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SPACING AND MOVEMENTS OF THE SALAMANDER *PLETHODON VEHICULUM*

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ABSTRACT: Territorial behavior among lungless salamanders of the family Plethodontidae has often been observed, but detailed investigations exist for only a few species. I examined spacing and movements of the western red-backed salamander, *Plethodon vehiculum*, through a mark-recapture study in the field and through laboratory experiments to test the hypothesis that adults defend feeding territories under cover objects. *Plethodon vehiculum* showed a high degree of site-specificity in the field and maintained relatively small home ranges. Home ranges of adult males, adult females, and juveniles were similar in size (mean distance between the two farthest captures for adult males = 2.47 m, for adult females = 1.71 m, for juveniles = 1.95 m). Few cover objects, however, were used exclusively by a single adult as would be expected if the salamanders were territorial. The pattern of multiple captures (adults within 10 cm of each other) showed no consistent seasonal trends. I examined the effect of soil moisture and distribution of food on the dispersion of *P. vehiculum* in indoor enclosures. Under test conditions, dispersion of *P. vehiculum* under cover objects did not indicate territoriality. Climatic conditions (cool and wet) in spring and autumn, when adults of *P. vehiculum* are active on the surface, are probably responsible for food (invertebrate prey) being readily available, thus rendering the defence of feeding territories uneconomical.

Key words: Plethodontidae; *Plethodon vehiculum*; Territoriality; Home ranges; Dispersion; Aggression; Salamander

TERRITORIALITY has long been suspected for plethodontid salamanders (Grant, 1955; Thurow, 1976), and Larson (1984) proposed that this behavior may be generally observed in the family Plethodontidae. Experimental demonstrations of territorial behavior, however, are few. Jaeger and co-workers (Jaeger, 1981; Jaeger and Gergits, 1979; Jaeger et al., 1982, 1986) showed that the eastern red-backed salamander, *Plethodon cinereus*, was territorial under laboratory conditions. Jaeger (1981) suggested that, in the field, adults of this species defend feeding territories under cover objects during summer, when dry conditions curtail foraging away from these relatively moist sites. Seasonal changes in patterns of dispersion of *P. cinereus* in the field support this suggestion, since each cover object tended to harbor only one adult in summer but not in spring (Jaeger, 1979).

The western red-backed salamander, *Plethodon vehiculum*, inhabits forested

areas along the Pacific rim in the northwestern United States and in southwestern Canada. Ecologically, *P. vehiculum* closely resembles *P. cinereus*: the two species are similar in size and external appearance, feed on the same types of prey, and occupy similar microhabitats. Therefore, their behavioral ecology might also be similar. Ample information exists on *P. cinereus*, providing a basis for comparisons.

I examined spacing and movements of *P. vehiculum* in the field and in the laboratory. A high degree of site-specificity and exclusive use of cover objects by individual salamanders in the field would indicate territoriality. In the laboratory, I examined the effect of soil moisture (Experiment 1) and distribution of food (Experiment 2) on the dispersion of *P. vehiculum*. I predicted that the salamanders would be territorial when the substrate is relatively dry but not when it is moist. I also predicted that the salamanders would defend territories when food is distributed evenly in defendable units under cover objects but not when it is dispersed in unpredictable, random locations away from the shelters. The treatments were designed

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to simulate environmental conditions likely experienced by the salamanders in a natural habitat; during dry, unfavorable conditions foraging takes place under cover objects, whereas during moist, favorable conditions the salamanders forage primarily in and on the leaf litter and on vegetation (Jaeger, 1972, 1978, 1979, 1980).

FIELD STUDY

Methods

I carried out a mark-recapture study of *P. vehiculum* on two plots (Plots A and B) in Goldstream Park, Vancouver Island, B.C., Canada (48°28' N, 123°32' W). Vegetation in the area consisted of mature forest with Douglas fir (*Pseudotsuga menziesii*), western red cedar (*Thuja plicata*), and Rocky Mountain maple (*Acer glabrum*) being the dominant tree species. Little light penetrated the forest canopy, and the ground vegetation was sparse. A layer of leaf litter covered both plots and was especially thick on Plot B. Deadfall in various states of decomposition, as well as moss-covered rocks, were abundant on the surface. Several layers of rocks of different sizes covered the entire area of Plot A and parts of Plot B. Both plots were situated on level ground and were well drained. The study area is described more fully elsewhere (Ovaska, 1987a).

