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Aneides vagrans is Absent from Angiosperm Crowns in an Old-growth Redwood Forest

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***Abstract*.—In the crowns of ancient Coast Redwood (*Sequoia sempervirens*) trees, large mats of soil anchored by ferns and other epiphytes provide refuge for the Wandering Salamander, *Aneides vagrans*. Similar mats are found in the crowns of understory angiosperm trees, but there have been no systematic efforts to search for salamanders there. We placed cover objects in the crowns and at the bases of four understory angiosperm trees (Big-leaf Maple, *Acer macrophyllum* and Red Alder, *Alnus rubra*) in the Redwood Experimental Forest in Klamath, California, and conducted 41 visual encounter surveys from February 2015 to June 2016. We did not find any *A. vagrans* in the crowns of angiosperm trees or on the forest floor directly below them in old-growth Redwood Forests, despite consistent captures of *A. vagrans* in and around the ancient conifers nearby at the same time. Because crown complexity and the availability of soil and crevices are significantly lower in angiosperms than in ancient conifers, angiosperms may not provide adequate habitat for *A. vagrans*.**

Key Words.—*Acer macrophyllum*; *Alnus rubra*; cover object; fern mat; Sequoia sempervirens; tree crown; Wandering Salamander

Introduction

The conifer forests that line the foggy coast from Sonoma to Del Norte County, California, USA, are home to the Wandering Salamander (*Aneides vagrans*), a species with an intriguing history. Besides its main distribution, a disjunct population of *A. vagrans* inhabits Vancouver Island, British Columbia, Canada, apparently the result of an accidental introduction in the 19th Century (Jackman 1998). For many years this species was not distinguished from its close relative, the Clouded Salamander (*Aneides ferreus*), which inhabits coastal forests from Del Norte County north through Oregon up to the Columbia River (Jackman 1998). Both species were originally characterized as ground-dwelling salamanders with climbing abilities, and were documented in terrestrial habitat such as large logs on the forest floor, talus, cracks and crevices in rocks and bark, stumps, woody debris, and brush piles (Wake 1965; Whitaker et al. 1986; Corn and Bury 1991). A couple of accounts acknowledged the remarkable climbing ability of these species, including one *A. vagrans* found 7 m above the ground in a dead tree (Van Denburgh 1916), and another of *A. ferreus* found up to 37 m above the ground in a snag (Leonard et al. 1993). These climbing abilities are perhaps less surprising considering their morphology: both species have rounded, prehensile tails, long limbs, and slender digits that include sub-terminal, square-shaped toe pads (Stebbins 2003; Petranka 2010), all of which assist in clinging and climbing. The role that climbing plays, however, in the ecology and life history of *A. vagrans*, at least, was underestimated for most of the 20th Century.

A serendipitous discovery of a clutch of eggs inside a fern mat that had been recently dislodged from the crown of a Coast Redwood (*Sequoia sempervirens*) was the first clue that *A. vagrans* could reside in the canopies of temperate redwood forests in Northern California (Welsh and Wilson 1995). Shortly thereafter, *A. vagrans* was observed directly living in the old-growth redwood canopy, occupying tunnels and cavities amidst epiphytic fern mats (usually composed of Leather Fern, *Polypodium scouleri*) high above the forest floor (Sillett 1999; Sillett and Bailey 2003). Spickler et al. (2006) documented the presence of *A. vagrans* in the canopy for extended periods of time, with some individuals found over 80 m off the forest floor, and estimated that a single old-growth redwood can support more than 30 individuals. *Aneides vagrans* does not require aquatic habitat for breeding because it has direct development (Stebbins 2003; Petranka 2010). Thus, an individual can complete its life cycle on land or in the canopy if the environment provides constant, moist refugia.

The fern mats found in the tall Coast Redwood and Sitka Spruce (*Picea sitchensis*) canopies may be the primary refugia for arboreal *A. vagrans*. The two most significant predictors of salamander abundance in a given tree are the average water storage of fern mats,

