# A Mark-Recapture Study of the Wandering Salamander, *Aneides vagrans*, in a Redwood Rain Forest Canopy

by

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A Thesis

Presented to

The Faculty of Humboldt State University

In Partial Fulfillment of the Requirements for the Degree

Master of the Arts in Biology

December 2004

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We certify that we have read this study and that it conforms to acceptable standards of scholarly presentation and is fully acceptable, in scope and quality, as a thesis for the degree of Master of Arts.

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# ABSTRACT

## A Mark-Recapture Study of the Wandering Salamander, *Aneides vagrans*, in a Redwood Rain Forest Canopy

James C. Spickler

I investigated seasonal activity, movement patterns, and habitat use of the wandering salamander, *Aneides vagrans*, in an old-growth forest canopy. During the fall and winter months from September 2000 to January 2003, a mark–recapture study of salamanders was conducted in the crowns of five large redwoods (*Sequoia sempervirens*) in Prairie Creek Redwoods State Park, Humboldt County, California. This represents a first attempt to describe the arboreal behavior of *A. vagrans*. A cover object approach limited damage to fragile canopy habitats. Litter bags were placed on 65 randomly selected fern mats, covering 10% of the total surface area of epiphytic fern (*Polypodium scouleri*) mats in each tree. Crack boards were also placed on one fern mat in each of two trees. These cover objects were then checked 2-4 times per month during the field season. Captured salamanders were marked by injecting tags near the base of the tail. A total of 52 captures were made of 40 individuals, including 15 recaptures. One salamander was captured on 4 occasions over the 3-year study period. Only one recaptured salamander moved (vertically 7 m) from its original point of capture. There was no evidence of territorial behavior by *A. vagrans* in the canopy. Salamander captures were compared to tree-level and fern mat-level variables with correlation analysis and stepwise regression. At the tree-level, the best predictor of salamander abundance was the total mass of fern mats in crotches. At the fern mat-level, the presence of crack boards accounted for 85% of the variability observed in captures, while the mass and height of the fern mat accounted for the remaining 6% explained by the model. Population estimates were made by applying the Lincoln-Peterson method to the capture data. This analysis revealed that individual redwoods can support at least 28 individual salamanders associated with fern mats. By virtue of their high water-holding capacities, large fern mats likely enable year-round occupation of the redwood forest canopy by *A. vagrans.* Anecdotal observations of *A. vagrans* and its close relative *A. ferreus* by scientists and forest activists strongly suggest that these salamanders also occupy additional habitats in forest canopies, especially rotting wood and fire cavities.

# ACKNOWLEDGMENTS

First and foremost I would like to thank members of my graduate committee for their support during this project. I thank Dr. Hartwell Welsh, Dr. Steve Sillett, and Dr. Sharyn Marks for securing research funding (USDA Forest Service in-house grant administered by Redwood Sciences Laboratory, USDA-FS), and for their time spent during the editing of this manuscript. I thank Dr. Steve Sillett and Dr. Michael Camann for their advice and assistance with the statistical analysis. I thank Dr. Scott Sillett for his help with the population estimation models used during our research. I would also like to thank Dr. Steve Sillett and Dr. Robert Van Pelt for the countless hours spent developing tree modeling techniques used to describe the incredible architectural complexities of ancient redwoods included in this study.

I thank the staff of Prairie Creek Redwood State Park for allowing us to conduct research in one of the most beautiful redwood forests on the planet. I thank Anthony Baker and Garth Hodgson for their support and assistance in obtaining research equipment. I would also like to thank John Christenson (Sandpiper Technologies, Manteca, CA) for his design expertise, and for developing monitoring equipment specifically for this project. I thank Dr. Sharyn Marks for providing lab space and equipment essential for developing our marking technique. I would also like to thank Jason Lowe and Andrea Herman for their insight and training in the use of injectable tags for marking salamanders.

I would also like to thank the many additional people that contributed to the success of this study. "Remedy" provided excellent observations of arboreal *Aneides*

*vagrans* while staging a year long tree sit to protest the logging of the mature redwoods. Dr. Steve Sillett, and Nolan Bowman of Eco-Ascension Research and Consulting, provided anecdotal observations of arboreal *Aneides ferreus* located in Douglas-fir forest in Oregon. I also want to thank many of my fellow graduate students and friends who assisted with field work and provided several anecdotal observations made during their own research endeavors, including: William Ellyson, Mark Bailey, Clint Jones, Anthony Ambrose, Brett Lovelace, Marie Antoine, Nolan Bowman, and Cameron Williams. Cameron deserves special thanks for all of his hard work as my field assistant. In spite of a hectic school schedule, and while developing his own graduate research, he faithfully conducted tree top salamander surveys. His enthusiasm and dedication to this project were invaluable. I also thank Nolan Bowman for all of his assistance with the business of Eco-Ascension Research and Consulting. His hard work made finishing this project a possibility in spite of my many other professional obligations.

Finally, I am grateful to my friends and family for their encouragement and support throughout this study. Last, but not least, I thank the *A. vagrans* in our study for sharing the wonder of their arboreal world.

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# INTRODUCTION

Forests dominated by *Sequoia sempervirens* (D. Don) Endl. (hereafter 'redwood') are the most massive on Earth. Redwoods growing on the wettest, most productive sites (i.e., alluvial terraces) can have a stand-level wood volume up to 10,000 $m^3$ $ha^{-1}$ and a biomass over 3000 tons $ha^{-1}$ (Sawyer et al. 1999). Individuals can exceed 112 m in height, 7 m in diameter, and have wood volumes greater than 1,000 $m^3$. These large redwoods are also some of the oldest and most complex trees on the planet. Many live to over 2000 years, and develop highly individualized crowns shaped by natural disturbances (Van Pelt 2001).

Disturbances (e.g., the falling of neighboring trees, broken leaders and branches, crown fires from lighting strikes) that increase light availability, or cause damage directly to the tree surfaces, often result in new growth from affected trunks and branches. In redwood, this new growth can be in the form of either plagiotropic branches or orthotropic trunks (hereafter 'reiterations'), each with its own set of branches (Sillett 1999). Reiterations can originate from other trunks, or from branches. When reiterations originate from a branch, the branch thickens in response to the added weight of the reiteration, creating a "limb." Large reiterations can support other reiterations, and their trunks and branches often become fused with each other as well as the main trunk (Sillett and Van Pelt 2001). The highly individualized crowns of complex redwoods offer a myriad of substrate and habitats for epiphytes and other arboreal organisms (Sillett and Bailey 2003).

Crown-level complexity in redwoods promotes accumulation of organic material, including epiphytes, on tree surfaces (Sillett and Bailey 2003). Crotches between the trunks, the upper surfaces of limbs and branches, and the top of snapped trunks provide platforms for debris accumulation. Vertical and horizontal sections of dead and rotting wood also provide materials and substrate for accumulations. Over time, this debris develops into canopy soil as organic materials decompose into humus, which provides a rooting medium for vascular plants. Eighteen species of vascular plants, including a spike moss, five ferns, five shrubs, and seven trees have been found growing epiphytically on canopy soils and rotting wood in redwoods (Sillett 1999, updated in 2003 by Sillett pers. obs.). The most abundant vascular epiphyte in redwood rain forests is the evergreen fern, *Polypodium scouleri* Hook. & Grev. (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). Large fern mats also tend to be internally complex, having tunnels and cavities between the rhizomes and dense roots, and interstitial space around embedded sticks (pers. obs.).

Another desiccation-sensitive species residing in the canopy of old-growth redwood forests is the wandering salamander (*Aneides vagrans*), a terrestrial amphibian belonging to the family Plethodontidae. Plethodontids are unique in that they are the only salamanders to have invaded the tropics, where many utilize arboreal habitats

(Lynch and Wake 1996). In spite of the high number of species that display arboreal reproduction in tropical forests, little is known about this phenomena beyond a few anecdotal accounts (e.g., Good and Wake 1993, McCranie and Wilson 1993). The first evidence that *A. vagrans* exists in forest canopies of northwestern California was the discovery of a clutch of eggs (later hatched and identified to be *A. vagrans*) found inside a *P. scouleri* fern mat that had been dislodged from the crown of a redwood being felled for lumber (Welsh and Wilson 1995). It was not until several years later that *A. vagrans* was observed directly in arboreal habitats in these forests (Sillett 1999).