I treated the two study plots somewhat differently, because it was not known what effects the searches would have on the habitat and on the behavior of the salamanders. On Plot A, I lifted all cover objects whereas on Plot B, I turned over only the larger rocks and logs. Plot A consisted of a 10 × 10 m area marked into 100 squares, each 1 × 1 m. Each square in turn was divided into four equal quadrats by imaginary lines. Thus, the plot consisted of 400 quadrats, each 0.5 × 0.5 m. I searched the area for salamanders every 2 wk from 19 March–3 November 1984. Two searches, on 3 April and 15 May, were made in 1985. I located the salamanders by gently lifting the moss, rocks, and logs on the surface layer and by sifting through the leaf litter with fingers, then carefully replacing the cover objects. I measured the length of the salamanders from the tip of the snout to

the anterior end of the vent (SVL) to the nearest 0.5 mm, and determined the sex of the adults. Males with SVL >41 mm and females with SVL >43 mm were considered adults (Peacock and Nussbaum, 1973). Sexually mature males could be distinguished from females by the presence of vent lobes and protruding, recurved premaxillary teeth (Arnold and Houck, 1982); these teeth could be readily felt by sliding a finger anteriorly on the underside of the snout of a male. I then clipped a unique combination of toes from each salamander by excising from 1–4 toes, with no more than two toes per foot being removed. I also used any abnormalities in toes and distinctive color patterns in identification. For each capture, I recorded the position of the salamander in the plot (quadrat number). I also noted the proximity of each salamander to others (≤ 10 or > 10 cm apart), because several cover objects were large enough potentially to accommodate a number of territories. The cut-off point was arbitrarily set at 10 cm, based on the assumption that the territories may be relatively small, and was similar to the value (15 cm) used by Jaeger (1979) in the analysis of dispersion of *P. cinereus* in the field. The salamanders were returned to their original locations within 15 min of capture.

Plot B covered an area of approximately 200 m² and was 50 m away from Plot A. I numbered all the larger logs and rocks (with an area of at least 300 cm² contacting the ground) on the plot and located the salamanders by turning over these cover objects once a week from 3 April 1984–30 May 1986. I carried out irregular searches in midsummer (July–August) and mid-winter (December–February), when few or no salamanders were on the surface. The total number of cover objects was 112 in 1984, 114 in 1985, and 117 in 1986, and the midpoints of these were mapped. Forty-three of the cover objects were logs, segments of logs, or pieces of bark, and 74 were either single rocks or distinct groups of rocks. Most were relatively small (only two logs were longer than 2 m) and supported a thick growth of moss.

I handled the salamanders caught on

Plot B as on Plot A, except that a maximum of three toes per individual was removed in 1985 and 1986. In 1984, I excised combinations of toes distinct from those on Plot A. As there were no movements between the plots, I used identification marks that duplicated those on Plot A in subsequent years. For each salamander, I noted the cover object under which it was found as well as its proximity to other salamanders (≤ 10 cm or > 10 cm apart). I calculated the distances moved by the salamanders from the centers of the cover objects and made no attempt to map the locations of the salamanders under particular logs and rocks in 1984. In 1985 and 1986, however, I measured the approximate positions of the salamanders under the larger cover objects (logs longer than 0.5 m or groups of several rocks).

I analysed the mark-recapture data using the Statistical Analysis System package (SAS Institute, 1985). The statistical tests used were standard tests described in Sokal and Rohlf (1981), and the data met the assumptions of parametric statistics. The minimum level of significance was set at $\alpha = 0.05$.

Results

I considered salamanders caught at least four times in 1 yr to be residents and those caught less than four times to be transients. I measured the distance between the two farthest captures for each resident to obtain an index of home range size. For animals caught during more than 1 yr, only data for the year with the greatest number of captures were included. Home ranges of *P. vehiculum* were relatively small on both plots, and the ranges of adult males, adult females, and juveniles were similar in size (one-way ANOVA, Plot A: $F = 0.31$, $df = 82$, $P > 0.25$; Plot B: $F = 1.82$, $df = 62$, $P > 0.10$; Fig. 1). The number of captures of adult males, adult females, and juveniles used in these analyses were also similar both on Plot A (males: $\bar{x} = 5.83$, $SD = 1.77$, $n = 23$; females: $\bar{x} = 5.09$, $SD = 1.38$, $n = 11$; juveniles: $\bar{x} = 5.00$, $SD = 1.17$, $n = 49$; one-way ANOVA: $F = 2.06$, $df = 82$, $P > 0.05$) and on Plot B (males: $\bar{x} = 5.23$, $SD = 2.24$, $n = 35$; females: $\bar{x} =$

