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Microhabitat Use and Movements of the Wandering Salamander, *Aneides vagrans*, on Vancouver Island, British Columbia, Canada

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In small terrestrial vertebrates, patterns of microhabitat use, individual movements, and spacing among individuals are reflections of species-specific morphology and physiology, local environmental conditions, occurrence of predators and parasites, and availability of resources. If resources are scarce but defensible, territories may be established (Brown and Orians, 1970). Spatial and movement patterns typical of territoriality include site-tenacity, overdispersion of individuals, and use of an area exclusive of potential competitors (Brown and Orians, 1970; Maher and Lott, 1995; Mathis et al., 1995). However, similar patterns of dispersion and movements might be produced as the result of minimizing energetic costs of moving, exploiting widely dispersed resources, and avoiding predation or unfavorable environmental conditions. Alternatively, under stressful environmental conditions individuals may aggregate in favorable microhabitats, which may be created partly by the aggregation itself (Arnold et al., 1991; Hutchison and Dupré, 1992; Blaustein and Walls, 1995).

Among terrestrial plethodontid salamanders, microhabitat use and spacing patterns are strongly influenced by recent weather conditions and the availability of cover on the surface (e.g., Grover, 1998). They find prey and mates on the surface, but surface activity is constrained by temperature and moisture (Cunningham, 1960; Heatwole, 1962; Jaeger, 1971, 1980; Fraser, 1976; Hutchison and Dupré, 1992). Burrows and cover objects (rocks, bark, and logs) provide diurnal protection from desiccation and predators and are especially important refugia during dry periods when foraging on the forest floor is not possible (Jaeger et al., 1995). Under such conditions, food can be a periodically limited resource (Jaeger, 1980), and territories may be established under cover objects or in burrows (Jaeger et al., 1982; Mathis, 1990; Nishikawa, 1990). Territoriality is common among terrestrial salamanders, although the function of territories is unknown for many species, and not all species are territorial (Hairston, 1981; Ovaska, 1987, 1988, 1993; Ovaska and Davis, 1992; Mathis et al., 1995).

The wandering salamander, *Aneides vagrans*, a terrestrial lungless salamander (family Plethodontidae), is a sibling species of the clouded salamander, *Aneides ferreus* (Jackman, 1998). Individuals can be found in moist terrestrial habitats, especially under exfoliating bark and in cracks and cavities of decomposing logs,

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TABLE 1. Characteristics of stations at Rosewall Creek, Vancouver Island, British Columbia, Canada. Station Type: B/GND = "bark on ground" (2–10 pieces of bark on the ground, spaces between layers of bark and under bark on ground); B/LOG = "bark on log" (space under bark on a log); WOOD = "wood" (pieces of rotten or solid wood, and spaces in split logs). SD = standard deviation. "Area" refers to the area covered by bark or wood at each station; % area in place refers to the percentage of the final total area estimated to have been found in place naturally and not created by rearrangement of materials before 3 May 1998.

| | Station type | | | |
	B/GND	B/LOG	WOOD	Total
Number of stations	75	83	44	202
Mean area (m²)	0.435	0.607	0.287	
SD (m²)	0.301	0.847	0.227	
Range (m²)	0.09–1.60	0.02–4.80	0.07–1.35	
Total area (m²)	32.66	50.34	12.65	95.65
% of total area	34.1%	52.6%	13.2%	100%
% area in place	41.2%	82.0%	8.7%	58.4%

stumps, and snags, in talus, and occasionally in trees (Guppy, 1946, 1953; Leonard et al., 1993; Welsh and Wilson, 1995; Corkran and Thoms, 1996). Territoriality has not been reported in *A. vagrans* or *A. ferreus*, but it has been demonstrated for male *Aneides aeneus* (Cupp, 1980), and intraspecific agonistic behavior is known in several other species of *Aneides* (Staub, 1993).

On Vancouver Island, British Columbia, Canada, *A. vagrans* is locally abundant, but its behavior and ecology are poorly known. I investigated microhabitat use, patterns of spacing, and movements of *A. vagrans* under natural conditions. Based on previous reports of *A. vagrans* and *A. ferreus* (e.g., Guppy, 1953; Stebbins, 1954; Mckenzie and Storm, 1970; Bury and Corn, 1988; Corn and Bury, 1991), I expected to find *A. vagrans* in spaces under loose bark and in decaying logs, and to avoid cover objects directly on the soil surface. If territorial, individuals should be site-tenacious, overdispersed, and use cover objects exclusive of other individuals (Ovaska, 1988), and if seasonally territorial, they should show seasonal or sexual variation in spacing patterns (Jaeger, 1979).