Scientific investigations of old-growth redwood forest canopies began in 1996 when S. C. Sillett began his professorship at Humboldt State University. The canopies of these forests had been unexplored except for a single, unpublished, ground-based study (Mulder and De Waart 1984). The immense height, complexity, and massiveness of the largest redwoods made access with traditional tree-climbing methods ineffective for research purposes. Climbers could access tall trees with these techniques, but the lateral movement required to fully explore arboreal habitats within large redwood crowns was still a challenge. Using arborist-style techniques and several new inventions, Sillett and his students began the botanical exploration of the world's tallest forest canopy (Sillett 1999). Several *A. vagrans* were observed during these initial studies. With one exception, all observations were made of individual and paired salamanders occupying tunnels and cavities in large fern mats. The one exception was, in fact, the very first direct observation by a researcher (Sillett) of an *A. vagrans* in the redwood canopy: a mummified adult found in a shallow trunk cavity located 88 m above the ground in a tree called Atlas. Prolonged and repeated access to redwood forest canopies is now a routine component of Sillett's research team at Humboldt State University, and incidental observations of arboreal *A. vagrans* continue to be made. This study focuses on wandering salamanders inhabiting a redwood rain forest canopy in Prairie Creek Redwoods State Park, Humboldt County, California, including several trees whose crowns have been explored by scientists since the late 1990s.

*Aneides vagrans* is a medium-sized salamander (mean snout-vent length 80 mm) that has 14-16 costal grooves along the body. Color variation between populations is common, but adults tend to be dark colored (brown, gray, or black), and have an irregular dorsal mottling of a lighter, golden-green color (Stebbins 2003; Davis 1991). Breeding occurs in the spring, and clutch sizes are between 6-9 (Welsh and Wilson 1995; Davis 1991). Wandering salamander have prehensile tails that are used to assist in climbing vertical surfaces (Petranka 1998; Spickler pers. obs.; Sillett pers. obs.). They also possess long limbs with slender digits bearing sub-terminal toe pads (Petranka 1998). *Aneides vagrans* has been described as a primarily terrestrial salamander that is occasionally found in trees and 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). Wandering salamanders occur 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 species' range in northern California extends from northern Siskiyou and Del Norte Counties south through western Trinity, Humboldt, and Mendocino Counties, and also into northwest Sonoma County (Stebbins 2003; Jackman 1998). During the initiation of our research, genetic evidence published by Jackman (1998) proposed that the clouded salamander (*Aneides ferreus*) be split into two separate species, thus creating a new species classification for the wandering salamander (*Aneides vagrans).* *Aneides vagrans* is now considered a sibling species to *A. ferreus*, which occurs primarily in western Oregon (Jackman 1998; Davis 2002a).

Like all other plethodontid salamanders, *A. vagrans* is lungless and respires exclusively through its skin and buccopharyx. 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 that 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 (e.g., Thorson 1955; Shoemaker et al. 1992; Cunningham 1969; Ovaska 1988; Cree 1989). This desiccation avoidance behavior is observed in terrestrial *A. vagrans* (Davis 2002b).

Although thought to be primarily terrestrial, *Aneides vagrans* has been described as the most arboreal of all salamanders in North America (Petranka 1998), but until this study, anecdotal observations were the only means by which to qualify this assertion. This study is thus the first attempt to describe what might be called "extreme" arboreal behavior of this species. The presence of wandering salamanders in the redwood forest canopy demonstrates that arboreal individuals are having their hydric requirements met within the tree crown. Prior to this study, observations of living *A. vagrans* in the redwood canopy were limited to fern mats, and the extent to which other potential habitats were being utilized was unclear. In order to acquire information on the ecology of arboreal *A. vagrans*, we investigated seasonal activity, movement patterns, and habitat use in the redwood canopy. As the first study of its kind, this required the development of techniques suitable for searching canopy habitats with minimal disturbance to substrates, capturing salamanders, and identifying individuals. We used a mark-recapture approach with visual encounter surveys (VES) and cover objects to estimate the size of within-tree populations and document movement patterns within and between tree crowns. We also correlated capture rates with fern mat and tree structure variables to assess their potential effects on *A. vagrans* numbers. We also examined anecdotal observations, from other scientists and forest activists, of *A. vagrans* in canopy habitats during seasons that we could not monitor our study trees directly.

# METHODS

## Study Area and Site Description

We studied *A. vagrans* populations in five redwood trees located in Prairie Creek Redwoods State Park (PCRSP), Humboldt County, California within an old-growth redwood forest near Boyes Creek. Annual rainfall in PCRSP is approximately 1.7 m, with summer temperatures ranging from 4° to 29° C and winter temperatures ranging from -1° to 16°C (based on data from 1971-2000; http://www.redwood.national-park.com/weather). Trees were selected from within a 1-hectare permanent reference stand (Figure 1) that is approximately 100m elevation and 7 km from the Pacific Ocean. Within the reference stand, redwood accounts for 93.7% of the trunk basal area (Sillett and Bailey 2003) with the remainder consisting of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), hemlock (*Tsuga heterophylla* (Raf.) Sarg.), Port Orford cedar (*Chamaecyparis lawsoniana* (A. Murr.) Parl.), cascara (*Rhamnus purshiana* DC.), big-leaf maple (*Acer macrophyllum* Pursh.), and California bay laurel (*Umbelluria californica* Nutt.). Understory vegetation is dominated by sword fern (*Polysticum munitum* (kauf.) Presl.), huckleberry (*Vaccinium ovatum* Pursh.), and redwood sorrel (*Oxalis oregano* Nutt.).

Study trees were not selected randomly; instead, we selected trees on the basis of size, structural complexity, and epiphyte abundance. Study trees 1 (hereafter 'Kronos') and 2 (hereafter 'Rhea') have interdigitating sections of their crowns, where fern-covered branches and limbs allow the possibility of salamanders moving from tree-to-tree without going to the ground. Tree 3 (hereafter 'Demeter') stands 16 m from Kronos

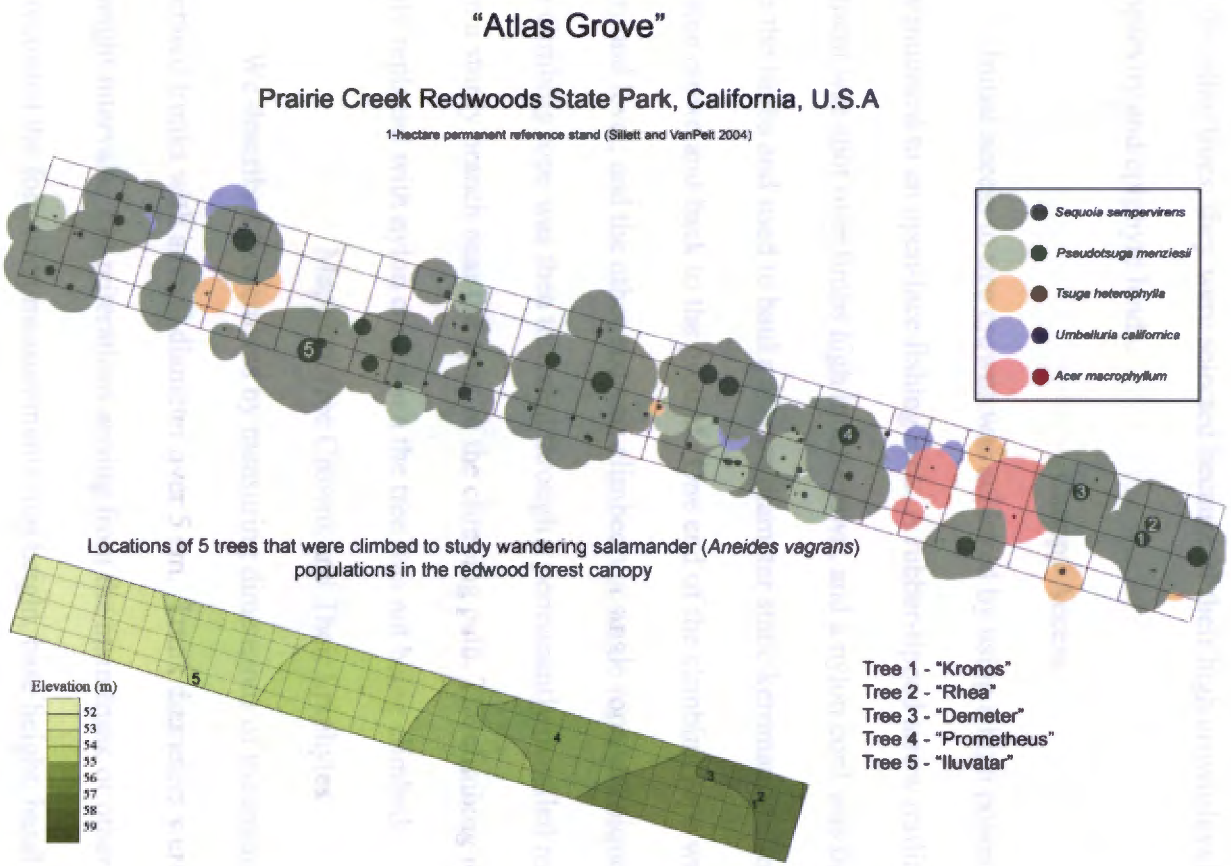

Figure 1. Stand map showing the locations of the 5 redwood trees surveyed in this study. Trees are located in "Atlas Grove," a 1-hectare permanent reference stand established by Sillett and VanPelt 2004. Grid lines are in 10-m increments. Legend describes the different species trunks (small circle) and crowns (larger circle) by color.

