



ALLEN  
PRESS



---

Population Structure, Growth, and Reproduction in a Vancouver Island Population of the Salamander *Plethodon vehiculum*

Author(s): Kristiina Ovaska and Patrick T. Gregory

Source: *Herpetologica*, Jun., 1989, Vol. 45, No. 2 (Jun., 1989), pp. 133-143

Published by: Allen Press on behalf of the Herpetologists' League

Stable URL: <https://www.jstor.org/stable/3892154>

#### REFERENCES

Linked references are available on JSTOR for this article:

[https://www.jstor.org/stable/3892154?seq=1&cid=pdf-reference#references\\_tab\\_contents](https://www.jstor.org/stable/3892154?seq=1&cid=pdf-reference#references_tab_contents)

You may need to log in to JSTOR to access the linked references.

---

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact [support@jstor.org](mailto:support@jstor.org).

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at <https://about.jstor.org/terms>



Allen Press and Herpetologists' League are collaborating with JSTOR to digitize, preserve and extend access to *Herpetologica*

JSTOR

*Herpetologica*, 45(2), 1989, 133–143  
© 1989 by The Herpetologists' League, Inc.

## POPULATION STRUCTURE, GROWTH, AND REPRODUCTION IN A VANCOUVER ISLAND POPULATION OF THE SALAMANDER *PLETHODON VEHICULUM*

KRISTINA OVASKA AND PATRICK T. GREGORY<sup>1</sup>

*Department of Biology, University of Victoria,  
Victoria, British Columbia, Canada V8W 2Y2*

**ABSTRACT:** We examined patterns of surface activity, population structure, sex ratio, growth, and reproduction in a population of the western red-backed salamander, *Plethodon vehiculum*, using mark-recapture methods, on southern Vancouver Island, British Columbia. Surface activity of adults consisted of spring (March–June) and autumn (September–November) periods with courtship taking place in the autumn. Juveniles remained above ground in midsummer after adults had disappeared, probably into underground refugia. Small salamanders (SVL  $\leq 30$  mm) were found under small rocks and away from discrete cover objects in the leaf litter and under moss more frequently than medium-sized ( $30 < \text{SVL} \leq 40$  mm) and large (SVL  $> 40$  mm) individuals. Growth was rapid during the first year of life (mean increase in SVL = 10.5 mm) and declined steadily thereafter with little growth taking place after sexual maturity was reached. Females attained sexual maturity at a larger size and reached a greater SVL than males. Individual females reproduced at intervals of 2 yr or more. The overall sex ratio of *P. vehiculum* with SVL  $> 40$  mm did not differ from 1:1, but males outnumbered females during most sampling periods, probably due to behavioral differences between the sexes. In general, the life history characteristics of *P. vehiculum* on southern Vancouver Island are similar to those of *Plethodon* in other temperate zone regions with the same length of time available for surface activity. However, annual variations in weather probably have a major effect on specific values of population parameters, and long-term studies are therefore needed to describe life histories adequately.

**Key words:** Population dynamics; Life history; Salamanders; Plethodontidae; *Plethodon vehiculum*

MEASUREMENT of life history traits in natural populations is fundamental for understanding the evolution of life history tactics and for providing a basis for the formulation and testing of specific evolutionary hypotheses. Of particular interest are comparisons of different populations of the same species in different locations to identify environmental effects. Comparison of different, but closely related, species in similar environments may provide evidence for phylogenetic constraints. Salamanders of the family Plethodontidae are in many ways ideal for studies of geographical variation. They are abundant and

have widespread distributions, and the evolutionary relationships among species are fairly well understood (Larson, 1984). In North America, plethodontids exhibit a highly disjunct distribution, and the genera *Plethodon* and *Aneides* consist of eastern and western components that have been separated for approximately 40 million years (Highton and Larson, 1979). Studies of ecology and behavior of North American plethodontids have focused mainly on eastern species while comparatively little is known about western forms. Data on western species are needed to understand the extent of behavioral, ecological, and genetic variation within this family of amphibians.

<sup>1</sup> Author to whom reprint requests should be sent.

The western red-backed salamander, *Plethodon vehiculum*, is abundant in moist forested habitats on the west coast of North America from southern Oregon to southern British Columbia. Peacock and Nussbaum (1973) studied reproductive ecology of *P. vehiculum* in Oregon, but little is known of the ecology and life history of this species elsewhere. However, there is a wealth of comparative information for other, phylogenetically and ecologically closely related species of *Plethodon*. We report and interpret our findings on habitat use, size structure, sex ratios, growth, and reproductive patterns in a population of *P. vehiculum* on southern Vancouver Island, British Columbia.

#### METHODS

We carried out a mark-recapture study of *P. vehiculum* on two plots (A and B) in Goldstream Park, Vancouver Island (48°28' N, 123°32' W). The climate in this area is characterized by mild, wet winters and summers that can be very dry. Snow and below-freezing temperatures are common from December–February. The study area is described in detail elsewhere (Ovaska, 1987).