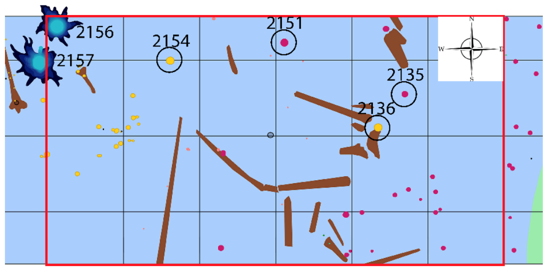

Figure 1. Map of the 60 × 30 m angiosperm understory plot, located in the Redwood Experimental Forest (Klamath, Del Norte County, California, USA) used to search for Wandering Salamanders (*Aneides vagrans*) from February 2015 to June 2016. Gridlines are at 10 m intervals. Focal trees are circled (2135, 2136, 2151, and 2154). Yellow dots are Bigleaf Maples (*Acer macrophyllum*), pink dots are Red Alders (*Alnus rubra*); the size of the dots represents trunk diameter (DBH). A single grey dot represents plot-center. Brown polygons represent downed trees and other woody debris. The plot boundary is indicated with a red border. Two Sitka Spruce (*Picea sitchensis*; 2156 and 2157) known to harbor *A. vagrans* are in the northwest corner of the plot. (Map courtesy of Robert Van Pelt).

and the mass of fern mats in canopy crotches (Spickler et al. 2006). The angiosperm understory within these old-growth forests also hosts epiphytic mats (usually composed of Licorice Fern, *P. glycyrrhiza*). We wondered whether *A. vagrans* use arboreal microhabitats in the angiosperm understory as well as in the conifer canopy. To answer this question, we placed cover objects in the crowns of four angiosperms, as well as on the ground below these trees, and checked these cover objects repeatedly for more than a year.

Materials and Methods

We conducted this study within a 60 m × 30 m research plot in the Redwood Experimental Forest (managed by the U.S. Forest Service) in Klamath, Del Norte County, California. *Aneides vagrans* were previously documented here in the crowns of tall conifers, and neighboring plots host ongoing research on these animals (unpubl. data). We placed cover objects in and under four angiosperm understory trees within the boundaries of the plot (Fig. 1): two Bigleaf Maple (*Acer macrophyllum*; trees 2154 and 2136) and two Red Alder (*Alnus rubra*; trees 2135 and 2151). We selected these trees because they are some of the largest understory trees inside the plot and they possess the most potential salamander habitat. We recorded the diameter at breast height (DBH) and height for all focal trees (Table 1). We measured height using the sine method (Larjavaara and Muller-Landau 2013). The elevation at the base of these understory trees is approximately 11 m above sea level. All four trees are within 20 m of each other, yet there is no overlapping of crowns. These angiosperm trees do not come into direct contact with the conifer crowns, but are within 20 m of tall Sitka Spruce and Coast Redwood that are known to harbor *Aneides vagrans* (pers. obs.).

We constructed flat and saddle-shaped cover objects from 2.54 × 15.2 × 15.2 cm redwood fence boards. We cut and assembled pairs of boards into 45.7 × 45.7 cm cover objects, with redwood spacers used to create a 1-cm gap between the top and the bottom boards (Fig. 2). This design exploits the preference of the species for narrow cracks in wood, rock, and other substrates, and has consistently yielded captures of *A. vagrans* in nearby conifer crowns (pers. obs.). We placed flat cover objects (n = 20) on the forest floor at the base of each focal tree, distributing them equally so that each tree had five cover objects under its crown. We placed cover objects at a random distance and azimuth from a given tree using a random number generator, with a maximum distance of 15 m from the center of the trunk. We secured saddle-shaped cover objects (n = 20) horizontally on lateral branches and vertically on trunk surfaces in the canopy using thin nylon cord (Fig. 3). We distributed these cover objects evenly among the focal trees and within individual tree canopies, with each tree hosting cover objects in the lower and upper

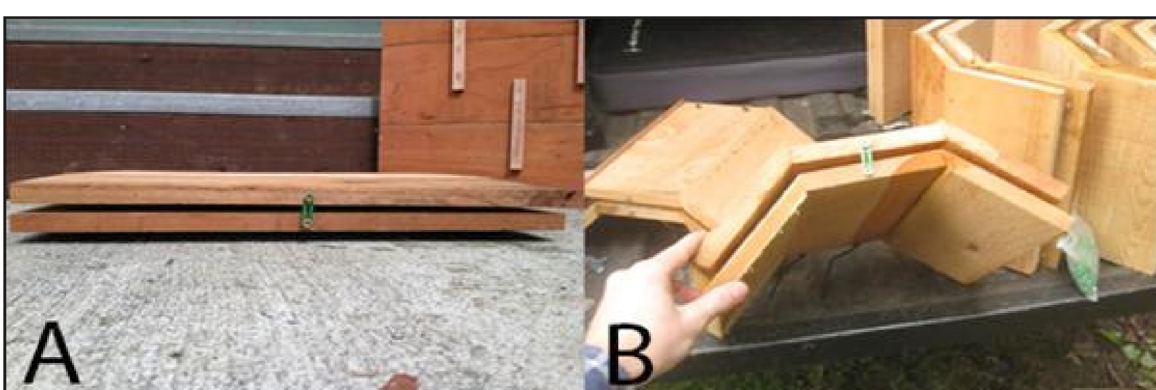

Figure 2. Two types of artificial cover objects constructed to provide refugia for Wandering Salamanders (*Aneides vagrans*). (A) Flat cover objects placed on the forest floor under focal hardwood trees; (B) Saddle-shaped cover objects placed in the canopy of focal hardwood trees. (Photographed by Christian Brown).