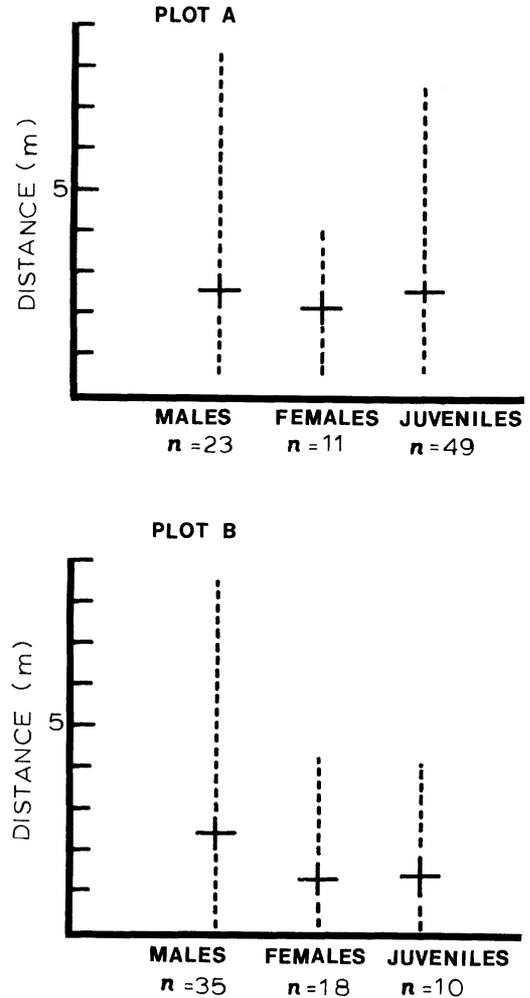


FIG. 1.—Distance between the two farthest captures of individual adult males, adult females, and juveniles on Plot A (top) and on Plot B (bottom). Horizontal bars = means, solid vertical bars = 2 SE, broken vertical bars = range.

4.78, $SD = 0.65$, $n = 18$; juveniles: $\bar{x} = 4.50$, $SD = 0.85$, $n = 10$; one-way ANOVA: $F = 1.82$, $df = 62$, $P > 0.10$). On Plot A, a sufficient number of captures existed for comparison of the size of home ranges of small ($SVL \leq 30$ mm) and large ($SVL > 30$ mm) juveniles. The distance between the two farthest captures of individuals was similar for the two size classes of juveniles (small: $\bar{x} = 2.57$, $SD = 1.91$, $n = 31$; large: $\bar{x} = 2.54$, $SD = 1.75$, $n = 18$; one-way ANOVA: $F = 0.02$, $df = 48$, $P > 0.25$).

Most cover objects on Plot B were used

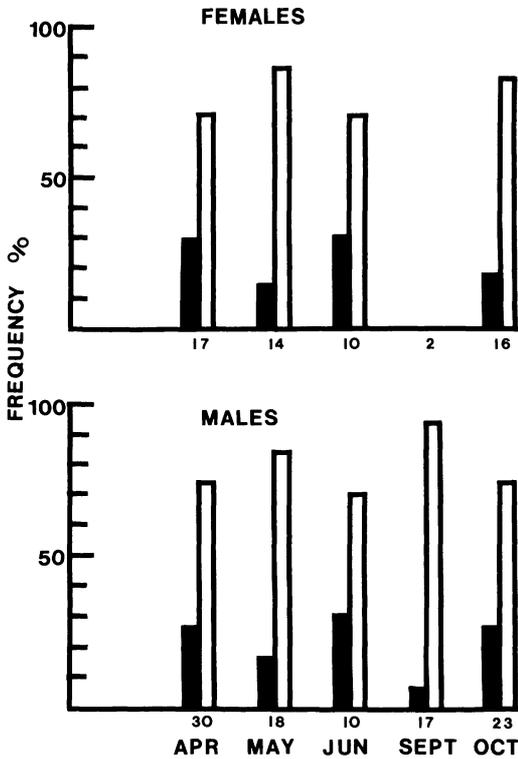


FIG. 2.—Proportion of cover objects used by one or by two or more adults of the same sex per month: 1984–1986 combined. Only cover objects with two or more captures of adult males or females per month were included. Solid bars = cover objects used by one individual, open bars = cover objects used by two or more individuals; number of cover objects below bars.