Plot A consisted of a 10 × 10 m area marked into 100, 1 × 1 m squares; each square in turn was divided into four equal quadrats. Thus, the plot consisted of 400, 0.5 × 0.5 m quadrats. We searched the area for salamanders every 2 wk from 19 March–3 November in 1984, and made two searches, on 3 April and 15 May in 1985. We located salamanders by lifting moss, rocks, and logs on the surface layer and by sifting through the leaf litter, and we then carefully replaced the cover objects. We 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, determined the sex of adults, and noted the reproductive condition of females. We considered a female reproductive if she had eggs visible through the abdominal wall with the diameter of the largest egg at least 2.5 mm. Females with smaller eggs never have sperm in the spermatheca (Peacock and Nussbaum, 1973) or spermatophore caps in their vent, which

would indicate recent mating (Ovaska, 1987; Peacock and Nussbaum, 1973). We considered males with vent lobes and protruding premaxillary teeth (Arnold and Houck, 1982) to be mature. We clipped a unique combination of toes from each salamander and also used any abnormalities in toes and distinctive color patterns in individual recognition. For each capture, we recorded the position of the salamander in the plot (quadrat number) and the type of microhabitat in which it was found (under a large rock with an area of at least 300 cm<sup>2</sup> contacting the ground, under a small rock, under a log, under the moss on top of a rock, under the moss on the ground, in the leaf litter, on the surface). The salamanders were returned to their original locations within 15 min of capture.

Plot B covered an area of approximately 200 m<sup>2</sup> and was 50 m away from Plot A. We numbered all large logs and rocks (with an area of at least 300 cm<sup>2</sup> 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. We carried out irregular searches in midsummer (July–August) and midwinter (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. We handled the salamanders caught on Plot B as on Plot A.

We analyzed the data using the Statistical Analysis System package (SAS Institute, 1985). All the statistical tests used are standard tests described in Sokal and Rohlf (1981). We applied the Yates' correction for continuity in  $\chi^2$ -tests whenever there was only 1 df. The level of significance was set at  $\alpha = 0.05$ .

#### RESULTS

##### *Recapture Frequency*

We captured 817 individuals of *P. vehiculum* on Plot A and 1258 on Plot B during the course of the study. Despite the large number of captures, we did not attempt to estimate the size of the total population by multiple recapture estimators.

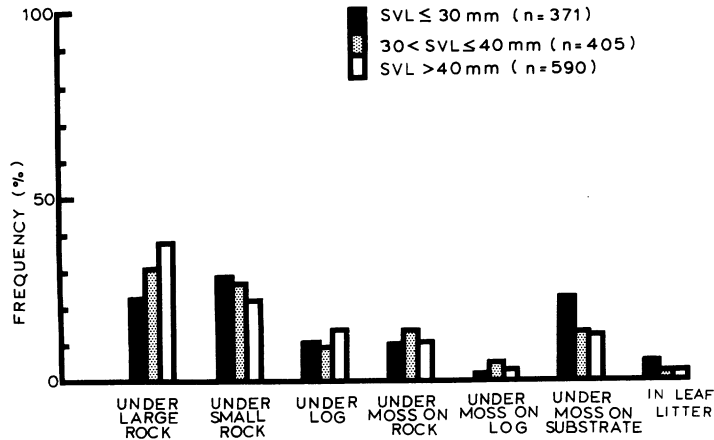


FIG. 1.—Use of cover types by *Plethodon vehiculum* of different size classes on Plot A.

We could not assume that catchability of salamanders was equal at any sampling occasion, as required by these models (Seber, 1982), mainly because an unknown proportion of the population was underground and unavailable for capture at any given time. Instead, we used quadrat sampling to estimate density of *P. vehiculum* on the surface of the forest floor. The number of captures of individuals ranged from 1–15. There were no differences in the frequency of recaptures among salamanders of different size-classes on Plot A, but smaller individuals were recaptured less often than larger ones on Plot B (Table 1). The pattern of recaptures for males and females with SVL > 40 mm differed on Plot A ( $\chi^2 = 20.68$ ,  $df = 5$ ,  $P < 0.001$ , individuals caught six or more times grouped together, 1984–1986 combined), and males were recaptured more frequently than females.

The use of different cover types (large rock, small rock, log, moss on rock, moss on log, moss on substrate, leaf litter) was related to the size of the salamanders (small: SVL ≤ 30 mm; medium: 30 < SVL ≤ 40 mm; large: SVL > 40 mm;  $\chi^2 = 49.60$ ,  $df = 12$ ,  $P < 0.00001$ ; Fig. 1). Small salamanders used small rocks rather than large rocks relatively more often than medium-sized and large individuals ( $\chi^2 = 17.60$ ,  $df = 2$ ,  $P < 0.0003$ ). They also were found away from discrete cover objects in leaf litter and under moss on substrate rela-

tively more frequently than medium-sized and large salamanders ( $\chi^2 = 21.33$ ,  $df = 2$ ,  $P < 0.0001$ ).

#### Population Structure

Juveniles formed a distinct size-class throughout their first year of life on Plot A (Fig. 2). Hatchlings started to appear in late autumn but were not caught in large numbers until the following spring. A second peak in the size-frequency distribution, probably representing salamanders in their second year, is evident during most months; it tends, however, to merge into the next peak consisting of several older age classes. Because of poor catchability of juveniles on Plot B (due to sampling

TABLE 1.—Recapture frequency of small (SVL ≤ 30 mm), medium (30 < SVL ≤ 40 mm), and large (SVL > 40 mm) *Plethodon vehiculum* on Plots A and B, all years combined.