and Rhea. Its crown does not interact with these trees, but its location near them could have permitted tree-to-tree movement if a salamander first went to the ground. Trees 4 (hereafter ‘Prometheus’) and 5 (hereafter ‘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.

## Canopy Access

Initial access to tree crowns was achieved by using a high powered compound bow mounted to an open-face fishing reel. A rubber-tipped arrow trailing fishing filament was shot over limbs high in the crown, and a nylon cord was then reeled back over the limbs and used to haul a 10 mm diameter static kernmantle climbing rope into the tree 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 (Jepson 2000). The climbing rope was then threaded through a permanently installed rope pulley hung from a sturdy branch near the apex of the climbing path. The climbing rope could then be easily replaced with nylon cord when the tree was not being climbed.

## Mapping Tree Crowns and Their Epiphytes

We described tree crowns by measuring dimensions of the main trunk and all reiterated trunks with a basal diameter over 5 cm. Trunk diameters were measured at 5 m height intervals. For reiterations arising from the main trunk or other reiterated trunks, we recorded the following measurements: top height, base height, basal diameter, and distance and azimuth (i.e., compass direction) of base and top from center of main trunk. For reiterations 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.

Three structural variables and 3 fern/humus mat variables were derived from the mapping data, including total fern/humus mass (kg), fern/humus mass in crotches, proportion of fern/humus mass in crotches, main trunk volume ($m^3$), reiteration volume, and limb volume. Volumes of main trunks, reiterations, and limbs were estimated by applying the equation for a regular conical frustum (i.e., volume= length x $\pi/3$ x (lower radius$^2$ + lower radius x upper radius + upper radius$^2$) to the diameter data (Table 1).

Table 1. Details of crown structure and fern/humus mats for the 5 redwoods included in this study.

| Study Tree | Total fern/humus mass (kg) | Fern/humus mass in crotches (kg) | Proportion of fern/humus mass in crotches (kg) | Main Trunk Volume ($m^3$) | Reiteration volume ($m^3$) | Limb volume ($m^3$) |
|---|---|---|---|---|---|---|
| Rhea | 229 | 13 | .059 | 359.3 | 1.2 | 1.5 |
| Kronos | 177 | 1 | .007 | 335.4 | 30.5 | 14.5 |
| Demeter | 51 | 19 | .364 | 389.7 | 20.2 | 6.4 |
| Prometheus | 305 | 250 | .820 | 598.5 | 63.1 | 3.2 |
| Iluvatar | 131 | 18 | .138 | 874.0 | 162.5 | 24.6 |

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, number of live fronds, average soil depth (calculated from multiple measurements with a metal probe), length of longest frond, and maximum number of pinnae per frond. We calculated surface areas of fern and humus mats by applying the equation for an ellipse: area = $\pi$ x 0.5(mat length) x 0.5(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: total mass (kg) = 0.0326 x volume ($cm^3$) + 33.9 x maximum frond length (cm) – 372 (Sillett and Bailey 2003, Table 1).

To better visualize individual tree crown complexity, we generated rotatable 3-dimensional models of tree crowns using Microsoft Excel and the crown structure data (Figure 2). Also, locations of fern mats and salamander captures were overlain on the crown models via their XYZ coordinates. We used this information to quantify movements of salamanders captured more than once during the study.

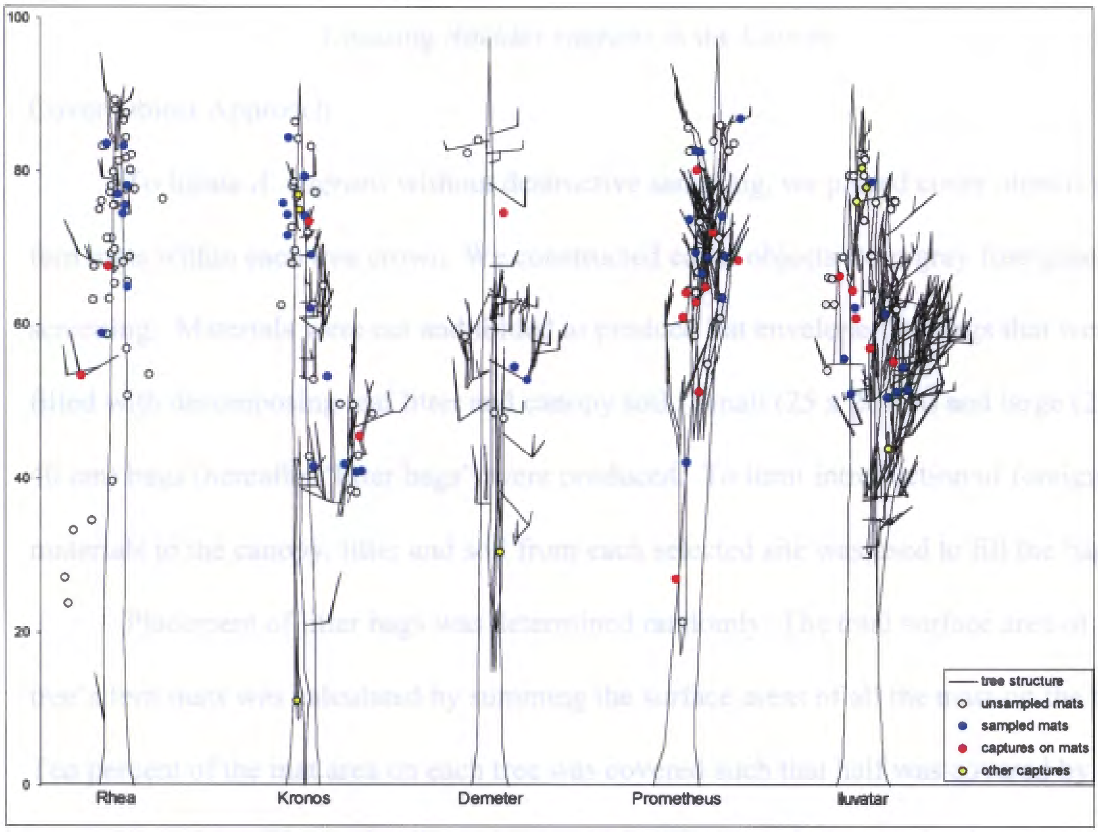

Figure 2. A 2-dimensional display (view angle= 120°) of the 3-dimensional crown structure of the 5 redwoods surveyed in this study. Main trunks, reiterated trunks, and limbs are indicated by thin, black lines. No branches are shown. Locations of fern mats and salamander captures are shown according to the legend. Note that "floating" symbols indicate locations on branches. "Sampled mats" are fern mats that were selected for placement of artificial cover objects. This procedure is described below in the section "Locating *Aneides vagrans* in the Canopy". Units are in meters.

## Locating *Aneides vagrans* in the Canopy

### Cover Object Approach

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. Materials were cut and folded to produce flat envelope-like bags that were filled with decomposing leaf litter and canopy soil. Small (25 x 20 cm) and large (25 x 40 cm) bags (hereafter 'litter bags') were produced. To limit introduction of foreign materials to the canopy, litter and soil from each selected site was 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, did not receive any litter bags. 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. Wood "squares" were placed underneath each litter bag, and directly on the fern mat surface, to maintain an adequate crawl space for salamanders under the litter bags. Each square was constructed from four 12-cm-length, 1-cm-thick strips of wood woven together in a lattice like fashion, and secured together with a staple gun.