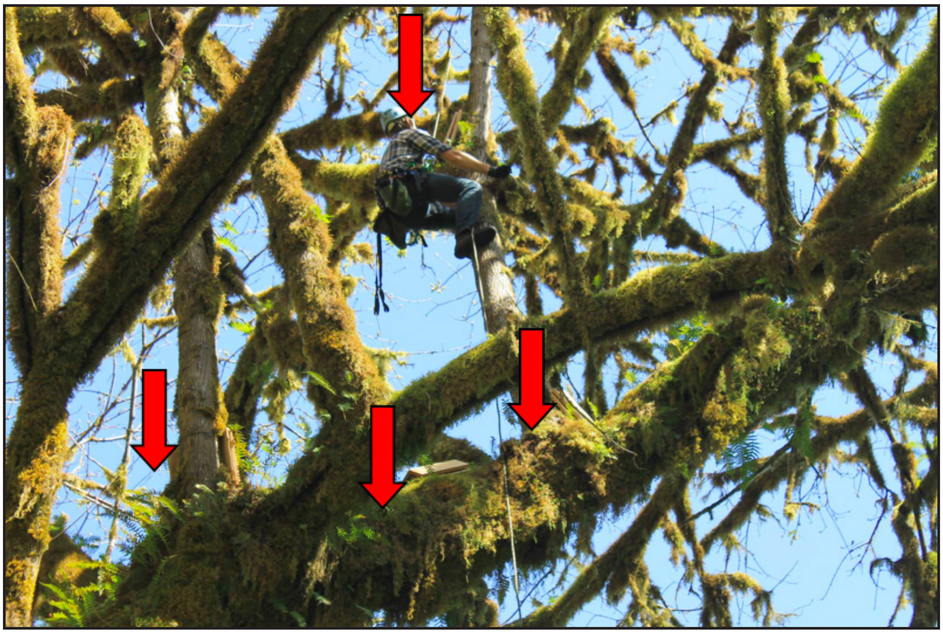

Figure 3. Cover objects (red arrows) placed in the crown of this Bigleaf Maple (*Acer macrophyllum*) to catch Wandering Salamanders (*Aneides vagrans*) as a researcher climbs. (Photographed by Morgan Brown).

crown. We selected the locations of cover objects within the canopy based on proximity to epiphyte mats, branch diameter, and safe climbing routes. We placed cover objects close to epiphyte mats to increase the chances of a resident salamander finding the board. We favored larger diameter branches because they host more surface area for salamanders, and we favored locations we could access without damaging the epiphyte mats or ourselves.

We surveyed the plot for salamanders two to three times per month, from February 2015 through June 2016, for a total of 41 visits. Each plot survey lasted roughly 6 h. We climbed all focal trees and searched for *A. vagrans* in arboreal cover objects, epiphyte mats, and on trunks by visual inspection and by using our hands and fingers to feel into any spaces with limited visibility. We also used our hands and fingers to feel under epiphyte mats from the sides, but our reach was limited as we were cautious not to sever any of the rhizomes anchoring the mats to the trees. For safety reasons, smaller branches near the upper crown that could not support a climber were only visually inspected. We also checked ground cover objects and flipped woody debris while navigating from cover object to cover object. We lifted and searched under woody debris, ranging in size from a few centimeters to a few meters, as it was encountered within the plot; however, because of its size, much woody debris in old-growth redwood forests could not be lifted.

Table 1. Species, diameter at breast height (DBH) and height of the four understory angiosperm trees (two Big-leaf Maple, *Acer macrophyllum* and two Red Alder, *Alnus rubra*) surveyed in the Redwood Experimental Forest (Klamath, Del Norte County, California) from February 2015 to June 2016. Tree IDs correspond to those in Figure 1.