| SVL  | No. of captures per individual |     |    |    |    |    |
|--|--------------------------------|-----|----|----|----|----|
|  | 1                              | 2   | 3  | 4  | 5  | 6+ |
| PLOT A   |                                |     |    |    |    |    |
| Small  | 135                            | 53  | 23 | 10 | 8  | 2  |
| Medium   | 140                            | 55  | 22 | 11 | 7  | 7  |
| Large  | 210                            | 63  | 32 | 14 | 11 | 14 |
| $\chi^2 = 7.58$ , $df = 10$ , $P = 0.67$ .     |                                |     |    |    |    |    |
| PLOT B   |                                |     |    |    |    |    |
| Small  | 214                            | 39  | 16 | 3  | 2  | 2  |
| Medium   | 236                            | 62  | 21 | 9  | 3  | 0  |
| Large  | 380                            | 110 | 70 | 33 | 16 | 42 |
| $\chi^2 = 71.15$ , $df = 10$ , $P < 0.00001$ . |                                |     |    |    |    |    |

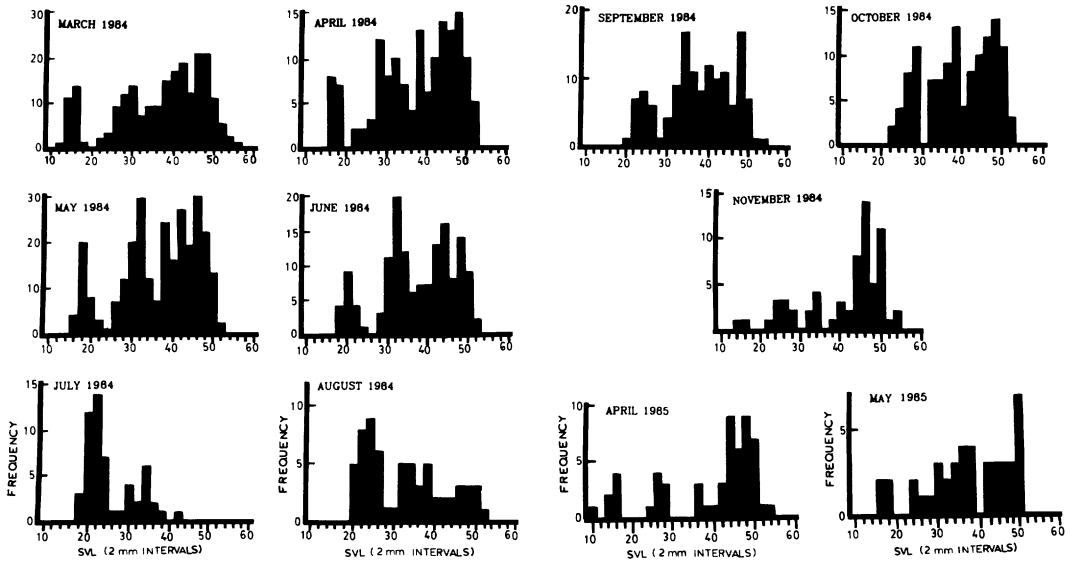


FIG. 2.—Size-frequency distribution of *Plethodon vehiculum* on Plot A per month. For individuals caught more than once in 1 mo, the mean of the measured values was used.

method), the smaller size-classes were greatly under-represented, and those data are not presented here.

The sex ratio of *P. vehiculum* with SVL > 40 mm did not differ from 1:1 on either plot (Plot A: 126 males, 110 females,  $\chi^2 = 0.95$ ,  $df = 1$ ,  $P > 0.05$ ; Plot B: 253 males, 264 females,  $\chi^2 = 0.19$ ,  $df = 1$ ,  $P > 0.05$ ), but the operational sex ratio (ratio of reproductive males to reproductive females) during most capture periods was biased towards males (Fig. 3). The sex of salamanders < 40 mm in SVL could not be determined by external examination.

Males matured at a smaller SVL than females and were, on average, smaller than reproductive females (males:  $\bar{x} = 46.7$  mm, mode = 48.0 mm, SD = 2.65, range = 38–54 mm,  $n = 335$ ; females:  $\bar{x} = 50.9$  mm, mode = 51.0 mm, SD = 2.60, range = 42–58 mm,  $n = 105$ ;  $t$ -test:  $t = 14.29$ ,  $P < 0.001$ ). If juvenile males and females grow at the same rate, then the examination of size-frequency histograms suggests that male *P. vehiculum* reach sexual maturity at the age of 3 yr, whereas the corresponding age for females is approximately 4 yr (Fig. 2).

#### Seasonal Patterns in Activity

Densities of *P. vehiculum* on the surface of the forest floor ranged from 0.30–1.16 individuals/m<sup>2</sup> and were greatest in March–June and in September–October on Plot A (Table 2). Occasional searches during snow-free periods in December–early February yielded no *P. vehiculum* during the course of the study, but we have encountered salamanders on mild winter days in other years. During July and August, the collections on Plot A consisted largely of small salamanders (Table 3). The relative disappearance of adults during July–August was correlated with moisture conditions, and the proportion of large salamanders increased sharply after rainfall (Table 3). Because we sampled salamanders found under cover objects and not in the leaf litter on Plot B, estimates of population density on the forest floor are not meaningful. However, the average number of salamanders per cover object per search on the plot yields an indication of annual and seasonal changes in relative density. The mean number of *P. vehiculum* per cover object varied little between