The study site was located 0.5 km south of Rosewall Creek (49°27'N, 124°46'W), Vancouver Island, British Columbia, Canada. The dominant trees were second-growth Douglas fir (*Pseudotsuga menziesii*), about 0.5 m diameter at breast height, and western hemlock (*Tsuga heterophylla*), but western red cedar (*Thuja plicata*), red alder (*Alnus rubra*), and broadleaf maple (*Acer macrophyllum*) also were present. In most areas, sword fern (*Polystichum munitum*) was the dominant ground species, but in some areas the ground was virtually devoid of undergrowth. Logs and woody debris, in various states of decomposition, were common. The climate in this area is characterized by mild, wet winters with temperatures often below freezing from December to February. Summers are generally dry, but under the cover of a dense forest canopy, spaces under bark and in decaying wood can remain relatively moist.

I established 202 stations, 3–10 m apart, along a 1.3-km primitive path that wandered through the site (details in Davis, 1991). Most stations were established with little or no modification of the natural habitat by simply locating naturally occurring loose bark on logs, wood or bark on the ground, or cracks in logs. Other stations were created by splitting logs or rearranging materials found at or within a few meters of the station. In all cases, the materials were arranged so that the spaces under or between bark and wood could be inspected with a minimum of disturbance. I established 64 stations between 15 June 1988 and 28 July 1988, and 138 stations between 3 and 26 May 1989.

I classified each station as one of three types: (1) "bark on ground" (B/GND), that is, spaces under bark on the ground; (2) "bark on log" (B/LOG), that is, spaces under bark on a log; or (3) "wood" (WOOD), that is, spaces between pieces of rotten or solid wood, and spaces within split logs. I estimated the covered surface area available at each station by multiplying the number of layers of bark or wood at each station by the product of the linear dimensions of the uppermost piece of bark or wood, measured to the nearest cm (Table 1).

From 15 June 1988 until 15 August 1990, I inspected all stations ($N = 64$ in 1988 and $N = 202$ after 26 May 1989) during daylight hours every three to four weeks. Salamanders were individually marked by toe-clipping, snout–vent length (SVL) measured, and sex determined by inspection of the cloacal vent. Adults were distinguished from juveniles on the basis of coloration (Storm, 1947; McKenzie and Storm, 1971). Adult salamanders were very active and difficult to restrain for measuring and sex identification, so I anesthetized them with Metofane (methoxyflurane). All salamanders were released within 15 min of capture.

In the analysis of individual movements, I eliminated repeated measurements of the same individual by analyzing only the first two captures of each individual. Because I did not record the position of a salamander within small stations (longest dimension < 2 m, $N = 173$), I assumed that the distance moved within each small station was equal to the longest linear dimension of that station. Movements between stations and within larger stations (longest dimension: $\bar{x} \pm SD = 6.24 \pm 5.19$, range = 2.0–20.3 m, $N = 29$) were measured to the nearest 0.1 m.
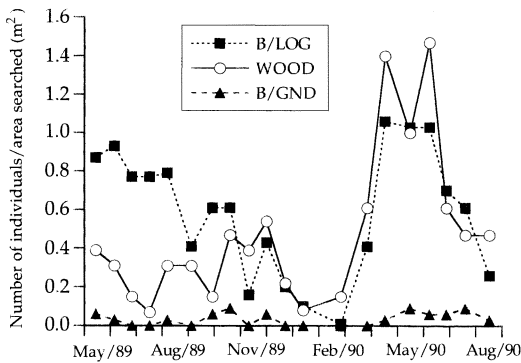
FIG. 1. Use of three microhabitats by *Aneides vagrans*. B/GND (bark on ground) indicated by solid triangles with dashed line (▲). B/LOG (bark on log) indicated by solid squares with dotted line (■). WOOD (crack in log or between wood) indicated by open circles with solid line (○). Plot represents 750 captures of 372 individuals on 20 searches of 202 stations between 26 May 1989 and 15 August 1990.