On two of the larger mats in Iluvatar and Prometheus, we deployed "crack board" cover objects in addition to litter bags. Crack boards were crafted from a pair of 2-cm-thick boards cut into 25 x 25 cm sections. Boards were placed together but separated by parallel 1-cm-thick strips of wood. These "spacers" created room between the boards for salamanders to occupy. The crack-board-style cover object was our original design for this study, but we greatly limited its use for fear of causing injury to climbers and tourists visiting the grove if the boards happened to fall from the trees, and most of them were removed during the installation of the litter bags. When we removed these crack boards, we were uncertain of their effectiveness. For curiosity's sake, however, we left two crack boards on a large mat in Prometheus and one crack board on a large mat in Iluvatar. These locations seemed stable enough to prevent loss of the boards during storms. As an extra precaution we also equipped these crack boards with small lengths of cord tied off to the tree.

Summer and spring observations were not possible in PCRSP due to climbing regulations in place to protect the nesting habitat of the marbled murrelet (*Brachyramphus marmoratus*) and northern spotted owl (*Strix occidentalis caurina*), both Federally listed under the Endangered Species Act as "threatened." Consequently, our field season was limited to the fall and winter, beginning late-September and continuing until the end of January during the three field seasons from 2000 to 2002. Cover objects were checked 2-4 times per month, weather permitting. In addition, we made weekly checks of litter bags and crack boards in Prometheus during the 2002-2003 field season. We also made one visit to Iluvatar during this time (Table 2). During each visit, all cover objects were checked. A description of salamander activity (e.g., walking on surface or resting under cover object) and the time and location of capture were recorded.

### Fiber-Optic Probe

On six occasions during the 2000-2001 field season, we attempted to locate *A. vagrans* in canopy habitats other than fern mats. Searches were conducted in the daylight following rain storms. We used an 8 cm diameter, 61 cm long fiberoptic gooseneck video probe (Sandpiper Technologies, Manteca, CA) to explore cavities and sections of dead wood in the tree crowns. The probe's infrared capability allowed us to search dark cracks and crevices otherwise impossible to search by hand. The probe provided video images received through special goggles worn by the operator. The "virtual reality" image made guiding the probe possible, while a digital 8mm recording device could be used to document the search.

### Hand Searching

On five occasions (3 nocturnal, 2 diurnal) following rain storms during the 2000-2001 field season, we performed visual encounter surveys (VES) to locate *A. vagrans* in tree crowns. Such surveys use time as a common denominator to allow comparison of captures per unit effort among sampling intervals (Crump and Scott 1994). Prior to a VES, a climber reached the treetop and started rappelling. At that point the timed search began and included hand searching as many potential salamander habitats as possible

Table 2. Search effort and number of *Aneides vagrans* captured in the crowns of 5 redwoods from September 2000 to January 2003. "Total captures" includes the "recaptures" value for that year.

| Year 1<br>(September 2000 – March 2001<br>First marking period) | Tree | Number of searches | Year 1 captures (# recaptures) |
|---|---|---|---|
| | Demeter | 15 | 3 (0) |
| | Rhea | 15 | 1 (0) |
| | Kronos | 15 | 4 (0) |
| | Iluvatar | 15 | 4 (0) |
| | Prometheus | 15 | 3 (0) |
| | | | Total 15(0) |

| Year 2<br>(September 2001 – January 2002<br>Second marking period &<br>First recapture period) | Tree | Number of searches | Year 2 captures (# recaptures) |
|---|---|---|---|
| | Demeter | 12 | 0 (0) |
| | Rhea | 12 | 1 (0) |
| | Kronos | 12 | 3 (1) |
| | Iluvatar | 12 | 6 (3) |
| | Prometheus | 12 | 15 (6) |
| | | | Total 25(10) |

| Year 3<br>(November 2002 – January 2003<br>Third marking period &<br>Second recapture period) | Tree | Number of searches | Year 3 captures (# recaptures) |
|---|---|---|---|
| | Iluvatar | 1 | 2 (0) |
| | Prometheus | 6 | 10 (4) |
| | | | Total 12(4) |

| Years 1-3 total # of captures (# recaptures) |
|---|
| 52 (14) |

along the rappelling path. The timed search ended when the climber reached the ground.

### Marking *Aneides vagrans*

Captured *A. vagrans* were taken to the ground and given a permanent and unique identifying mark. We used 1 x 2 mm fluorescent alpha-numeric tags (Northwest Marine

Technologies, Inc., Seattle, WA) that were injected subcutaneously on the ventral side of the tail immediately posterior to the vent. Photographs of dorsal patterning were taken for smaller salamanders that could not be tagged easily with the injector (i.e., the base of the tail was too small for the width of the injector). Marked animals were then returned to their point of capture (i.e., sampling with replacement).

We anesthetized *A. vagrans* prior to injection of the tags using a pH neutral solution of MS-222 (3-aminobenzoic acid ethyl ester; Sigma Chemical Company, St. Louis, Missouri, catalog #A-5040). Neutral pH was achieved by combining 1.0 g MS-222 + 2.4 g sodium bicarbonate dissolved in 500 ml of distilled water. Salamanders were submerged in the solution until they became completely immobile. This level of anesthetization generally took 2-5 min and was attained when the salamander could be rolled onto its back without making an attempt to right itself. This degree of immobilization lasted 5-10 min, during which time we made the following measurements: snout to vent length (i.e., from tip of snout to anterior margin of vent), total length (i.e., tip of snout to tip of tail), 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 descriptions and pictures of injuries or other identifying marks. The entire procedure took 2-3 min to complete, at which time the salamander would be placed in distilled water until fully recovered from the effects of the MS-222. The same data were collected for salamanders that were re-captured later in the study; in all cases salamanders were anesthetized prior to re-measurement.

## Data Analyses

We used stepwise multiple regression analysis to evaluate potential effects of individual fern mat characteristics on salamander abundance in those mats with cover objects (n =65). The following independent variables were included: percentage of fern mat surface covered by bags, total area covered by bags, fern mat mass, surface area, and height. The number of crack boards on each mat (i.e., 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 captures per mat.

Potential effects of fern/humus mats and tree structure on *A. vagrans* abundance were evaluated using correlation analysis. Tree-level independent variables included total fern/humus mass (kg), mass of fern/humus in crotches, and the proportion of total mass in crotches. Tree structure variables included main trunk volume ($m^3$), reiteration volume, and limb volume. The dependent variable was the number of marked animals per tree. We corrected for sampling effort by dividing the lowest number of visitations per tree (27) by the highest number of visitations per tree (up to 33). We eliminated the potentially confounding effects of crack boards by removing those 2 mats from the data set (i.e., mat #18 in Iluvatar and mat #44 in Prometheus) prior to the analysis.

*A. vagrans* abundance was estimated with the Lincoln-Petersen method. We used the unbiased estimator for population size ($N$):

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

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 there are short-comings with 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 a first approximation of salamander numbers a particular habitat type (i.e., fern mats and humus accumulations).

## Anecdotal Observations

The inaccessibility of study trees during the spring and summer greatly limited our observations of *A. vagrans* behavior and activity patterns. Fortunately, several interesting observations were made by forest activists participating in "tree sits" and by scientists working in the canopy on research unrelated to this study; locations are described in figure 3. A review of these observations is given in the results section under the subheading "Restricted Season and Incidental Observations".

Figure 2. Location of study site in Prairie Creek Redwoods State Park represented by red circle 1. Location of anecdotal observations represented by black circles 2 thru 8.

# RESULTS

Diurnal and nocturnal VES were quickly abandoned during our study. We determined that hand searching canopy habitats was destructive and altered substrates too much to be used for a long-term study. Soil and debris often fell from the fern mats during searching, and searching under bark flakes often required pulling the flake off of the tree, thus destroying potential habitat for other salamanders. Visual encounter surveys at night were also destructive and impractical. Attempting to find a salamander on a fern mat or other substrate was made nearly impossible due to the shadows produced by head lamps and the fern fronds; shadows cast by fern fronds and small branches would give the appearance that the substrate underneath these objects was moving. The fiber-optic gooseneck video probe also was not effective for locating salamanders during our study. The complexity and depth of many of the hollows and cavities in the tree usually made guiding the probe impossible. Attempts to search inside of fern mats with the probe also were thwarted when organic material would block the lens of the fiber optic camera, requiring it to be removed and cleaned.