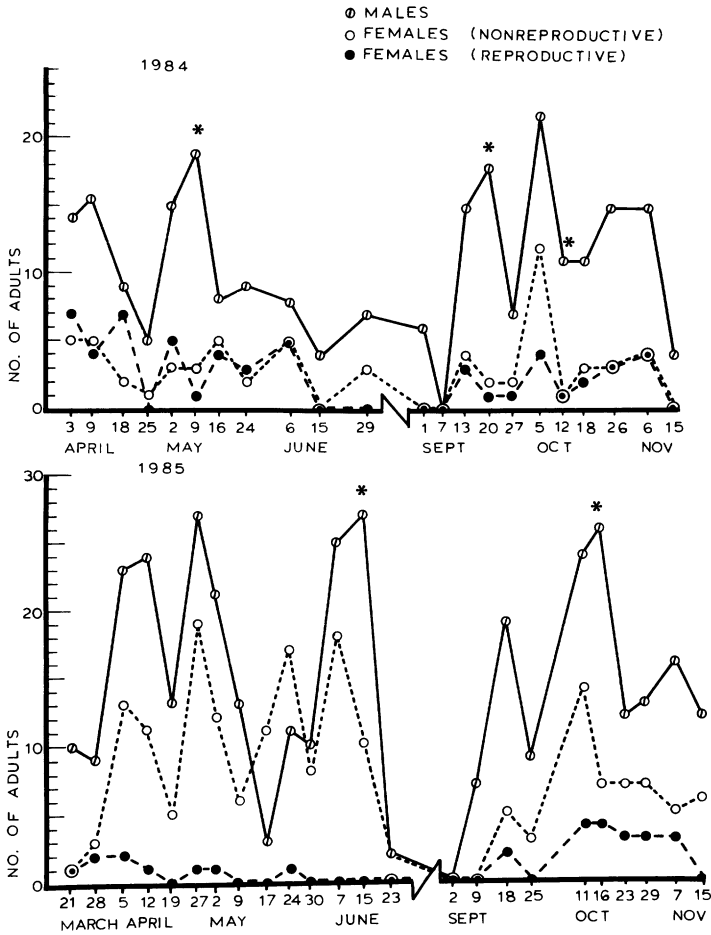


FIG. 3.—Number of adult males and females (reproductive and nonreproductive) per sampling period on Plot B. \* denotes dates when males outnumbered females (reproductive and nonreproductive),  $\chi^2$ -test,  $P < 0.05$ .

1984 and 1985, the years for which complete data exist (1984:  $\bar{x} = 0.35$ ,  $SD = 0.185$ ; 1985:  $\bar{x} = 0.33$ ,  $SD = 0.170$ ;  $t$ -test:  $t = 0.81$ ,  $df = 22$ ,  $P = 0.44$ ). As on Plot A, densities were highest in spring and autumn (March–May:  $\bar{x} = 0.31$  individuals/cover object,  $SD = 0.124$ ; September–November:  $\bar{x} = 0.40$ ,  $SD = 0.160$ , all years combined) and lowest in summer (June–August:  $\bar{x} = 0.23$ ,  $SD = 0.235$ , all years combined). The number of captures of *P. vehiculum* under cover objects on Plot B was greater during wet (rain within the previous 48 h) than during dry (no rain within the previous 48 h) sampling periods in spring, March–May, and autumn, Sep-

tember–November ( $t$ -test:  $t = 5.44$ ,  $P < 0.001$ ; Table 4).

#### Growth Rates

Annual increment in SVL (adjusted to 365 days) was greatest for salamanders in their first year of life and decreased steadily thereafter (Table 5). Little growth could be detected in salamanders with SVL  $> 45$  mm. Individual variation in growth was high, especially among small *P. vehiculum*. The negative values obtained for larger individuals presumably represent measurement errors. Figure 4 shows growth curves for selected individuals on

TABLE 2.—Number of captures of *Plethodon vehiculum* on Plot A per month.

| Month     | No. captures | No. searches/<br>100 m <sup>2</sup> | No./m <sup>2</sup> |
|-----------|--------------|-------------------------------------|--------------------|
| 1984      |              |                                     |                    |
| March     | 232          | 2                                   | 1.16               |
| April     | 156          | 1.5                                 | 1.04               |
| May       | 349          | 2.5                                 | 1.40               |
| June      | 172          | 2                                   | 0.86               |
| July      | 60           | 2                                   | 0.30               |
| August    | 66           | 2                                   | 0.33               |
| September | 151          | 2                                   | 0.76               |
| October   | 150          | 2                                   | 0.75               |
| November  | 66           | 2                                   | 0.33               |
| 1985      |              |                                     |                    |
| April     | 56           | 1                                   | 0.56               |
| May       | 43           | 1                                   | 0.43               |
| Total     | 1501         | 20                                  | 0.75               |

Plot A and illustrates seasonal patterns in growth.

#### Reproductive Patterns of Females

Based on captures of females with spermatophore caps in their vents (two in September, 13 in October, 19 in November; 1984–1986 combined), indicating recent mating, the courtship season peaked in October–November. We found no recently mated females in spring. Reproductive females disappeared from the catchable population after 6 June in 1984 and 24 May in 1985 on Plot B (Fig. 3). One female had enlarged ovarian eggs in October 1984 but not the following March.