Tree ID	Species	DBH (cm)	Height (m)
2135	*Alnus rubra*	63.5	26.1
2136	*Acer macrophyllum*	90.5	23.9
2151	*Alnus rubra*	88.3	25.6
2154	*Acer macrophyllum*	87.4	22.6

Results

In spite of our extensive search, we found no evidence that *A. vagrans* are using the crowns of angiosperms; we did not find any *A. vagrans* in our plot during this study. Many salamanders were found in and under our cover objects during ground surveys, but the only species observed were Ensatina (*Ensatina eschscholtzii*) and California Slender Salamander (*Batrachoseps attenuatus*). No amphibians of any species were observed in the angiosperm canopy.

Discussion

Despite the presence of apparently suitable habitat, we found no evidence that *A. vagrans* use the crowns of trees in the angiosperm understory at the Redwood Experimental Forest. There are several possible explanations. Absence of evidence is not necessarily evidence of absence: that we did not find any *A. vagrans* in the angiosperm understory does not necessarily mean that they were not there. Because epiphytic mats are sensitive refugia that can take decades to establish, we were careful not to disturb any mats while surveying the understory crowns; it is possible that the salamanders were there but simply hidden from view beneath the mats. While *A. vagrans* are known to hide under fern mats in tall conifer crowns, they also frequently abandon fern mats to hunt from cover objects (pers. obs.). During the same time period over which we failed to locate salamanders in or under our understory cover objects, researchers captured numerous *A. vagrans* from cover objects distributed at similar densities in a redwood crown just outside of our plot (unpubl. data). It is also possible that cover objects in the canopy were not used because they had not had been present long enough to be colonized by salamanders. In another study, *A. vagrans* took 4–5 mo to colonize newly created habitat (Davis 2002); however, this explanation is unlikely because our cover objects were surveyed for 16 mo, over two wet seasons. Taking our data at face value, then, why would *A. vagrans* occupy the tall conifers but not the understory angiosperms?

In the old-growth canopy, the two most significant predictors of presence and abundance of *A. vagrans* are fern mat size and water-holding capacity (Spickler et al. 2006). While a single large redwood crown can support a complex network of fern mats of different sizes, heights, and aspect, the much smaller understory angiosperm trees are characterized by much less complexity and typically host only one or two relatively small epiphyte mats. The presence of smaller, likely drier mats could be responsible for the lack of *A. vagrans* in the angiosperm crowns.

Furthermore, the epiphyte mats observed in the angiosperm crowns differ in composition from old-growth redwood epiphyte mats. In the angiosperm understory, mats of *P. glycyrrhiza* are abundant while mats of *P. scouleri* are rare. In the redwood canopy *P. scouleri* dominates, while *P. glycyrrhiza* is only occasionally encountered and never forms large mats (Sillett 1999; Sillett and Bailey 2003). Gametophytes of *P. scouleri* can establish directly on redwood bark in the moist, shaded areas of the crown and on accumulations of composted leaf litter that get held up on large branch surfaces and crotches (Sillett and Bailey 2003). *Polypodium scouleri* has persistent leaves that aid soil formation by capturing and holding canopy debris. Fronds eventually die, but are held on to by the rhizomes as they decompose back into the fern mat surface. Rhizomes also eventually die, but when they decompose they leave behind voids in the mat that are used by *A. vagrans* (pers. obs.). Conversely, in the angiosperm understory the mats are composed of tightly woven carpets of bryophytes (Cobb et al. 2001), primarily *Isothecium myosuroides* (Slender Mouse-tail Moss), which *P. glycyrrhiza* uses to establish and shelter its rhizomes. There is little to no organic soil underneath, just the rhizomes of the bryophytes and ferns in a dense, carpet-like layer on the bark. Bryophytes, including *I. myosuroides*, are known to recolonize *Acer macrophyllum* before any species of fern (Cobb et al. 2001). As soon as the summer dry-down begins, *P. glycyrrhiza* fronds dry out, fall off, and blow away; they flush again only in the fall or winter, after the rains return and the moss is rehydrated (pers. obs.). Thus, soils cannot form because the moss is so dominant; interestingly, the moss that dominates these angiosperms does not thrive in the redwood canopy.

It is also possible that the angiosperms lack certain habitat requirements for *A. vagrans* that the conifers provide, most notably interstitial spaces approximately 1 cm wide. *Aneides vagrans* can be found in moist terrestrial habitats such as exfoliating bark, in cracks and cavities of decomposing logs, stumps, snags, and in talus (Leonard et al. 1993; Welsh and Wilson 1995; Davis 2002; Stebbins 2003). They are known to use deep, damp cracks for oviposition (Stebbins 2003; Petranka 2010), and individuals have been observed foraging from cracks in bark in the crowns of old-growth conifers, using a sit-and-wait predation strategy (pers. obs.). However, cracks and crevices are not common features in the angiosperm crowns, and the bark of angiosperms does not tend to peel or exfoliate readily enough to provide large amounts of suitable habitat. It seems that no matter where *A. vagrans* are found, be it in tall conifers, fallen logs, or even on talus slopes, they are seeking out narrow cracks and crevices that the angiosperm understory simply does not provide.

