with a single female. We also found two females together with no male present and two males together with no female present. Twice we found a pair of salamanders on the same fern mat but not within the same cover board: a male with a female and a male with another male. Males did not appear to be defending females from other males, and neither sex appeared to be defending a particular site, both of which are major components of territorial behavior (Brown and Orians 1970; Jaeger et al. 1982; Mathis et al. 1995). Similar behaviors were observed in terrestrial *A. vagrans* on Vancouver Island, British Columbia (Davis 2002a). Although arboreal *A. vagrans* in redwood forests appear to be acting similarly to terrestrial individuals in British Columbia, we did not sample during either the breeding season (presumably spring) or the summer. Arboreal *A. vagrans* may behave differently during certain times of the year if resources, such as nest sites, prey items, or moist habitats, become limited.

Seasonality.—The seasonal restrictions on canopy research in old-growth redwood forests prevented us from sampling salamanders for eight months of the year, including the summer dry season. When considering the hydric constraints of plethodontid salamanders, it is likely that *A. vagrans* would be less active on forest canopy surfaces during the dry season. Anecdotal observations of *A. vagrans*, as well as observations of other species of *Aneides*, suggest otherwise however. Arboreal *Aneides* may be most active during the drier and warmer spring and summer given the strong marine influences that contribute to mild temperatures and high relative humidity during these seasons in the coastal redwood forest (Sawyer et al. 2000).

Green salamanders (*Aneides aeneus*) use arboreal habitats seasonally (Waldron and Humphries 2005). These animals over-winter in rock outcrops and migrate into woody or arboreal habitats (primarily hardwoods) during the onset of spring. They remain in these habitats throughout the summer and breeding season before returning to rock outcrops sometime in October and November. Green Salamanders prefer larger (in diameter) and more complex trees having a variety of visible cavities. On dry days individuals are often found under the flaky and furrowed bark of several different tree species. The maximum height above the ground where Green Salamanders have been observed is 21 m at the mouth of a tree hollow (Waldron and Humphries 2005). Gordon (1952) noted a decrease in Green Salamander abundance during the dry season, but Waldron and Humphries (2005) demonstrated that the salamanders may be climbing into the canopy where they remain throughout the summer and cannot be easily detected from the ground.

It is unlikely that *A. vagrans* utilizes arboreal habitats seasonally like *A. aeneus*. Anecdotal observations do not support such a scenario but instead suggest year-round residency. At most, *A. vagrans* may shift its use of particular microhabitats within the canopy, but it remains unclear which suitably moist locations might be preferred during different seasons.

Effects of tree- and fern mat-level variables on salamanders.—Our mat-level analysis indicated an effect of cover boards on number of salamanders. Nearly half of the *A. vagrans* captured during our study were found in cover boards even though their use was quite limited. By placing cover boards on top of fern mats we may have created a preferred habitat type. This assertion is supported by observations that dead wood substrates were favored by terrestrial *A. vagrans* populations in Vancouver Island, British Columbia (Davis 2002b). It is unclear whether the salamanders captured in our cover boards were residents of the fern mat on which the boards were placed, originally residing in the tunnels and other complexities of the fern mat, or if placing the cover boards on the fern mat created a habitat allowing foraging individuals from other parts of the tree the opportunity to stay and take up residence. The paucity of recaptures under litter bags suggests that *A. vagrans* prefers crevices but will use litter bags opportunistically for cover while foraging.

Future research.—Future studies should examine how *A. vagrans* uses other habitats besides fern mats, since the preponderance of cover board captures as well as anecdotal observations suggest that *A. vagrans* inhabits crevices, cavities, and lodged woody debris at least as much as it does soil beneath ferns (*P. scouleri*). Crevices and cavities are difficult to search manually in a non-destructive fashion, and we discourage this activity. Placing cover boards adjacent to these sites would

allow capture of salamanders coming out to forage on other tree surfaces without permanently altering the habitat. Cover boards also create new habitats within tree crowns for salamanders and their prey. The entrance to natural and artificial crevices and cavities could be monitored continuously (even during summer months when canopy access is restricted) via motion-sensitive, infrared video cameras. Microclimate data could also be compared to videos to determine preferred conditions for foraging and also to document salamander behavior throughout the annual cycle. Identification of salamanders via videos would be possible using a visual implant fluorescent elastomer marking technique and by marking individuals on their dorsal surfaces.

Hopefully our discovery of resident arboreality in *Aneides vagrans* will trigger a renewed interest in studying adaptations of plethodontid salamanders to the use of arboreal habitats. For example, the recently described modification (Sapp 2002) of the typical plethodontid courtship tail-straddling walk (Houck and Arnold 2003) from linear to circular in the genus *Aneides* may be an adaptation to arboreality.

Conservation implications.—Resident populations of arboreal salamanders in old-growth forests may be top predators of diverse, heterotrophic communities fueled by the productivity of epiphytes and the trees themselves. Such ecosystems appear to be lacking in younger forests regenerating on logged-over land. Only 4% of the original old-growth redwood forests remain, and second-growth forests originating before 1930 are scarce (Noss 2000). Nearly all regenerating redwood forests are younger than rotation age (~ 50 years) and consisting of trees less than 40 m tall with small branches. As a consequence of their simple structure, the biological diversity of young redwood forests is low, and many old-growth-associated plants and animals are now restricted to a few National and State Parks (Sawyer et al. 2000; Cooperrider et al. 2000). Redwood forests capable of supporting arboreal salamanders are rare outside of these Parks. Even within the Parks, epiphytic vascular plants and associated soil communities do not occur in the crowns of small trees despite their proximity to large trees, because the structural complexity (e.g., large limbs and reiterated trunks) necessary to support these organisms develops very slowly. Thus, the arboreality of *A. vagrans* in redwood forests may be a phenomenon restricted to a tiny portion of the landscape. Further investigations to establish a basis for the conservation of *A. vagrans* and associated organisms in protected forests are warranted.

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A Wandering Salamander (*Aneides vagrans*) from Humboldt County, California (United States). (Photograph by: William Leonard, ©2004. All Rights Reserved.)





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