by several large (SVL >40 mm) *P. vehiculum* each month (March–November), and only a small proportion of the cover objects was occupied exclusively by one individual ($\bar{x} = 7.43\%$, $SD = 7.60$). I considered only cover objects with at least two captures of large salamanders and omitted those used by reproductive females [eggs visible through the abdominal wall with the diameter of the largest egg at least 2.5 mm, Ovaska (1987a)] to eliminate potential bias towards pairs resulting from courtship activity. Similar patterns are evident for males and females. Most cover objects with at least two captures of sexually mature females with SVL >43 mm were used by several females each month throughout the year, and comparable trends were observed for adult males with SVL >41 mm (Fig. 2).

The proportion of large salamanders (SVL >40 mm) in multiple captures (within 10 cm of each other, omitting groups that included reproductive females) showed seasonal trends in 1984 ($\chi^2 = 14.00$, $df = 5$, $P < 0.016$) but not in 1985 ($\chi^2 = 10.22$, $df = 6$, $P > 0.10$; Fig. 3). I compared the frequency of male-male, female-female, and male-female pairs (two adults within 10 cm of each other, reproductive females excluded) under cover objects. Unexpectedly, pairs consisting of adult males and nonreproductive females were more frequent than those consisting of adults of the same sex (14 male-male, 7 female-female, and 36 male-female pairs; $\chi^2 = 11.55$, $df = 2$, $P = 0.003$).

LABORATORY EXPERIMENTS

Collection and Maintenance of the Salamanders

Adult *P. vehiculum* were collected from southern Vancouver Island. Prior to the experiments, the salamanders were housed individually in 1-l glass jars filled with moist moss. The jars were kept in a basement laboratory where the experiments were conducted. Light entering through a small window maintained a natural light-dark cycle in the basement, and the temperature remained between 9–14 C. The salamanders were given the opportunity to feed to satiation with *Drosophila* once a week. They were kept a maximum of 6 wk in captivity before the experiments, and no individual was used more than once.

I applied the Yate's correction for continuity in χ^2 -tests when there was only 1 df. Multivariate analysis of variance of cover object use was performed using the MANOVA program in the Statistical Package for Social Sciences (SPSSx User's Guide, 1985). The level of significance was set at $\alpha = 0.05$.

Experiment 1—Effect of Soil Moisture on Salamander Dispersion

Procedures.—The experiment was carried out in two 175 × 103 cm indoor enclosures, the bottoms of which were covered with dark forest soil up to a depth of 3 cm. A 5 cm rim of fiberglass tape along

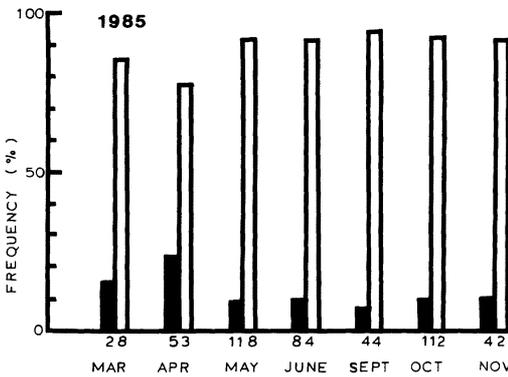
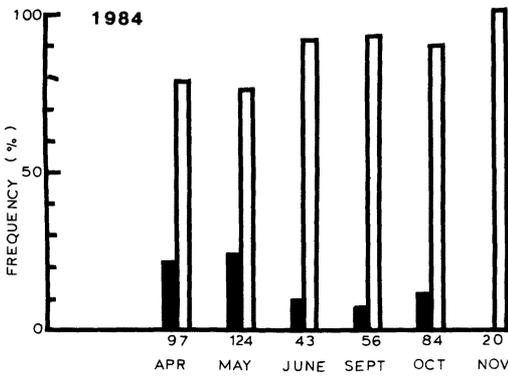


FIG. 3.—Proportion of *P. vehiculum* with SVL > 40 mm in multiple captures (within 10 cm of each other) in 1984 and in 1985. Solid bars = multiple captures, open bars = single captures; number of captures below bars.

the sides and on top of the pen prevented the salamanders from climbing out. Ten pieces of plywood (14 × 17 cm) topped with moss and arranged in two rows along the long side of the enclosure (18 cm from the nearest side and 23 cm from each other) were placed in each pen. In Treatment 1, the soil was allowed to dry after an initial soaking, except that the soil under the cover objects was sprayed daily. In Treatment 2, all the soil was kept moist by daily spraying. Soil samples were taken every third day to monitor the moisture content (difference between wet and dry mass/dry mass × 100). The soil samples were dried to a constant weight in an oven at 105 C.