Further investigation is needed to test some of these potential explanations for the absence of *A. vagrans* in the angiosperm understory. Future studies could attempt to quantify the size and water holding capacity of the angiosperm epiphyte mats for comparison with tree-level quantities of ferns, soils, and water in tall redwoods (Sillett and Bailey 2003; Spickler et al. 2006; Sillett and Van Pelt 2007). Additionally, available crack-space could be quantified and compared in tall conifer crowns and angiosperm crowns. Such differences in microhabitat features might help explain why *A. vagrans* uses conifer canopy habitat but apparently not the angiosperm understory.

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Literature Cited

Cobb, A.R., N.M. Nadkarni, G.A. Ramsey, and A.J. Svoboda. 2001. Recolonization of Bigleaf Maple branches by epiphytic bryophytes following experimental disturbance. Canadian Journal of Botany 79:1–8.

Corn, P.S., and R.B. Bury. 1991. Terrestrial amphibian communities in the Oregon Coast Range. Pp. 304–317 *In* Wildlife and Vegetation of Unmanaged Douglas-Fir Forests. Ruggiero, L.F, K.B. Aubry, A.B. Carey, and M.H. Huff (Eds.). General Technical Report PNW–GTR–285. U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, Oregon, USA.

Davis, T.M. 2002. Microhabitat use and movements of the Wandering Salamander, *Aneides vagrans*, on Vancouver Island, British Columbia, Canada. Journal of Herpetology 36:699–703.

Jackman, T.R. 1998. Molecular and historical evidence for the introduction of clouded salamanders (Genus *Aneides*) to Vancouver Island, British Columbia, Canada, from California. Canadian Journal of Zoology 76:1570–1580.

Larjavaara, M., and H.C. Muller-Landau. 2013. Measuring tree height: a quantitative comparison of two common field methods in a moist tropical forest. Methods in Ecology and Evolution 4:793–801.

Leonard, W.P., H.A. Brown, L.C. Jones, K.R. McAllistar, and R.M. Storm. 1993. Amphibians of Washington and Oregon. Seattle Audubon Society, Seattle, Washington, USA.

Petranka, J.W. 2010. Salamanders of the United States and Canada. Smithsonian Institution Press, Washington, D.C., USA.

Sillett, S.C. 1999. The crown structure and vascular epiphyte distribution in *Sequoia sempervirens* rain forest canopies. Selbyana 20:76–97.

Sillett, S.C., and M.G. Bailey. 2003. Effects of tree crown structure on biomass of the epiphytic fern *Polypodium scouleri* (Polypodiaceae) in redwood forests. American Journal of Botany 90:255–261.

Sillett, S.C., and R. Van Pelt. 2007. Trunk reiteration promotes epiphytes and water storage in an old-growth redwood forest canopy. Ecological Monographs 77:335–359.

Spickler, J.C., S.C. Sillett, S.B. Marks, and H.H. Welsh, Jr. 2006. Evidence of a new niche for a North American salamander: *Aneides vagrans* residing in the canopy of old-growth redwood forest. Herpetological Conservation and Biology 1:16–26.

Stebbins, R.C. 2003. A Field Guide to Western Reptiles and Amphibians. 3rd Edition. Houghton Mifflin Company, Boston, Massachusetts, USA.

Van Denburgh, J. 1916. Four species of salamanders new to the state of California, with a description of *Plethodon elongatus*, a new species, and notes on other salamanders. Proceedings of the California Academy of Sciences, 4th Series 6:215–221.

Wake, D.B. 1965. *Aneides ferreus*. Pp. 16.1–16.2 *In* Catalogue of American Amphibians and Reptiles. Riemer, W.J. (Ed.). American Society of Ichthyologists and Herpetologists, Kensington, Maryland, USA.

Welsh, H.H., Jr., and R.A. Wilson. 1995. *Aneides ferreus* (Clouded Salamander) reproduction. Herpetological Review 26:196–197.

Whitaker, J.O., C. Maser, R.M. Storm, and J.J. Beatty. 1986. Food habits of Clouded Salamanders (*Aneides ferreus*) in Curry County, Oregon. The Great Basin Naturalist 46:228–240.

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