We caught a total of 20 individual females (SVL > 43 mm) in spring (March–June) of more than 1 yr. Six of these (30%) had at least a biennial reproductive cycle,

TABLE 3.—Number of small (SVL ≤ 30 mm), medium (30 < SVL ≤ 40 mm), and large (SVL > 40 mm) *Plethodon vehiculum* on Plot A in July and August of 1984.

| Date      | Small | Medium | Large | Rain within<br>the previous<br>48 h |
|-----------|-------|--------|-------|-------------------------------------|
| 6 July    | 13    | 3      | 0     | no                                  |
| 12 July   | 17    | 9      | 0     | no                                  |
| 20 July   | 8     | 0      | 0     | no                                  |
| 27 July   | 9     | 0      | 1     | no                                  |
| 6 August  | 25    | 21     | 14    | yes                                 |
| 22 August | 8     | 0      | 0     | no                                  |

TABLE 4.—Captures of *Plethodon vehiculum* under cover objects on Plot B during wet (rain within the previous 48 h) and dry (no rain within the previous 48 h) sampling days. March–May and September–November, 1984–1986.

| Moisture condition | No. of sampling days | No. of captures | Mean no. of captures/<br>period ± SE |
|--------------------|----------------------|-----------------|--------------------------------------|
| Wet                | 33                   | 1555            | 47.12 ± 2.74                         |
| Dry                | 15                   | 357             | 23.80 ± 1.95                         |

and 14 (70%) reproduced triennially or less often (Table 6). No female that we followed reproduced annually.

## DISCUSSION

### Surface Activity

Growth and reproduction of terrestrial plethodontids are probably related to the length of time available for foraging on the forest floor (Houck, 1977; Jaeger, 1980; Semlitsch and West, 1983). Little or no feeding is thought to take place when the salamanders are below the surface (Fraser, 1976a,b; Maiorana, 1976). Variation in patterns of moisture and temperature most likely governs the level of seasonal activity. In general, eastern plethodontids and those western species inhabiting montane regions have a period of dormancy in the winter, when subfreezing conditions prevent surface activity. The coastal western species, on the other hand, disappear into underground retreats for the summer months, which can be very dry along the Pacific Rim in North America (Houck, 1977).

The surface activity of *P. vehiculum* on southern Vancouver Island consisted of an autumn (September–November) and a spring (March–June) period during the course of the study. Subfreezing temperatures in December–January and lack of rainfall in July–August probably limited surface activity at these times. The disappearance of adults in midsummer appeared directly related to the lack of moisture, because the infrequent heavy rains at this time were followed by brief surges of activity. We have also encountered *P. vehiculum* on the surface on mild days in midwinter, suggesting that weather rather

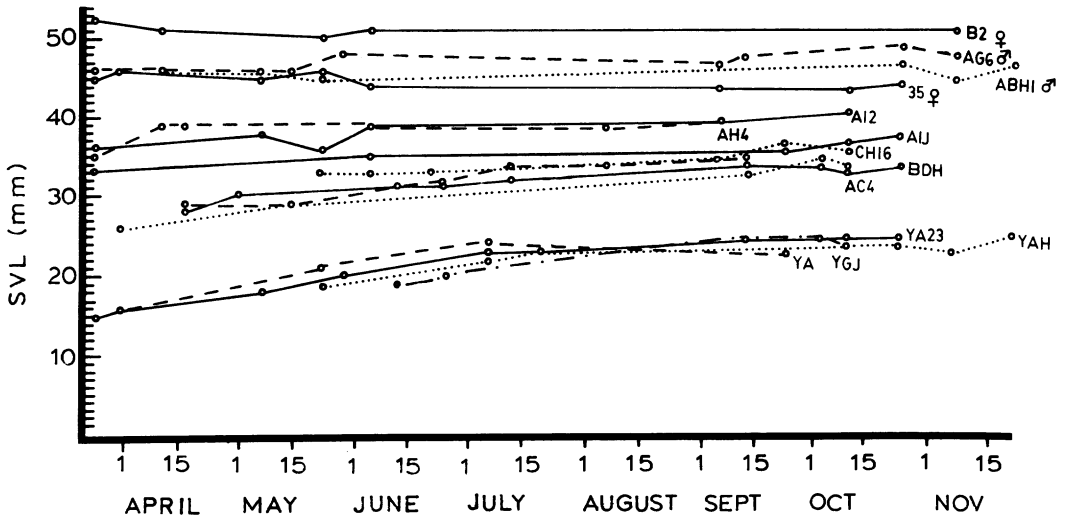


FIG. 4.—Selected growth patterns for individual *Plethodon vehiculum* on Plot A in 1984.

than endogenous factors directly influences the periods of dormancy. We caught more *P. vehiculum* under cover objects during wet than dry sampling periods in spring and autumn. This suggests that part of the population disappears from the surface, probably into underground retreats, even during short-term dry periods. Fraser (1976a) reported a similar pattern for *Plethodon hoffmani*. The percentage of the population on the surface at any one time, and the factors governing it, are virtually unknown for any plethodontid salamander. Peacock and Nussbaum (1973) found *P. vehiculum* on the forest floor during all months of the year except in August in Oregon. Milder winters there probably provide a longer period for surface activity than at the study site on Vancouver Island.