I placed six individually marked male and six female *P. vehiculum* in each pen and, after 1 wk of acclimatisation, record-

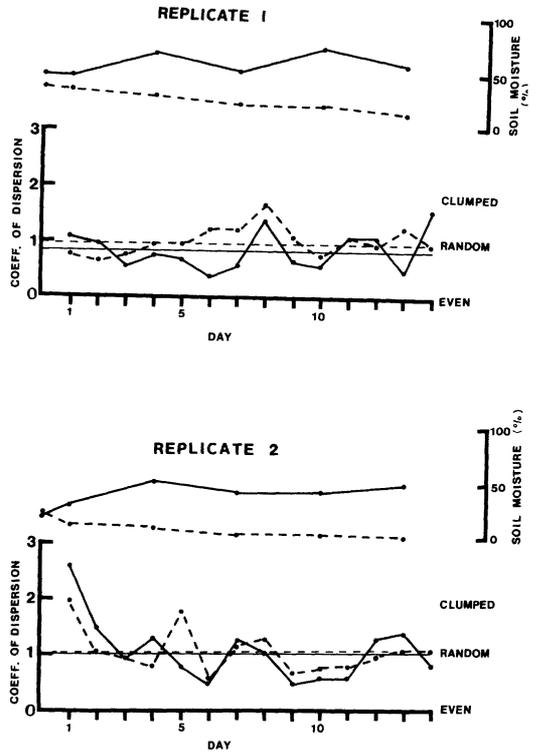


FIG. 4.—Coefficient of dispersion (CD) per day for *P. vehiculum* under cover objects in Experiment 1. Broken line = Treatment 1 (soil between cover objects dry), solid line = Treatment 2 (soil moist); straight horizontal lines = mean CD for Treatment 1 (broken line) and for Treatment 2 (solid line). Soil moisture (%) is shown above for the two treatments.

ed their positions under the cover objects each morning (0700–1000 h) for 14 days. All the females were nonreproductive, and the experiment was performed outside the mating season (June–July 1985) to eliminate potentially confounding effects resulting from courtship activity.

The salamanders were given an opportunity to feed to satiation on *Drosophila* the day before the experiment. They were fed again on the third day with 12 small earthworms placed in each pen, but not thereafter. The soil may have contained prey items, but these were not measured. There were two replicates of each treatment. The soil and the moss were changed after each replicate to remove any pheromonal markings present, and the treatments were switched between the enclosures.

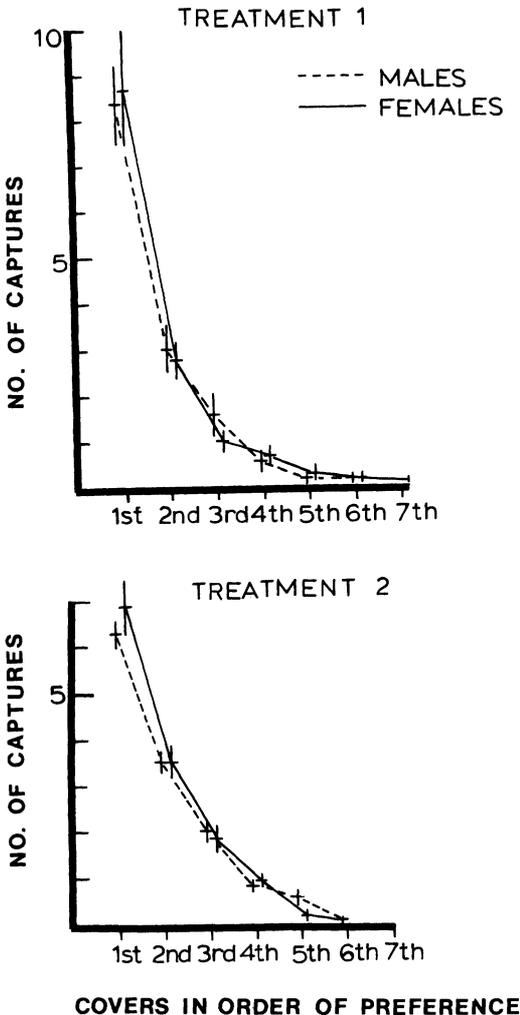


FIG. 5.—Number of captures of male and female *P. vehiculum* under cover objects in Experiment 1. Cover objects are listed in the order of most use by individuals. Maximum number of captures possible = 14, number of males = number of females = 12 for each treatment. Treatment 1 = soil dry, Treatment 2 = soil moist, horizontal bars = means, vertical bars = 2 SE. Two independent replicates combined for each treatment.

