Reproductive Biology and Population Structure of the Western Red-backed Salamander, *Plethodon vehiculum* (Cooper)

Robert L. Peacock and Ronald A. Nussbaum

Phoenix High School, Phoenix, Oregon and Department of Zoology,
Oregon State University, Corvallis, Oregon 97331

ABSTRACT—Certain aspects of the life history of *Plethodon vehiculum* from Benton and Lincoln Cos., Oregon, were studied. Mating occurs primarily from November through January with oviposition in the spring. The number of yolky ovarian ova is a function of body size; the mean for all sizes was 10.4/female. Incubation is in the summer, with hatching in the fall at 13 to 15 mm SVL. Growth rates for both sexes are about 10 mm SVL/year for the first 3 years. Both sexes mature between their second and third years: males at 42 mm SVL and females at 44 mm SVL. Females have a biennial gonadal cycle as has been described for other species of *Plethodon,* and males have an annual cycle. Spermatogenesis begins in the spring and culminates in the fall. Mature females are larger (mean SVL = 49.1 mm) than mature males (mean SVL - 45.7 mm). In general, *P. vehiculum,* a western plethodon, has a life history similar to that of eastern small and eastern large plethodons.

* * *

The genus *Plethodon* can be divided into 3 natural groups (Grobman, 1944; Highton 1962a): the eastern large plethodons, the eastern small plethodons, and the western plethodons. Highton (1956, 1962b) and Pope and Pope (1949) described the reproductive cycle of the slimy salamander, *Plethodon glutinosus,* an eastern large plethodon; and Sayler (1966) studied the reproductive ecology of the red-backed salamander, *Plethodon cinereus,* an eastern small plethodon. Werner (1971) provided further notes on *P. cinereus,* and the reproductive biology of a second eastern small plethodon, the northern ravine salamander, *Plethodon richmondi richmondi,* was studied by Angle (1969). The geographically isolated Jemez Mountains salamander, *Plethodon neomexicanus,* is thought to be related to the eastern small plethodons (Highton, 1962a); and its reproductive biology has recently been examined (Reagan, 1972). To date, none of the western plethodons has been studied in any detail with regard to the reproductive cycle and population structure.

The western red-backed salamander, *Plethodon vehiculum,* occurs in the humid coastal forests of western Oregon and Washington and is found northward as far as southwestern British Columbia, including Vancouver Island. Although common throughout its range, little is known of its habits and life history. There are no records of eggs collected in the field; however, gravid females have been induced to oviposit during the month of May in the laboratory (Stebbins, 1951). Dumas (1953) suggested that in Oregon *P. vehiculum* has no well-defined breeding season, and that in some males "testicular activity" occurs throughout the year.

The purpose of this investigation was to gain an understanding of the reproductive biology and population structure of *P. vehiculum* within a limited geographic area, in order to form a basis for comparison with other populations of *P. vehiculum* and with other members of the genus, both on the species and group level.

MATERIALS AND METHODS

In this study, 1002 *P. vehiculum* were collected at monthly intervals from April 1969 to July 1970 in Benton and Lincoln Counties, Oregon. August, 1969 was eliminated from analysis because dry, hot weather prevented us from collecting an adequate sample.

All measurements were made on preserved specimens. The animals were killed in 0.2 per cent chlorobutanol, straightened and fixed in 10 per cent buffered formalin for 24 hrs, washed in water for 24 hrs, and preserved in 50 per cent isopropyl alcohol. Snout to vent (SVL) measurements were made with vernier calipers from the tip of the snout to the anterior angle of the cloaca. Internal measurements were made with an ocular micrometer in a stereomicroscope, and included lengths of testes and ovaries, and diameters of testes, vasa deferentia, ovaries, and oviducts measured at three points (anterior, middle, and posterior). Measurements were recorded for both the right and left reproductive tracts. However, there were no significant differences between right and left sides, so with the exception of egg counts, only data for the right side are presented below.

To determine the time of mating and the length of time spermatozoa were retained by the female, a portion of tissue immediately posterior to the pelvic girdle was removed by dissection as explained by Sayler (1966). This tissue, including the cloaca and spermatheca, was embedded in paraffin using the dioxane method, sectioned (9μ), and mounted on slides. The sections were stained in a modified alum hematoxylin stain and counterstained in eosin Y as described by Galigher and Kozloff (1964).

The progress of the spermatic wave was determined by examination of smears taken at different regions of the testes and vasa deferentia. Males were considered sexually mature if the testes and/or vasa deferentia contained spermatozoa. Adult females were distinguished from subadult females on the basis of the size of ovarian eggs and SVL. It was impossible to accurately determine sex, by macroscopic means, of salamanders smaller than 30 mm SVL. For the purpose of this study, *P. vehiculum* 30 mm SVL and less were classed as unsexed juveniles.

MALE REPRODUCTIVE CYCLE

There is no evidence of spermatogenesis in males less than 41 mm SVL. Monthly variation in the size of the testes of mature males ($\geqslant$42 mm SVL) is summarized in Table 1. The diameter of the posterior portion of the testis increases in the spring to attain maximum size in June. Similarly, the maximum diameters of the middle and anterior portions of the testis occur in June and July. Minimum sizes are September and October for the posterior testis and December for both the middle and anterior testis. The testis is longest in June and shortest in December. Since testicular enlargement indicates active spermatogenesis, these data suggest that spermatogenesis begins in spring, progresses through the summer, and culminates in the fall.