I used the Kruskal-Wallis test to compare microhabitat use among seasons (Zar, 1999). To avoid using the same individual more than once in this analysis, I selected one observation randomly from all captures of each individual between 26 May 1989 and 15 August 1990. Seasons were defined by convenience (summer 1989: May through August; autumn 1989: September through November; winter 1989–1990: December through February; spring 1990: March through May; summer 1990: June through August), and only searches with more than five salamanders were used. The significance level was set at $\alpha = 0.05$, and as a postsignificance test, I ran Dunn's multiple comparison test when $P < 0.05$ (Zar, 1999). The Kruskal-Wallis test was calculated using InStat 3.0 (GraphPad Software, Inc., www.graphpad.com); other calculations were done with the Statistical Analysis System (SAS Institute, Inc., Cary, NC).

Salamanders were consistent in their use of B/GND and B/LOG stations in 1989 and 1990: B/GND stations were little used during any part of the year, whereas B/LOG stations represented an important microhabitat (Fig. 1). During the active season of 1989, B/LOG was the primary microhabitat, but WOOD stations became at least as important as B/LOG stations in 1990. These differences among microhabitats were significant, except for the winter season when few salamanders were found (Kruskal-Wallis; summer 1989: $H = 10.35$, $P = 0.006$; autumn 1989: $H = 6.9$, $P = 0.031$; winter 1989–1990: $H = 3.71$, $P = 0.156$; spring 1990: $H = 7.26$, $P = 0.027$; summer 1990: $H = 8.41$, $P = 0.015$; $N = 372$). Dunn's test was significant for B/GND versus B/LOG for all seasons tested (summer 1989: $P < 0.01$; autumn 1989, spring 1990, and summer 1990: $P < 0.05$), but no other comparisons were statistically significant.

Of the 456 salamanders captured between 15 June 1988 and 15 August 1990, 176 (38.6%) were recaptured at least once. Movements of *A. vagrans* among stations (approximately 10 m apart) were rare ($N =$

12), and individuals often were recaptured at the same location within a station. Of the distances between the locations of first two captures of an individual salamander, 133 (75.6%) were ≤ 2 m, and 166 (94.3%) were ≤ 10 m (median = 1.65 m, $\bar{x} \pm SD = 2.79 \pm 4.26$, range = 0.0–38.5, $N = 176$). No differences were detected in the distances moved among juveniles ($N = 139$), males ($N = 18$), and females ($N = 19$; Kruskal-Wallis, $H = 2.95$, df = 2, $P = 0.23$). Few individuals were captured in more than one season; thus, it was not possible to compare the movements of the same individuals among seasons. The mean distances moved were not significantly different among seasons (spring: $\bar{x} \pm SD = 4.04 \pm 6.62$ m, $N = 54$; summer: $\bar{x} \pm SD = 2.29 \pm 2.65$ m, $N = 88$; autumn: $\bar{x} \pm SD = 2.04 \pm 1.57$, $N = 20$; winter: $\bar{x} \pm SD = 2.19 \pm 2.31$, $N = 14$; ANOVA, $F_{3,172} = 2.30$, $P > 0.08$).

The interval between the first and second captures ranged from 17 days to 497 days ($\bar{x} \pm SD = 74.4 \pm 86.2$, $N = 176$), but there was no significant relationship between the number of days and the distance moved between captures (Spearman rank correlation, $r_s = 0.147$, $t = 1.96$, df = 174, $0.05 < P < 0.10$).

To determine whether there were seasonal changes in spacing behavior, I calculated the mean distance between any adjacent pair of salamanders at the same station for each season. The mean distances between salamanders in different seasons were not significantly different (spring: $\bar{x} \pm SD = 0.97 \pm 1.34$ m, $N = 153$; summer: $\bar{x} \pm SD = 1.19 \pm 1.91$ m, $N = 243$; autumn: $\bar{x} \pm SD = 1.09 \pm 1.27$, $N = 66$; winter: $\bar{x} \pm SD = 1.34 \pm 1.53$, $N = 18$; ANOVA, $F_{3,476} = 0.65$, $P > 0.58$).