Results.—I calculated a coefficient of dispersion, CD, (variance/mean) daily for each treatment with the number of salamanders per cover object as the variable. $CD > 1$ indicates a clumped, $CD = 1$ a random, and $CD < 1$ an even dispersion pattern (Pielou, 1977). Occasionally a salamander could not be located and was probably buried in the soil as it usually appeared the following day.

The coefficient of dispersion fluctuated around 1.0 under both treatments (Fig. 4). The salamanders showed a high degree of site-specificity and spent most of their time under a few of the available cover objects (Fig. 5). There were no differences in cover use between males and females or between treatments (2×2 MANOVA with treatment and sex as independent variables and the number of captures under first, second, third, fourth, and fifth + sixth most used cover objects by individuals as dependent variables: treatment effect—Wilks Lambda = 0.82, hypothetical df = 5, $P = 0.167$; sex effect—Wilks Lambda = 0.92, hypothetical df = 5, $P = 0.627$; treatment \times sex effect—Wilks Lambda = 0.88, hypothetical df = 5, $P = 0.412$).

Experiment 2—Effect of Distribution of Food on Salamander Dispersion

Procedures.—The experiment was conducted in two 81×94 cm indoor enclosures that were filled to a depth of 3 cm with moist peat moss. A 5 cm rim of fiberglass tape along the sides and on top of the pen prevented the salamanders from climbing out. Each pen was provided with eight 14×17 cm plywood cover objects distributed along the perimeter of the enclosure in a circular pattern (approximately 5 cm from the nearest side and 12 cm from the adjacent cover objects). Under each piece of plywood was a sheet of tinted plexiglass of dimensions equal to the cover. The cover objects were raised 1 cm off the substrate at one end by inserting a piece of lath under one side of the plywood.

In Treatment 1, a small plastic dish (3.4 cm diameter, 1.8 cm deep) was buried up to its rim under each cover object, and a mealworm (approximately 1 cm in length) was deposited in each dish every third day for 30 days. In Treatment 2, eight dishes were similarly buried but in random locations between the cover objects. The locations of the dishes were changed every third day when a mealworm was also deposited in each one. Preliminary studies indicated that this amount of food was am-

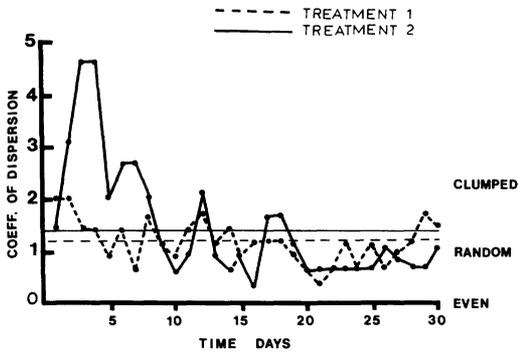


FIG. 6.—Coefficient of dispersion (CD) per day for *P. vehiculum* under cover objects in Experiment 2. Broken line = Treatment 1 (food concentrated under cover objects), solid line = Treatment 2 (food randomly dispersed between cover objects); straight horizontal lines = mean CD for Treatment 1 (broken line) and for Treatment 2 (solid line).

ple to satisfy the energetic needs of the salamanders.

I placed eight individually marked adult *P. vehiculum* (males and nonbreeding females) in each pen and recorded their positions under the cover objects daily for 30 days. I then calculated a coefficient of dispersion for each day with the number of salamanders per cover object as the variable. A total of eight adult *P. vehiculum* (referred to as intruders) was introduced to each pen, two per night, on days 31, 32, 33, and 34. All introductions took place after dark, the time of day corresponding to the natural activity period of the salamanders. The plywood covers were removed just prior to the introductions, exposing the plexiglass to facilitate observation. I recorded the reactions of the residents towards the intruders for 50 min under dim (2 m from a 25 W light bulb) light and then replaced the plywood covers. I noted the positions of the intruders under the cover objects (with residents or under vacant cover objects) the following morning, when I also removed the intruders but left the residents in the pen. The experiment was carried out in June–July 1984.