Juveniles disappeared from the surface

TABLE 5.—Absolute growth rates (in mm) of *Plethodon vehiculum* of different size classes per year. Only data for individuals recaptured 365 ± 80 days apart are included (adjusted to 365 days). Data for 1984–1985 and 1985–1986 combined.

| Initial SVL   | $\bar{x}$ | SD  | Min. | Max. | n   |
|---------------|-----------|-----|------|------|-----|
| SVL ≤ 25      | 10.5      | 3.8 | 5.6  | 17.2 | 10  |
| 25 < SVL ≤ 35 | 4.8       | 2.3 | 0    | 10.8 | 25  |
| 35 < SVL ≤ 45 | 1.7       | 1.8 | -2.0 | 7.7  | 48  |
| SVL > 45      | 0.3       | 1.5 | -3.2 | 3.6  | 105 |

later than adults in summer, and first-year young could be found above ground even during the driest periods in July and August. Semlitsch and West (1983) reported a similar pattern for *P. websteri* in South Carolina, where juveniles disappeared from the surface approximately a month later than adults after the onset of dry weather in summer. Juvenile *P. cinereus* also exhibit similar behavior in Virginia (Jaeger, personal communication). This appears somewhat puzzling, because small

TABLE 6.—Reproductive patterns of individual females caught on Plot B in the spring (March–June) of more than 1 yr. R = reproductive (eggs visible through the abdominal wall and the diameter of the largest egg at least 2.5 mm); N = nonreproductive.

| 1984               | 1985 | 1986 | No. of females |
|--------------------|------|------|----------------|
| At least biennial  |      |      |                |
| N                  | ?    | N    | 2              |
| N                  | R    | N    | 2              |
| R                  | N    | ?    | 1              |
| N                  | R    | ?    | 1              |
| Total              |      |      | 6              |
| At least triennial |      |      |                |
| N                  | N    | ?    | 2              |
| ?                  | N    | N    | 8              |
| N                  | N    | R    | 3              |
| R                  | N    | N    | 1              |
| Total              |      |      | 14             |



salamanders dehydrate faster than larger individuals due to their greater surface-area to volume ratios (Spotila, 1972). Small salamanders may not possess sufficient fat reserves to allow for a prolonged dormancy. Juvenile reptiles also often enter hibernation later than adults (e.g., *Sceloporus orcutti*: Weintraub, 1968; *Sceloporus jarrovi*: Ruby, 1977; *Sauromalus obesus*: Smits and Yorke, 1979). This is also found among hibernating mammals (e.g., *Spermophilus lateralis*: Twente and Twente, 1967; *Napaezopaus insignis*: Wrigley, 1972). Small salamanders may be able to obtain sufficient moisture from dew or to utilize moist microhabitats that are unavailable to larger individuals, or they may be excluded from limited underground refuges.

#### Growth Rates

The minimum SVL of hatchlings during this study was 10 mm, but individuals between 15 and 17 mm were more common. On the basis of size at hatching for other species of *Plethodon* with similar-sized eggs, Peacock and Nussbaum (1973) postulated that *P. vehiculum* hatches at approximately 15 mm SVL. Absolute growth rates were greatest during the first year of life and decreased steadily thereafter. Little growth occurred after sexual maturity was reached. The mean absolute increment during the first year, 10.5 mm in SVL, is within the range reported for other terrestrial plethodontids (Hairston, 1983; Houck, 1977; Semlitsch and West, 1983) and is almost identical to what Peacock and Nussbaum (1973) found for *P. vehiculum* in Oregon. This is somewhat surprising, because the longer time available for surface activity there should result in more growth than on Vancouver Island. Peacock and Nussbaum collected *P. vehiculum* during all months throughout the winter, but how many days between the sampling dates were actually favorable for surface activity is unknown. The activity period in Oregon may not be sufficiently longer than on Vancouver Island to permit more growth.

Individual growth patterns showed a

great deal of variability, especially during the first year of life. Jaeger (1980) found that individual variation in foraging success (number of prey items in the stomach/mm of SVL) was great for *P. cinereus* on the forest floor and varied up to 49 times between individuals on any given day. Such variation may result from local differences in the quality of foraging sites or from variation in the amount of time individual salamanders spend underground. Both of these factors could contribute to variability in growth rates. Low vagility of small salamanders, as well as their requirement of prey of small size, may attenuate the effects of patchiness of habitat for these individuals.

Mature females were larger than males, as Peacock and Nussbaum (1973) also found for *P. vehiculum*. Females could attain a greater size by growing faster during the early years and/or by reaching sexual maturity later than males. The sex of immature salamanders could not be determined by external examination, and therefore it is not possible to distinguish between these possibilities. Clutch size shows a positive correlation with body size of females in many plethodontids (Tilley, 1977). A similar relationship exists for *P. vehiculum* (Peacock and Nussbaum, 1973), and may partly explain the relatively large body size achieved by females at sexual maturity compared with that of males.

#### Sex Ratios

The overall sex ratio of *P. vehiculum* with SVL > 40 mm was 1:1 as Peacock and Nussbaum (1973) also reported. The sex ratio during any given capture period, however, was variable and tended to be biased towards males at all times of the year. The number of recaptures of male *P. vehiculum* was greater than that of females, suggesting behavioral differences in activity between the sexes. Males may spend more time on the surface of the forest floor than females in search of mating opportunities. The operational sex ratio was greatly biased towards males during any one sampling period presumably because males, unlike females, reproduce annually.

### Reproduction

Courtship in eastern species of *Plethodon* is usually interrupted by the winter and occurs in autumn and early spring with oviposition taking place in late spring–early summer (Houck, 1977). Timing of courtship in western *Plethodon* is less well known. Peacock and Nussbaum (1973) found that male *P. vehiculum* were in breeding condition from autumn to spring, but that the proportion of males having sperm in the vasa deferentia decreased after January. Field observations of recently mated females by the same authors supported the notion that the mating season peaked in December–January in Oregon. We commonly found females with spermatophore caps in the vent between September and November but never in spring, suggesting that autumn is the primary mating season for *P. vehiculum* on Vancouver Island. Only females with large eggs (diameter > 2.5 mm) had spermatophore caps, and these females probably oviposited the following spring. Peacock and Nussbaum (1973) reported that spent females never had sperm in the spermatheca, indicating that sperm are not stored over several breeding seasons. The disjunction of insemination and oviposition allows a female to mate as soon as her eggs reach a certain size, thus ensuring fertilization. Why autumn rather than spring should be the primary mating season is not known. Although multiple matings were not observed in the field, laboratory data indicate that females are capable of mating several times during one mating season (Ovaska, 1987). The lack of such observations in the natural habitat may merely reflect low catchability of reproductive females. Multiple inseminations also are known to occur in *Desmognathus ochrophaeus* (Tilley and Hausman, 1976) and in *Ensatina eschscholtzii* (Stebbins, 1954).