During a diurnal VES in Iluvatar, however, we located the remains of a single adult size *A. vagrans* in a shallow trunk cavity. Much like Dr. Sillett's first observation of *A. vagrans* in the redwood canopy, this mummified individual was found in an exposed location above 80 m.

## Effect of Fern Mat Characteristics on *A. vagrans* Captures

The effects of fern mat characteristics on the number of *A. vagrans* captures and recaptures were evaluated separately for a total of 65 fern mats (i.e., only those with cover objects) in 5 trees. Total number of *A. vagrans* captured, including recaptures, was positively correlated with number of crack boards ($R^2 = 0.85$, $P < 0.0001$), area covered by litterbags ($R^2 = 0.38$, $P < 0.0001$), fern mat mass ($R^2 = 0.28$, $P < 0.0001$), and fern mat area ($R^2 = 0.22$, $P < 0.0001$). No correlations 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 crack 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 $R^2 = 0.91$, $P < 0.03$) were all correlated with number of captures.

The strongest variable affecting the number of *A. vagrans* captured was not a physical characteristic of the fern mats at all. It was merely an artifact of our sampling technique. More salamanders were captured on fern mats with crack boards than on mats with only litter bags; in fact, this variable accounted for over 85% of the variation in number of captures. In Prometheus, the total number of captures on one fern mat (#44) was 15, representing 5 individuals. All of the captures were made in the 2 crack boards present at the site in spite of the fact that this fern mat also had 8 litter bags, all within close proximity to the crack boards (Figure 4). Nine of the 15 captures were recaptures, including 4 of salamander X70 (see Appendix). This was a large male who had apparently taken up residence in an area that included both of the crack 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 (i.e., P09, P18, and P16). On fern mat #18 in Iluvatar, there was a total of 9 captures representing 7 individuals.

Figure 4. Canopy researcher searching crack boards and litter bags on fern mat #44 in study tree # 4 (Prometheus).

Seven of these were made in a crack board, while the remaining two were made under a litter bag located 0.75 m away.

### Tree-level Effects of Ferns/Humus on *A. vagrans*

At the tree-level, we explored relationships among 3 fern/humus variables (i.e., total mass, crotch mass, proportion of total mass in crotches), 3 structure variables (i.e., main trunk volume, reiteration volume, limb volume), and the number of marked salamanders per tree. The best predictor of salamander abundance at the tree level was crotch mass ($r = 0.79$, $P = 0.11$), followed by proportion of mass in crotches ($r = 0.64$, $P$

= 0.24), total mass ($r = 0.58$, $P = 0.31$), main trunk volume ($r = 0.45$, $P = 0.44$), reiteration volume ($r = 0.44$, $P = 0.46$), and limb volume ($r = 0.16$, $P = 0.79$). Small sample size (n = 5 trees) prohibited further analysis of tree-level effects.

### Lincoln-Petersen Population Estimations

During our study a total of 52 salamander captures were made, including 14 recaptures. Salamanders were found in all 5 study trees, with the most captures in Prometheus (28), and the least in Rhea (2). Small sample sizes forced us to use entire field seasons as sampling intervals (Table 2). Thus, *A. vagrans* abundance was estimated once for three trees (Prometheus, Iluvatar, and Kronos) in January 2002 for animals marked in the first field season and marked or recaptured in the second field season, 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. There were insufficient data to make any tree-level population estimates for two of the trees (Demeter and Rhea). However, we combined data from the five trees to calculate a crude estimate for these trees collectively in January 2002, based on animals marked in the first field season and marked or recaptured in the second field season (Table 3). Number of visits, along with capture and re-capture data for each field season are summarized in Table 2.

### Movement of Previously Captured *A. vagrans*

Evidence of between-tree movement of marked salamanders, via interacting crowns or the ground, was not observed during our study. In fact, we obtained no evidence that *A. vagrans* return to forest floor habitat at any time during the year. Based on our study and anecdotal observations made outside or our field season (see below), it appears that *A. vagrans* occupy forest canopy habitat year-round. Individuals appeared to move only short distances, or not at all. Of the 14 recaptures made during our study, 13 were of individuals found in the same locations as their initial captures. The only 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.

Table 3. Estimated sizes of *Aneides vagrans* populations in 3 individual trees and 5 trees combined for 2002, and 2 individual trees for 2003, using the Lincoln-Petersen mark-recapture method. Estimates are only for the portion of the population using fern mats.

| | Salamander Abundance | |
|---|---|---|
| Tree | January 2002 | January 2003 |
| Prometheus | 8 | 28 |
| Iluvatar | 9 | 18 |
| Kronos | 6 | - |
| Five Trees Combined | 50 | - |

## Restricted Season and Incidental Observations

Restricted canopy access during spring and summer greatly limited our arboreal observations of *A. vagrans* during these periods. The few observations that have been made during these times were incidental and often made while canopy researchers were conducting surveys for organisms that the restrictions were designed to protect (e.g., marbled murrelet and spotted owl). In addition, salamander observations were made by non-scientists occupying trees illegally. It is understandable that the protection of these "listed" 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 leaves 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.

### Activist "Tree Sitters" in Northern California

The willingness of tree sitters to disregard the law, and their resolve to stay aloft for extended periods, often enables them to make observations that scientists working under research permits cannot. In the spring of 2002, an activist named "Remedy" began a tree sit on Pacific Lumber Company private lands. Remedy, along with other activists, established sleeping platforms in several large redwoods near Freshwater, Humboldt County, California in hopes of saving a mature forest from logging. She succeeded in staying aloft for nearly a year before being forcibly removed and arrested for trespassing. In that period she made observations of a pair of wandering salamanders that shared her arboreal home.

On seven separate 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 platform. The original leader of the tree had failed at an approximate height of 40 m; Remedy's 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 formed around the break created the cavity that the salamanders occupied. Interestingly, 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 she described their behavior as "moving independently as if unaware of each other." She explained that most of the salamander activity was limited to the area on and around the fern mat, but on two occasions she saw a salamander moving out along branches and continuing to the outer crown where she could no longer see it. All of Remedy's observations were made during early evening and under similar microclimatic conditions: dry substrate with elevated air humidity. She described the conditions as "warm and muggy, perfect weather for flying insects." Her impression was that the salamanders were more affected by temperature than by moisture; she never observed animals moving during the rain or immediately thereafter. She also noted that there was limited flying insect activity during and immediately after rain storms. Her 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 Remedy believes that the evenings became too "cold" for foraging.

The most notable *A. vagrans* observation that Remedy made during her tree-sit is the only documented observation of an *A. vagrans* predating an insect while in the canopy. She described how the salamanders would often move a short distance, stop and wait for a period, and then continue moving. One evening, Remedy observed 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 predated without hesitation. After a moment, the salamander continued moving along the branch to the outer crown.

Remedy also described similar observations that were made by another activist 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 02 February 2003 he observed a pair of *A. vagrans* come on to his platform "in search of food." He watched them for several minutes before they continued off into the darkness.

### Summer observations in Humboldt Redwoods State Park, California

On 17 September 2002, an *A. vagrans* observation was made by biologists Dr. Steve Sillett and HSU graduate student Anthony Ambrose while crown-mapping a large redwood in Humboldt Redwoods State Park. The observation was made at 0800 hrs during warm conditions with high air humidity and low cloud cover; the tree's bark was completely dry. A single adult *A. vagrans* was observed moving vertically along the trunk at a height of 93 m. The salamander's path was completely exposed with no canopy soil or cavities nearby. Sillett recorded the salamander crawling up the trunk via a digital video recorder (See attached CD for video file "ANVA footage") until it disappeared from view, having traveled several m vertically. The nearest area in which this *A. vagrans* could have found cover was in a cavity of rotten wood located 100.6 m above the ground, but even this site was very exposed and dry.