Results.—After an initial clumped pattern under Treatment 1, the coefficients of dispersion fluctuated around 1.0 (random) under both treatments (Fig. 6). The salamanders showed a high degree of site-

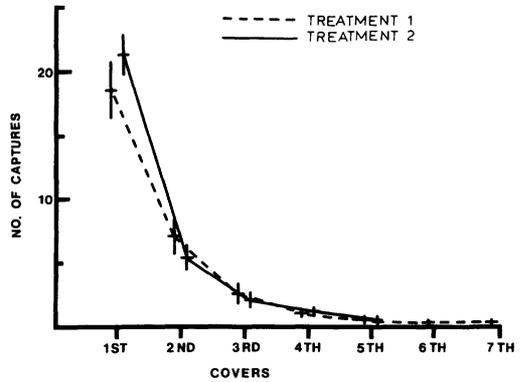


FIG. 7.—Number of captures of individual *P. vehiculum* under cover objects in Experiment 2. Cover objects are listed in the order of most use by individuals. Maximum number of captures possible = 30, number of individuals = 8 for each treatment. Treatment 1 = food under cover objects, Treatment 2 = food randomly dispersed between cover objects, horizontal bars = means, vertical bars = 2 SE.

specificity and spent most of their time under a few of the available cover objects (Fig. 7). There were no differences in cover use by the salamanders between the two treatments (1×2 MANOVA with treatment as independent variable and the number of captures under first, second, third, fourth, and fifth + sixth most used cover objects by individuals as dependent variables; Wilks Lambda = 0.51, hypothetical $df = 5$, $P = 0.184$). The residents were usually totally passive towards the intruders during the introductions, even when approached by the latter. Only two of the total of 16 intruders were attacked (once each) and both by the same resident, a large male, under Treatment 1. The positions of the intruders under the cover objects on the morning following the introductions were independent of whether the cover objects were occupied by residents or not [Treatment 1: seven intruders under occupied covers (total of 44 occupied covers), one intruder under a vacant cover (total of 20 vacant covers), Fisher's Exact-test, $P = 0.213$; Treatment 2: six intruders under occupied covers (total of 46 occupied covers), two intruders under vacant covers (total of 18 vacant covers), Fisher's Exact-test, $P = 0.599$]. The salamanders under Treatment 1 did not consume significantly more mealworms (30,

or 37.5% of 80) than those under Treatment 2 (18, or 22.5% of 80; $\chi^2 = 3.60$, $df = 1$, $P < 0.10$).

DISCUSSION

Plethodon vehiculum maintained relatively small home ranges in the field, and most movements between captures of individual salamanders were < 3 m. These results are in accordance with observations for other plethodontids which indicate that surface movements of these salamanders are limited [e.g., Barbour et al. (1969) for *Desmognathus fuscus*; Hendrickson (1954) for *Batrachoseps attenuatus*; Kleeberger (1985) for *D. monticola*; Merchant (1972) for *Plethodon jordani* and *P. glutinosus*; Nishikawa (1986) for *P. jordani* and *P. glutinosus*]. Male *Aneides aeneus* (Gordon, 1961), *P. jordani* (Madison, 1969; Madison and Shoop, 1970; Merchant, 1972), and *P. glutinosus* (Merchant, 1972) wandered more widely than females, but this difference is statistically significant only for *P. jordani*. In contrast, Kleeberger and Werner (1982) found that home ranges of female *P. cinereus* were larger than those of males. The distance between the two farthest captures did not differ among adult males, adult females, and juveniles of *P. vehiculum*, although the longest movements (up to 8.5 m) were by males.

If these salamanders were territorial, one would expect to find exclusive use of cover objects in addition to site-specificity. Several adults, however, shared the use of a cover object on a monthly basis. It is possible that territories are not stationary but are maintained for a transient period of time. Keen and Sharp (1984) and Keen and Reed (1985) suggested, based on experiments in the laboratory and in field enclosures, that *Desmognathus monticola* possesses mobile territories and defends feeding sites under the cover object where it happens to be feeding.