The reproductive cycles of females show considerable intra- and interspecific variability, but such cycles are often not annual among plethodontids in the temperate zone (Tilley, 1977). Within the genus *Plethodon*, annual reproduction has been

reported for a coastal population of *P. cinereus* (Houck, 1977), for *P. glutinosus* at the southern part of its range (Highton, 1956), and for *P. websteri* in South Carolina, where the length of active season is about 8 mo (Semlitsch and West, 1983). Peacock and Nussbaum (1973) found that about half of the mature females of *P. vehiculum* were in reproductive condition at any one time, and they inferred that females reproduced every other year. Reproductive histories of individual females from our study indicate that *P. vehiculum* may reproduce every third year or even less often on Vancouver Island. Similar low rates of reproduction also occur in *P. larsoni*, a western montane species (Herrington and Larsen, 1987). A 3-yr study is not long enough to examine the regularity of reproductive cycles in animals with such a low frequency of reproduction. Tilley (1977) suggested for *D. ochrophaeus* and Hairston (1983) for *P. jordani* that reproductive patterns of individual females may be flexible and may reflect the ability of the females to accumulate sufficient energy reserves for breeding; this in turn may be influenced by fluctuations in environmental conditions. The low frequency of reproduction found for *P. vehiculum* could be a result of adverse environmental conditions during or immediately prior to the study and may not represent a general pattern. Flexibility in reproduction could be a response to uncertainty in yearly patterns of rainfall and thus the time available for foraging.

Maternal care occurs in most terrestrial plethodontids, and females brood their clutches for several months, during which time they forego foraging (Forester, 1974, 1979; Organ, 1961). Houck (1977) suggested that biennial or less frequent reproductive patterns of female plethodontids may be a consequence of brooding behavior, as the females will not have enough time for foraging and acquiring energy for the development of a new clutch the following year. The relative energetic costs of parental behavior for female *P. vehiculum*, however, may not be extensive, because the entire adult population

disappears underground in summer when brooding takes place.

#### Habitat Use

Hatchlings started to appear on the surface in late autumn but were not caught in large numbers until the following spring. Peacock and Nussbaum (1973) found that hatchlings did not appear in collections until the ground was soaked with rain in late autumn-early winter. They suggested that the young remain in the vicinity of the nests for some time, as hatchlings of *P. cinereus* do (Burger, 1935; Piersol, 1910; Test, 1955). Hatchlings, therefore, may not usually be encountered on the forest floor until they disperse from these localized sites.

Salamanders of different size classes used different cover types on Plot A. Small salamanders were frequently found under small cover objects or under moss or leaf litter on the forest floor, whereas larger individuals preferred rocks and logs of larger size. This difference in habitat use likely accounts for the low catchability of juveniles on Plot B, where only the larger cover objects were lifted. Keen (1982) found that adults of both *Desmognathus monticola* and *D. fuscus* showed a preference for large cover objects over small ones and suggested that these cover objects provide consistently moist microhabitats where the salamanders can forage and be protected from predators.

#### Conclusions

Population characteristics of *P. vehiculum* appeared similar to those of other species of *Plethodon* in areas with a temperate climate and consisted of (a) rapid growth in the first year of life with little growth occurring after sexual maturity is reached, (b) a high degree of individual variation in growth, especially during the first year, (c) even adult sex ratios, (d) maturation of females at a larger size than males, and (e) less frequent than annual reproductive patterns for females. The length of time available for surface activity probably influences these characteristics by governing feeding rates. The pat-

terns of surface activity (seasonal patterns, the proportion of the population on the surface at any one time) are likely shaped by environmental and social factors, and the examination of their interactions in populations living under different climatic regimes provides a fruitful area for further study.

*Acknowledgments.*—This paper is based on material from a Ph.D. dissertation of the senior author submitted to the University of Victoria. Support for the study came from a Natural Sciences and Engineering Research Council (NSERC) Postgraduate Scholarship to KO and from a NSERC Operating grant to PTG. We thank reviewers of an earlier version of this paper for their helpful comments.