## Arboreal Observations of Clouded Salamanders (*Aneides ferreus*) in Coastal Oregon

Since there have been so few descriptions of the arboreal behavior of any salamander species, incidental observations of *A. ferreus* are summarized here to offer potential insights into the arboreal behavior of this very close relative of *A. vagrans*. On three separate occasions in 2002, biologists (Spickler and Bowman of Eco-Ascension Research and Consulting) observed adult *A. ferreus* while studying the nesting behavior of the red-tree vole *Arborimus pomo* in the old-growth Douglas-fir forest canopy of coastal Oregon (BLM forest lands, Salem and Eugene Districts). Observations were made in the summer (July-August) during periods with high humidity and on moist substrates. Observations were made midday, and 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, Steve 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 the moss *Antitrichia curtipendula* on a large branch approximately 30 m above the ground. After he disturbed it, 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

## Techniques for Locating and Capturing Arboreal Salamanders

One of the most challenging aspects of our study was locating *A. vagrans* in the canopy while limiting impact to fragile fern mat habitats. Climbing directly on fern mats was not an option since a careless boot placement, or even slight contact with a climbing rope, almost always caused compaction or the loss of organic material. In a study designed to monitor a population over time, and one that requires several visits to a site over several years, the cumulative effects of such damage would be substantial. Other habitats were also difficult to search directly in a non-destructive fashion. Even if one were able to locate *A. vagrans* in crevices, capturing the salamander without permanently altering the substrate was nigh impossible. We found that creating artificial cover objects (i.e., litter bags and crack boards) and then monitoring them for use by *A. vagrans* was the most effective way to capture salamanders while limiting impact on canopy surfaces.

Artificial cover objects are commonly employed in mark-recapture studies of terrestrial salamanders (Fellers and Drost 1994; Droege et al. 1997). Until our study, this technique had never been used to study arboreal salamanders. Our litter bag design had two major disadvantages. Over time the litter inside of the bags decomposed, and the bags began to conform to the surface contours of the mats, eventually adhering to the substrate via fungal mycelia. This resulted in the eventual loss of the space between the litter bag and the fern mat. Our solution to this problem (i.e., placing wood "squares" under the bags) was somewhat effective, but some of the bags became entangled in mycelia nonetheless. The other disadvantage of litter bags was that their use was restricted to flat upper surfaces of fern mats; they could not be stabilized on other sloping surfaces that might be suitable for salamanders (e.g., upper sides of trunks and limbs receiving stemflow). In spite of these limitations, litter bags were easy to install, safe to use, and effective for capturing salamanders, although they were not nearly as effective as crack boards.

Our crack boards were designed to simulate preferred terrestrial habitats of *A. vagrans*: 6 mm spaces between bark and heartwood with a smooth firm surface (Stebbins 2003; Davis 1991). Although *Aneides vagrans* can occasionally be found among leaf litter on the forest floor (pers. obs), this species is most commonly found under the splintered wood of recently fallen trees or its exfoliating bark (Davis 2002b; Stebbins 2003). Similar crevice structures are common in the crowns of old redwoods, but our VES and fiber optic probe approach to searching these habitats was not practical or effective. In retrospect, salamanders in wood cracks, cavities, or under bark flakes could have been captured by placing crack boards adjacent to or on these structures.

Future mark-recapture studies utilizing many crack boards in each tree may yield superior tree-level population estimates for *A. vagrans.* We suggest a modification of the crack board design in this study. Crack boards placed on fern mats are clearly effective for locating salamanders, and they can be deployed much in the same way as we did litter bags. They can also be used to sample vertically-oriented substrates, which would mimic habitats described as “crevices.” The sturdiness of the boards allows them to be mounted. By attaching the bottom board directly to the tree via stainless steel screws (to avoid oxidation and subsequent damage to the tree) or straps, and then mounting the top board to the bottom board via latches, the cover objects could be installed on just about any bark or wood surface on the tree. Capturing salamanders inside the crack boards would require that the top board be removed carefully. The space between the bottom board and the mounting surface would also provide habitat that should be checked. If a salamander were found "under" the bottom board it could be coaxed from its shelter, thus avoiding having to remove the board entirely. Prior to attempting to remove a salamander from inside or under a crack board, we recommend that a small tarp or bag be placed beneath the site to catch the salamander if it falls or attempts to jump. To increase safety when using the crack boards, we also recommend securing each board with a separate piece of cord tied to the tree. This would greatly reduce the likelihood of boards falling from the tree and striking someone below in the unlikely event that the screws, straps, or latches failed.

## Effects of Tree- and Mat-level Variables on Salamander Abundance

The results of our correlation analysis are likely spurious due to multiple co-linearity issues between variables at the tree and fern mat level. Stepwise multiple regression analysis comparing fern mats (N=65) was possible and will be addressed here, but sample size was too low to use the same analysis to compare capture rates between individual trees (n = 5). Regardless, the correlation analysis of tree-level variables suggests relationships important to the ecology of *A. vagrans* in the forest canopy.

## Fern/Humus Mats

A notable result of our mat-level analysis was the effect of crack boards on number of salamanders. Nearly half of the *A. vagrans* captured during our study were found in crack boards even though their use was quite limited. By placing crack boards on fern mats we may have created a "preferred" habitat type on top of fern mats. This assertion is supported by the observation 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 crack boards were residents of the fern mat on which the crack boards were placed, originally residing in the tunnels and other complexities of the fern mat, or if placing the crack 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.

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 feeding habits of arboreal *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 pers. comm.) 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 (*ibid.*). 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 being harvested for the development of equations to predict fern mat mass. Also, an egg cluster of *A. vagrans* was found within a *P. scouleri* mat on a freshly fallen redwood (Welsh and Wilson 1995). We know from these observations that the tunnels and spaces 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). 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 tree (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 or altogether impossible during dry periods. This idea is supported by the discovery of the two mummified individuals near the tops of two trees (see also Maiorana 1977).

### Individual Tree Effects

Our correlation analysis of tree-level effects on salamander abundance suggests that mass of epiphytic material (e.g., ferns and canopy soil) and location of this material within the crown (e.g., in crotch or on limb) are more important than crown-level complexity *per se*. A very old tree whose crown reflects the millennia in the form of limb reiterations may support far less suitable habitat for *A. vagrans* than a younger tree with more large crotches or deep cavities. Canopy soils on limbs drain faster than those in crotches (Allen et al. 2004, Ambrose 2004) and thus may become too dry for perennial occupancy by salamanders. Trees with crotches and deep rot cavities likely provide ideal arboreal habitats for *A. vagrans* in old-growth forest canopies, enabling this fascinating species to breed and live its entire life within a tree crown.

Microclimate data from fern mats show that crotches have more stable moisture and temperature regimes than branches or limbs (Ambrose 2004). Compared to those on branches or limbs, crotch mats hold more water per unit mass and store water longer (*ibid.*). Furthermore, canopy soils in crotches have higher bulk densities and lower hydraulic conductances than soils on branches or limbs (Allen et al. 2004), providing relatively stable refugia from desiccation during the dry season. It may be that these habitats are essential to the survival of arboreal *A. vagrans*. We did not measure climatic variables of fern mats in our study trees, but congruent studies have accomplished this in other trees (Ambrose 2004, Sillett unpubl.). Recent developments in wireless sensor technology (Sillett, pers. comm.) will provide opportunities to fully characterize relationships between salamanders and canopy microclimates.

## Movement and Territoriality

If a salamander finds a habitat within its home range 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 findings support these observations.

On 6 occasions we captured more then one salamander on a fern mat. Twice we found 2 males in a crack board with a single female. We also found 2 females together with no male present and 2 males together with no female present. Twice we found a pair of salamanders on the same fern mat but not within the same crack board: a male with a female and a male with another male. Males do not appear to be defending females from other males, and neither sex appears 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, it should be noted that 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.

## Population Estimations

The presence of crack boards in only two of the trees, Prometheus and Iluvatar, presents a sampling problem for population estimations. Statistically, the groups “trees with crack boards” and “trees without crack boards” should be analyzed separately, but the low capture and recapture numbers makes this impossible in our study. Therefore, our population estimations, along with the fern mat and tree-level analyses using salamander capture data, should be viewed with suspicion. Regardless, this information is interesting and likely a conservative estimate of arboreal *A. vagrans* number in each tree. A future study using crack boards exclusively, and on a variety of canopy surfaces, would provide the number of capture/recapture needed for strong population estimates. However, given the complexity of these arboreal habitats, a removal method of sampling (see Salvido 2001) would probably yield better estimates, especially if it were conducted during the warm season (see below).