If *P. vehiculum* held such mobile territories, then the salamanders should be evenly dispersed under cover objects during any one capture period. The pattern of multiple captures (adults within 10 cm of each other) is somewhat difficult to interpret due to the fluctuating numbers of

P. vehiculum between capture periods and also due to the relatively large number of unoccupied cover objects at any one time. There were no consistent seasonal trends in the proportions of adults found in single and multiple captures, although multiple captures were more frequent in spring 1984 than in summer of the same year. Jaeger (1979) found that, despite constant surface densities, groups consisting of several adult *P. cinereus* were common in spring but not in summer, when each cover object tended to harbor only one adult. He suggested that the salamanders switch to territorial behavior when dry conditions in summer restrict foraging movements and confine the salamanders to these moist sites. The frequency of multiple captures of *P. vehiculum* in spring 1984, however, probably reflected higher densities at this time rather than changes in spacing resulting from the drying of the forest floor. The proportions of multiple captures in the fall remained similar to those in summer, and this pattern of multiple captures was not observed in 1985.

Experiments in indoor enclosures, where the dispersion of food and the soil moisture were manipulated, failed to reveal territoriality. The dispersion of *P. vehiculum* appeared random under all the experimental treatments, and the salamanders (apart from one individual) did not show aggression towards intruders. In addition, the intruders introduced into the pens positioned themselves randomly under the cover objects regardless of whether these were occupied by residents or not. Dumas (1956) also found that *P. vehiculum* was randomly dispersed in terraria with respect to conspecific individuals.

The extent to which the artificial conditions affected behavior of *P. vehiculum* is unknown, but results of other laboratory experiments (Ovaska, 1987b) also support the suggestion that these salamanders are not territorial. Agonistic behavior (threat displays and biting) was largely confined to encounters between males during the peak of the courtship season in autumn and thus appeared primarily associated with mating.

The climate along the Pacific rim in the

northwestern United States and southwestern Canada is characterized by mild, wet winters and summers that may be very dry. On southern Vancouver Island, adults of *P. vehiculum* are active from September–November and from February–June but disappear, probably into underground retreats, during midwinter and midsummer (Ovaska, 1987a). Rainfall is frequent during the active periods of the salamanders, and low temperature usually prevent the ground from drying. Food (small invertebrates) is therefore likely to be readily available, rendering the defence of feeding territories uneconomical for *P. vehiculum*.

The conditions leading to the evolution of territorial behavior among plethodontid salamanders are to a great extent unknown. Experiments on territoriality of *P. cinereus* from different parts of its range would be instructive, because this species has a relatively wide geographical range encompassing several climatic regimes. Information on a number of species, both territorial and nonterritorial, would further elucidate the conditions under which territoriality is exhibited.

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FEEDING ASYMMETRY AFFECTS TERRITORIAL DISPUTES BETWEEN MALES OF *PLETHODON CINEREUS*

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ABSTRACT: An experiment was conducted to study the interactions between paired males of the red-backed salamander, *Plethodon cinereus*, when both were residents of neighboring areas and the amount of food received per individual was asymmetric (i.e., "low" and "high" levels). The low food level was the minimum number of *Drosophila virilis* required per day by a salamander, without loss or gain of body mass; the high food level was double that amount. Salamanders fed low food levels spent significantly more time inside the burrow and in escape behavior. This suggests that males in food-poor territories avoid escalated aggressive disputes with males in food-rich territories.

Key words: Salamander; *Plethodon cinereus*; Territoriality; Food asymmetry

TERRITORIALITY can be defined as a suite of behavior patterns by an individual (resident) defending an area (territory) against invasion by other individuals (intruders) (Brown and Orians, 1970). Several studies have examined the behavioral interactions between residents and intruders (e.g., Barnard and Brown, 1982; Davies, 1981), and usually in these studies, residents defeat intruders in disputes over territorial ownership. The observation that "the resident always wins" (Davies, 1978) can be explained by a resident's advantage that leads to an asymmetry in the contest (Maynard Smith and Parker, 1976). There are several reasons why a resident should have an advantage (Parker and Rubenstein, 1981), one of which is that residents have a better knowledge of the disputed area. Barnard

and Brown (1983) eliminated the resident's advantage in their experiment with shrews (*Sorex araneus*) by allowing both contestants to be "residents" in the same area. The only asymmetry, then, was the amount of food that each contestant received before the encounter. They found that the resident that experienced the lower density of food won more disputes. However, Maynard Smith and Parker (1976), with simple "Hawk-Dove" models of game theory, predicted that an increase in aggressive behavior should be favored as the value of the resource increases. Rubenstein (1981) found that pygmy sunfish invest more in fighting under conditions of clumped prey than in conditions of dispersed prey, which is consistent with the Hawk-Dove models.