#### LITERATURE CITED

- ARNOLD, S. J., AND L. D. HOUCK. 1982. Courtship pheromones: Evolution by natural and sexual selection. Pp. 173-312. In M. H. Nitecki (Ed.), *Biochemical Aspects of Evolutionary Biology*. University of Chicago Press, Chicago.
- BURGER, J. W. 1935. *Plethodon cinereus* (Green) in eastern Pennsylvania and New Jersey. *Am. Nat.* 69:578-586.
- FORESTER, D. C. 1974. Parental Care in *Desmognathus ochrophaeus* Cope (Urodela: Plethodontidae): A Behavioral Study. Ph.D. Dissertation, North Carolina State University, Raleigh, North Carolina.
- . 1979. The adaptiveness of parental care in *Desmognathus ochrophaeus* (Urodela: Plethodontidae). *Copeia* 1979:332-341.
- FRASER, D. F. 1976a. Empirical evaluation of the hypothesis of food competition in salamanders of the genus *Plethodon*. *Ecology* 57:459-471.
- . 1976b. Coexistence of salamanders in the genus *Plethodon*: A variation of the Santa Rosalia theme. *Ecology* 57:238-251.
- HAIRSTON, N. G. 1983. Growth, survival and reproduction of *Plethodon jordani*: Trade-offs between selective pressures. *Copeia* 1983:1024-1035.
- HERRINGTON, R. E., AND J. H. LARSEN. 1987. Reproductive biology of the Larch Mountain salamander, *Plethodon larselli*. *J. Herpetol.* 21:48-56.
- HIGHTON, R. 1956. The life history of the slimy salamander, *Plethodon glutinosus*, in Florida. *Copeia* 1956:75-93.
- HIGHTON, R., AND A. LARSON. 1979. The genetic relationships of the salamanders of the genus *Plethodon*. *Syst. Zool.* 28:579-599.
- HOUCK, L. D. 1977. Life history patterns and reproductive biology of neotropical salamanders. Pp. 43-72. In D. H. Taylor and S. I. Guttman (Eds.), *The Reproductive Biology of Amphibians*. Plenum Press, New York.
- JAEGER, R. 1980. Fluctuations in prey availability and food limitation for a terrestrial salamander. *Oecologia* 44:335-341.
- KEEN, W. H. 1982. Habitat selection and interspe-

- cific competition in two species of plethodontid salamanders. *Ecology* 63:94-102.
- LARSON, A. 1984. Neontological inferences of evolutionary pattern and process in the salamander family Plethodontidae. Pp. 119-217. *In* M. K. Hecht, B. Wallace, and G. T. Prance (Eds.), *Evolutionary Biology*, Vol. 17. Plenum Press, New York.
- MAJORANA, V. C. 1976. Size and environmental predictability for salamanders. *Evolution* 30:599-613.
- ORGAN, J. A. 1961. Studies on the local distribution, life history, and population dynamics of the salamander genus *Desmognathus* in Virginia. *Ecol. Monogr.* 31:189-220.
- OVASKA, K. 1987. Social Behavior of the Western Red-backed Salamander, *Plethodon vehiculum*. Ph.D. Dissertation, University of Victoria, Victoria, British Columbia.
- PEACOCK, R. L., AND R. A. NUSSBAUM. 1973. Reproductive biology and population structure of the western red-backed salamander, *Plethodon vehiculum* (Cooper). *J. Herpetol.* 7:215-224.
- PIERSOL, W. H. 1910. The habitats and larval state of *Plethodon cinereus erythronotus*. *Trans. Can. Inst.* 8:469-492.
- RUBY, D. E. 1977. Winter activity in Yarrow's spiny lizard, *Sceloporus jarrovi*. *Herpetologica* 33:322-333.
- SAS INSTITUTE. 1985. SAS User's Guide: Statistics, Version 5 ed. SAS Institute, Cary, North Carolina.
- SEBER, G. A. F. 1982. The Estimation of Animal Abundance and Related Parameters, 2nd ed. Macmillan, New York.
- SEMLITSCH, R. D., AND C. A. WEST. 1983. Aspects of the life history and ecology of Webster's salamander, *Plethodon websteri*. *Copeia* 1983:339-346.
- SMITS, A. W., AND C. D. YORKE. 1979. Winter activity and mortality in juvenile chuckwallas (*Sauromalus obesus*). *J. Herpetol.* 14:100-101.
- SOKAL, R. R., AND F. J. ROHLF. 1981. *Biometry*, 2nd ed. W. H. Freeman, San Francisco.
- SPOTILA, J. R. 1972. Role of temperature and water in the ecology of lungless salamanders. *Ecol. Monogr.* 42:95-125.
- STEBBINS, R. C. 1954. Natural history of the plethodontid salamanders of the genus *Ensatina*. *Univ. California Publ. Zool.* 54: 47-124.
- TEST, F. H. 1955. Seasonal differences in populations of the redbacked salamander in southeastern Michigan. *Pap. Michigan Acad. Sci. Arts Letters* 40:137-153.
- TILLEY, S. G. 1977. Studies of the life histories and reproduction in North American plethodontid salamanders. Pp. 1-41. *In* D. H. Taylor and S. I. Guttman (Eds.), *The Reproductive Biology of Amphibians*. Plenum Press, New York.
- TILLEY, S. G., AND J. S. HAUSMAN. 1976. Allozymic variation and occurrence of multiple inseminations in populations of the salamander *Desmognathus ochrophaeus*. *Copeia* 1976:734-741.
- TWENTE, J. W., AND J. A. TWENTE. 1967. Seasonal variation in the hibernating behavior of *Citellus lateralis*. Pp. 47-63. *In* C. P. Lyman, E. Schonbaum, and F. E. South, Jr. (Eds.), *Mammalian Hibernation III*. Oliver & Boyd, London.
- WEINTRAUB, J. D. 1968. Winter behavior of the granite spiny lizard, *Sceloporus orcutti* Stejneger. *Copeia* 1968:708-712.
- WRIGLEY, R. E. 1972. Systematics and biology of the woodland jumping mouse, *Napaeozapus insignis*. *Illinois Biol. Monogr.* 47:1-118.

Accepted: 1 August 1988

Associate Editor: Raymond Semlitsch