## Anecdotal Observations of *Aneides* in Forest Canopies

The seasonal restrictions on canopy research in old-growth redwood forests prevent salamander sampling for much (i.e., 8 months) of the year. When considering the hydric constraints of plethodontid salamanders, it seems logical to assume that *A. vagrans* would be less active on forest canopy surfaces during the dry season. But the anecdotal observations compiled here contradict that rationale. These observations suggest that *A. vagrans* may be more active during warmer periods with no precipitation and with little or no wind. But these weather conditions are also the times when the tree sitters may have been most active, because they might spend cooler and wetter periods inside their shelters trying to escape the elements. It is possible that *A. vagrans* were still active during these times, but that this activity went undetected by the activists. Still, their observations during dry conditions are interesting and suggest the possibility that *A. vagrans* in canopy habitats can endure conditions too dry for terrestrial plethodontid salamander activity.

The details of Dr. Sillett's observation of a single *A. vagrans* moving vertically above 93 m under dry conditions are somewhat astonishing. The video documentation of the encounter suggests that this salamander was under no hydric duress and that its activity was not provoked by the biologists. Although the salamander's final destination was not determined, the entrance to the cavity above 100 m in the tree was exposed and dry. A likely possibility is that the interior of the cavity was sufficiently moist and that the salamander was retreating to this refugium. This salamander may have simply been moving between two points within his home range. Regardless, an ecophysiological study comparing rates of cutaneous water loss between arboreal *A. vagrans* its close terrestrial relative, *Aneides flavipunctatus*, would be informative. It may also be interesting to compare the same between arboreal *A. vagrans,* and individuals captured in terrestrial habitats.

# CONCLUSION

Much of what we knew about *A. vagrans* prior to this study came from research on *A. ferreus* populations in Oregon as well as on disjunct populations of *A. vagrans* in British Columbia. Our research was the first attempt to study an arboreal salamander in the canopy environment. The presence of *A. vagrans* in old-growth redwood forests is amazing when you consider the hydric constraints facing plethodontid salamanders. Our results not only suggest canopy features and ecological processes important to arboreal salamanders, but they also indicate the general role of water-storing canopy soil in the amelioration of microclimatic conditions for desiccation-sensitive arboreal biota. Furthermore, they add to the limited knowledge of the life history and ecology of *A. vagrans* and describe techniques suitable for future research with this and other arboreal salamander species in old-growth forests.

The effects of epiphytes, canopy soil, and tree structure on within-crown microclimates continue to be quantified (Ambrose 2004, Sillett unpubl.). Future studies on *A. vagrans* in the redwood canopy could examine the microclimatic determinants of salamander activity if they were conducted within the crowns of trees equipped with sensor arrays (e.g., Sillett currently has 6 large redwoods with such arrays.) These systems continuously quantify light, wind, rain, air temperature and humidity, temperatures and moisture contents of canopy soil and rotten wood, and leaf wetness at multiple locations throughout the crowns.

Future studies should examine how *A. vagrans* uses other habitats besides fern/humus mats, since the preponderance of crack-board captures as well as anecdotal observations suggest that *A. vagrans* prefers crevices and cavities and lodged coarse woody debris over humus or canopy soil beneath *P. scouleri*. Crevices and cavities are difficult to search manually in a non-destructive fashion, and we discourage such manual searching in future studies. Placing crack boards adjacent to these sites would allow capture of salamanders coming out to forage on other tree surfaces without permanently altering the substrate. Crack boards also create habitats within the crown for salamanders and their prey. The entrance to natural and artificial crevices and cavities could then be monitored continuously (even during summer months when canopy access is restricted) via motion-sensitive, time-lapse, infra-red cameras, which provide an accurate time stamp. Microclimate data could then be compared to video footage to determine preferred conditions for foraging and also to document salamander behavior throughout the annual cycle. Video footage showing marked and unmarked salamanders could be used to generate more accurate tree-level population estimates. Identification of salamanders via video footage would be possible using a visual implant fluorescent elastomer (VIE) marking technique (Northwest Marine Technologies, Shaw Island, Washington) and by marking individuals on their dorsal surfaces.

Conducting research in tall canopies is a challenging venture. Our triumphs and failures will serve an example to others who attempt studies on arboreal *A. vagrans* and other tree-dwelling amphibians around the world. Canopy access and research techniques continue to advance. Future studies of *A. vagrans* in old-growth redwood forest can benefit from these advances and allow the life history and ecology of these incredible animals to be more fully understood and appreciated.

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# APPENDIX A

Morphological data and capture information for *A. vagrans* encountered in 5 large redwood trees near Boyes Creek, Prairie Creek Redwoods State Park, California. "Tree" refers to the study tree where the capture occurred. "Capture Date" refers to the day the capture was made. "ANVA Tag No." refers to the identification code given to each salamander when it was first captured, or it refers to the identification code recorded when a salamander was recaptured. "Found With" refers to the identification code of the other salamander(s) captured with the salamander being described. "Location" refers to the fern mat where the capture occurred. "SVL" refers to the measurement from the tip of the snout to the posterior of the vent. "Total Length" was measured from the tip of the snout to the tip of the tail. "Weight in Grams" was recorded post anesthetization. "No. Overlapping Folds" refers to the number of costal folds that overlapped when the posterior and anterior limbs were adpressed to the side of the salamander's abdomen. "Height" refers to the height above ground (m) of the capture location. "Surface Area of F. Mat" refers to the surface area of the fern mat ($m^2$) where the capture occurred. "F. Mat Mass in kg" refers to the estimated dry mass of the fern mat where the capture occurred. "Site Description" refers to the cover object type or the habitat away from a fern mat where the capture occurred: LL = leaf litter, BF = bark flake, c. board = crack board, lg L. bag = large litter bag, sm L. bag = small litter bag. The labels n/c and n/a indicate "not collected" and "not applicable," respectively. The datum proceeded by * refers to an *A. vagrans* that died in captivity, and ** represents a measurement made on a salamander that was missing a portion of its tail.

| Tree | Capture Date | ANVA Tag No. | Found With | Location | SVL | Total Length | Weight in Grams | No. Overlapping Folds | Sex | Height | Surface Area of Mat | Mat Mass in kg | Site Description |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Demeter | 11/02/00 | X74 | n/a | #779 | 6.50 | 12.40 | 5.10 | 1 | M | 74.6 | 1.32 | 13.4 | lg L. bag |
| Demeter | 11/30/00 | P04 | n/a | #782 | 5.40 | 9.90 | 2.50 | 0 | juv | 30.5 | 0.88 | 7.9 | sm L.bag |
| Demeter | 03/13/01 | P08 | n/a | #782 | 4.50 | 10.20 | 2.10 | 1 | juv | 30.5 | 0.88 | 7.9 | sm L.bag |
| Rhea | 10/12/00 | X69 | n/a | #747 | 6.20 | 12.01 | 4.60 | 0 | n/c | 53.4 | 2.2 | 24.3 | lg L. bag |
| Rhea | 11/03/01 | P14 | n/a | #733 | 5.02 | 9.45 | 2.10 | 0 | juv | 67.6 | 2.27 | 20.3 | sm L.bag |
| Kronos | 03/07/00 | X62 | n/a | n/a | 6.30 | 11.84 | 3.70 | 0 | M | 77 | n/a | n/a | under decaying BF |
| Kronos | 03/10/00 | X63 | n/a | n/a | 3.50 | 6.58 | 0.70 | 0.5 | juv | 11 | n/a | n/a | In deadwood |
| Kronos | 09/22/00 | X66 | n/a | n/a | n/c | n/c | n/c | n/c | M | 70 | n/a | n/a | in deadwood |
| Kronos | 10/10/00 | X67 | n/a | #709 | 5.50 | 9.90 | 2.70 | 0 | M | 73.4 | 0.72 | 14.6 | sm L.bag |
| Kronos | 10/27/01 | P12 | n/a | #3 | 5.86 | 11.02 | 3.10 | 1.5 | M | 45.4 | 1.34 | 9.1 | sm L.bag |
| Kronos | 11/10/01 | No#2 | n/a | #3 | 4.20 | 8.10 | 1.00 | 1 | Juv | 45.4 | 1.34 | 9.1 | lg L. bag |
| Kronos | 11/26/01 | No#2 | n/a | #3 | 4.20 | 8.10 | 1.00 | 1 | Juv | 45.4 | 1.34 | 9.1 | lg L.bag |
| Iluvatar | 12/08/99 | * | n/a | #17 | n/c | n/c | n/c | n/c | F | 66.4 | 0.562 | 1.2 | LL on mat |
| Iluvatar | 12/08/99 | y1y2 | n/a | #17 | n/c | n/c | n/c | n/c | n/c | 66.4 | 0.562 | 1.2 | LL on mat |
| Iluvatar | 12/12/99 | Mummy #2 | n/a | n/a | n/c | n/c | n/c | n/c | n/c | 80.5 | n/a | n/a | In shallow hollow |
| Iluvatar | 02/16/00 | X60 | n/a | n/a | n/c | n/c | n/c | n/c | M | 76.1 | n/a | n/a | BF on branch collar |
| Iluvatar | 03/19/00 | X65 | n/a | n/a | 6.16 | 11.58 | 3.60 | 1 | M | 78 | n/a | n/a | BF on trunk |
| Iluvatar | 10/23/00 | X71 | x73 | #18 | 6.30 | 11.90 | 4.20 | 1 | F | 64.5 | 5.011 | 40.9 | c. board |
| Iluvatar | 10/23/00 | x73 | x71 | #18 | 6.20 | 12.00 | 4.50 | 0 | F | 64.5 | 5.011 | 40.9 | c. board |
| Iluvatar | 12/02/00 | p06 | n/a | #18 | 6.40 | 13.20 | 4.50 | 1.5 | F | 64.5 | 5.011 | 40.9 | c. board |
| Iluvatar | 12/20/00 | p07 | n/a | #18 | 6.40 | 12.10 | 4.40 | 0 | F | 64.5 | 5.011 | 40.9 | c. board |
| Iluvatar | 11/03/01 | p13 | n/a | #22 | 4.35 | 8.23 | 1.20 | 0.5 | Juv | 57 | 0.471 | 0.1 | sm L.bag |
| Iluvatar | 11/10/01 | p13 | n/a | #18 | 4.35 | 8.23 | 1.20 | 0.5 | Juv | 64.5 | 5.011 | 40.9 | Incindental on mat |