Salamanders seldom used B/GND stations but were often found at the B/LOG stations, and this pattern was the same in both years. However, the pattern with respect to the WOOD stations was very different between years. In the spring of 1989, WOOD stations were used much less than B/LOG stations, but by October 1989 they were at least as important as B/LOG stations (Fig. 1). This pattern might have arisen as a consequence of when the stations were established. Before 3 May 1989 more than 40% of the B/GND stations and 82% of the B/LOG stations were in place for nearly a year or more, but only 8.7% of the WOOD stations were available (Table 1). Apparently, it took four to five months for the salamanders to move into the newly created WOOD microhabitat, suggesting that individuals rarely move from familiar parts of their home range, that the newly created spaces were initially unsuitable, or both. Thus, differential use of B/LOG and WOOD stations is probably an artifact of when the stations were created, and they probably represent equivalent microhabitats with the common element being a substrate of wood.

These results show that individuals move only short distances, are site-tenacious and return periodically to particular spots within their home ranges. Many species of small terrestrial plethodontid salamanders are site-tenacious and have small home ranges of a few square meters (Hendrickson, 1954; Cunningham, 1960; Madison, 1969; Kleeberger and Werner, 1982; Ovaska, 1988; Gergits and Jaeger, 1990; Nishikawa, 1990; Mathis et al., 1995; Stebbins and Cohen, 1995). If a salamander finds a spot within its home range

with favorable moisture and feeding characteristics, it is probably advantageous to remain at that spot or to return to it frequently. Individuals may benefit by remaining close to familiar escape routes from predators, feeding spots, or retreats that are used when microclimatic conditions become unfavorable. Also, ranging over a wider area may involve increased risks of desiccation or exposure to predators (Jaeger, 1980).

Site-tenacity is one of four criteria that characterize territoriality; the others are defense of an area, advertisement by display behavior, and exclusion of potential competitors from the defended area (Brown and Orians, 1970; Jaeger et al., 1982; Mathis et al., 1995). Territoriality arises under conditions of limited and defendable resources (Brown, 1964), but the spaces under bark on logs used by *A. vagrans* are extensive with abundant but transient prey, and particular locations might not be worth defending. Logs with suitable microhabitats for *A. vagrans* are spatially separated with little movement among them, and both juveniles and adults are found together frequently. Thus, it is possible that many of the salamanders inhabiting a particular log are closely related, and inclusive fitness could be lowered if territorial behavior were directed toward unrecognized relatives (Wilson, 1975; Jaeger et al., 1995). If territorial, *A. vagrans* residents should exhibit agonistic and display behavior, and they should expel conspecific intruders from defended areas. Although *A. vagrans* exhibits intraspecific agonistic and display behavior under laboratory conditions, residency status does not predict the outcome of such interactions, the intensity of agonistic behavior is relatively low, and expulsion of intruders has not been demonstrated (Davis, 2002). These observations suggest that *A. vagrans* is not territorial, but more work is needed to resolve this question.

Bury and Corn (1988) reported that 81% of the *A. ferreus* (total: $N = 79$) they found in Oregon were associated with logs, either inside logs (34%) or under the bark on logs (47%). Similarly, Corn and Bury (1991) reported that *A. ferreus* ($N = 166$) in Oregon were usually found under the bark on logs or in cavities within logs of younger decay classes but was rarely found in contact with the soil. My results establish that these are the primary microhabitats for *A. vagrans* in the spring, summer, and autumn and that microhabitat use is similar between these species. In the winter, *A. vagrans* might move to subterranean retreats or deep within larger logs, but there are no data that bear directly on this question. Larger logs with exfoliating bark and internal cavities seem to be especially important habitat elements for this species, both as diurnal retreats and for reproduction (Davis, 1991), and should be retained in managed forests. Where forestry activities result in relatively even-age forests that contain uniform types, amounts, and decay classes of logs, suitable microhabitat for *A. vagrans* may become limited as logs pass beyond favorable decay stages. Additional study of the long-term effects of forestry practices on this species is needed to test this hypothesis.

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Effects of Collection on Weight, Length, and Sex Ratio of Red-Spotted Newts, *Notophthalmus viridscens*

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Declines in amphibian populations have been noted
worldwide and have recently gained international at-
tention (Barinaga, 1990; Wyman, 1990; Wake, 1991;
Gibbons et al., 2000). A variety of factors have con-
tributed to these declines, including habitat destruc-
tion (Aubry et al., 1987; Dodd, 1991), pollution (Cooke
1973, 1981), and disease (Cunningham et al., 1993). A
factor that has been mentioned as causing an addi-
tional stress on some amphibian populations is collec-

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