| Tree | Capture Date | ANVA Tag No. | Found With | Location | SVL | Total Length | Weight in Grams | No. Overlapping Folds | Sex | Height | Surface Area of Mat | Mat Mass in kg | Site Description |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Iluvatar | 12/09/01 | p19 | x71, p20 | #18 | 6.85 | 12.85 | 4.70 | 1.5 | M | 64.5 | 5.011 | 40.9 | c. board |
| Iluvatar | 12/09/01 | p20 | x71, p19 | #18 | 7.10 | 12.55 | 5.90 | 0 | M | 64.5 | 5.011 | 40.9 | c. board |
| Iluvatar | 12/09/01 | x71 | p19, p20 | #18 | 6.40 | 12.01 | 3.40 | 1 | F | 64.5 | 5.011 | 40.9 | c. board |
| Iluvatar | 12/16/01 | x73 | n/a | #18 | 6.40 | 12.12 | 4.20 | 0 | F | 64.5 | 5.011 | 40.9 | lg L.bag |
| Iluvatar | 01/24/03 | no#5 | n/a | #18 | 4.71 | 9.05 | 1.7 | 1 | Juv | 64.5 | 5.011 | 40.9 | lg L.bag |
| Iluvatar | 01/24/03 | no#6 | n/a | #28 | 6.80 | 11.90 | 4.3 | 1.5 | M | 55.2 | 0.715 | 2.6 | sm L. bag |
| Prometheus | 01/12/00 | r1r2 | n/a | #43 | 6.44 | 11.81 | 3.31 | n/c | M | 65 | n/a | n/a | sm L.bag |
| Prometheus | 10/19/00 | x70 | n/a | #44 | 6.80 | 12.40 | 4.90 | 0.5 | M | 61 | 3.039 | 46.4 | c. board |
| Prometheus | 12/02/00 | p05 | n/a | #44 | 6.10 | 12.40 | 4.10 | 1 | F | 61 | 3.039 | 46.4 | c. board |
| Prometheus | 09/22/01 | p09 | n/a | #44 | 6.32 | 11.78 | 3.60 | 0 | M | 61 | 3.039 | 46.4 | c. board |
| Prometheus | 09/22/01 | p10 | n/a | #14 | 5.02 | 9.83 | 2.10 | -2 | Juv | 72 | 6.103 | 93.3 | lg L.bag |
| Prometheus | 10/15/01 | p11 | n/a | #46 | 5.54 | 10.33 | 2.60 | 1 | F | 52.6 | 4.18 | 138 | lg L.bag |
| Prometheus | 11/03/01 | no#1 | n/a | #11 | 1.30 | 2.40 | 0.10 | 0 | Juv | 80.1 | 0.47 | 1.2 | sm L.bag |
| Prometheus | 11/03/01 | x70 | n/a | #44 | 6.78 | 12.02 | 5.00 | 1 | M | 61 | 3.039 | 46.4 | c. board |
| Prometheus | 11/10/01 | p05 | n/a | #44 | 5.80 | 11.40 | 2.70 | 1 | F | 61 | 3.039 | 46.4 | c. board |
| Prometheus | 11/10/01 | p09 | n/a | #44 | 6.30 | 14.58 | 3.60 | 0 | M | 61 | 3.039 | 46.4 | c. board |
| Prometheus | 11/10/01 | p15 | n/a | #14 | 6.37 | 12.10 | 4.50 | 0.5 | F | 72 | 6.103 | 93.3 | sm L.bag |
| Prometheus | 11/26/01 | no#3 | n/a | #48 | 3.53 | 6.54 | 1.83 | 0 | Juv | 27 | 0.565 | 1.7 | lg L.bag |
| Prometheus | 11/26/01 | p09 | x70, p16 | #44 | 6.30 | 14.58 | 3.50 | 0 | M | 61 | 3.039 | 46.4 | c. board |
| Prometheus | 11/26/01 | p16 | p09, x70 | #44 | 6.24 | 11.20 | 3.60 | 1 | F | 61 | 3.039 | 46.4 | c. board |
| Prometheus | 11/26/01 | x70 | p09, p16 | #44 | 6.80 | 12.20 | 4.70 | 1 | M | 61 | 3.039 | 46.4 | c. board |
| Prometheus | 12/04/01 | p17 | n/a | #14 | 5.52 | 10.40 | 2.40 | 1 | M | 72 | 6.103 | 93.3 | lg L.bag |
| Prometheus | 12/04/01 | p18 | x70 | #44 | 6.01 | 11.01 | 3.70 | 0 | M | 61 | 3.039 | 46.4 | c. board |

| Tree | Capture Date | ANVA Tag No. | Found With | Location | SVL | Total Length | Weight in Grams | No. Overlapping Folds | Sex | Height | Surface Area of Mat | Mat Mass in kg | Site Description |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Prometheus | 12/04/01 | x70 | p18 | #44 | 6.80 | 12.20 | 4.80 | 1 | M | 61 | 3.039 | 46.4 | c. board |
| Prometheus | 11/21/02 | no#4 | n/a | #22 | 4.61 | 8.54 | 1.4 | 0 | F | 64.2 | 1.901 | 6.5 | sm L.bag |
| Prometheus | 11/21/02 | p05 | n/a | #44 | 6.00 | 11.89 | 3.2 | 1 | F | 61 | 3.039 | 46.4 | c. board |
| Prometheus | 11/21/02 | p21 | n/a | #14 | 6.00 | 11.29 | 2.8 | -2 | F | 72 | 6.103 | 93.3 | sm L.bag |
| Prometheus | 11/21/02 | p22 | n/a | #22 | 6.45 | 10.92 | 3.5 | -1.5 | F | 64.2 | 1.901 | 6.5 | sm L.bag |
| Prometheus | 11/21/02 | p23 | n/a | #39 | 5.57 | 10.36 | 2.7 | 1 | F | 63.6 | 1.901 | 10.9 | lg L.bag |
| Prometheus | 12/07/02 | p05 | n/a | #44 | 6.00 | 11.89 | 3.2 | 1 | F | 61 | 3.039 | 46.4 | c. board |
| Prometheus | 12/18/02 | p09 | n/a | #44 | 6.42 | 14.70 | 3.80 | 0.5 | M | 61 | 3.039 | 46.4 | c. board |
| Prometheus | 12/18/02 | x70 | n/a | #44 | 6.80 | 12.30 | 4.60 | 1 | M | 61 | 3.039 | 46.4 | c. board |
| Prometheus | 01/24/03 | no#7 | n/a | #14 | 4.80 | 8.00** | 1.3 | 0 | F | 72 | 6.103 | 93.3 | sm L. bag |
| Prometheus | 01/24/03 | no#8 | n/a | #41 | 2.54 | 5.30 | 0.9 | 0 | Juv | 68.4 | 0.126 | 3.2 | sm L. bag |