By late fall (November) the vasa deferentia have swollen to maximum size (Fig. 1), and the posterior portions are particularly enlarged at this time. From September to December, 100 per cent of the mature males examined had spermatozoa in their posterior vasa deferentia (Table 2). Based on these observations, males may be in breeding condition from fall to early spring. However, the decrease in size of the vasa deferentia in December and January (Fig. 1), and the lowered percentage of males with spermatoza in their posterior vasa deferentia in January and thereafter suggests that November to January may be the peak season for spermatophore transfer. Field observations support the contention that peak mating activity occurs during these months. Thirteen females, collected at 3 different localities within the study area had spermatophores in their cloacae. Eight of these were found in December and 5 in January. In

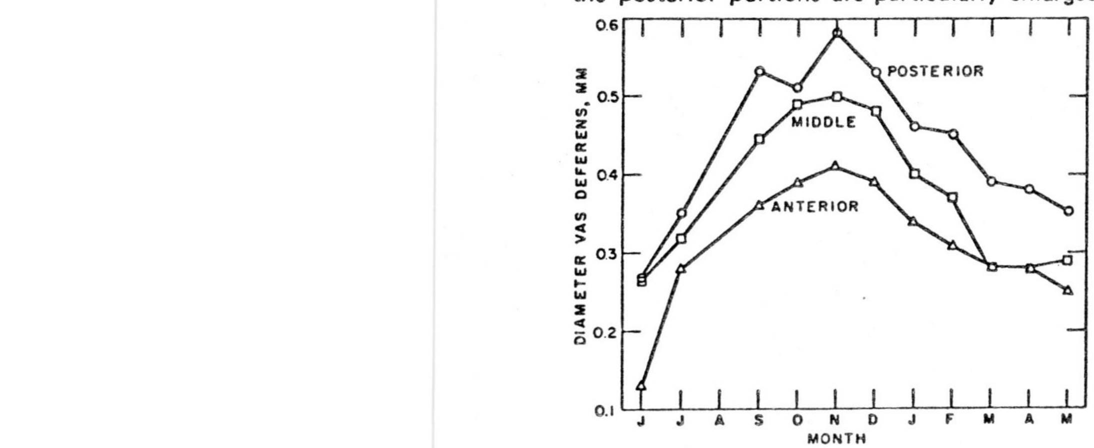
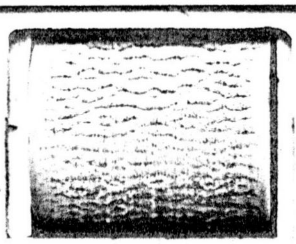


FIGURE 1. Seasonal variation in the diameter of the vas deferens in mature *P. vehiculum*.

TABLE 1. Condition of the male reproductive organs during each month of the year except for August. $\bar{x}$ = mean, R = range, SE = standard error.

		Snout-vent length	Testis length	Anterior testis diameter	Middle testis diameter	Posterior testis diameter	Anterior vas deferens diameter	Middle vas deferens diameter	Posterior vas deferens diameter	n
June	$\bar{x}$	45.0	12.3	2.20	2.50	2.40	0.13	0.27	0.27	6
	R	42.0-48.0	10.3-14.7	2.00-2.40	2.40-2.70	2.00-2.70	0.00	0.00	0.00	
	SE	1.04	0.66	0.07	0.06	0.11	0.00	0.00	0.00	
July	$\bar{x}$	47.3	12.1	2.20	2.40	2.10	0.28	0.32	0.35	10
	R	42.7-49.9	10.0-13.3	1.10-2.70	1.30-2.70	1.20-2.70	0.13-0.40	0.27-0.53	0.27-0.53	
	SE	0.64	0.31	0.15	0.13	0.16	0.02	0.04	0.04	
September	$\bar{x}$	44.5	10.1	2.10	2.00	1.40	0.36	0.44	0.53	14
	R	42.3-47.4	8.10-11.5	1.60-2.50	1.30-2.40	0.70-1.90	0.27-0.40	0.27-0.53	0.27-0.67	
	SE	0.52	0.31	0.07	0.08	0.08	0.02	0.02	0.02	
October	$\bar{x}$	49.5	10.5	1.90	2.20	1.40	0.39	0.49	0.51	10
	R	45.3-51.6	8.70-12.3	0.93-2.40	1.60-2.40	0.93-2.00	0.27-0.40	0.40-0.53	0.40-0.67	
	SE	0.68	0.36	0.13	0.09	0.12	0.01	0.02	0.03	
November	$\bar{x}$	47.8	10.4	1.90	2.10	1.60	0.41	0.50	0.58	9
	R	42.1-53.3	9.20-12.0	1.20-2.70	1.70-2.70	1.20-2.00	0.27-0.53	0.40-0.53	0.53-0.80	
	SE	1.20	0.39	0.15	0.11	0.10	0.03	0.02	0.03	
December	$\bar{x}$	44.4	9.20	1.50	1.70	1.50	0.39	0.48	0.53	23
	R	42.0-47.1	6.90-12.1	1.10-2.30	1.30-2.10	1.30-2.10	0.27-0.40	0.40-0.53	0.40-0.67	
	SE	0.35	0.24	0.06	0.05	0.05	0.01	0.01	0.02	
January	$\bar{x}$	45.4	9.70	1.60	1.90	1.60	0.34	0.40	0.46	33
	R	42.1-49.6	6.00-12.0	0.67-2.30	1.30-2.80	0.80-2.30	0.13-0.40	0.13-0.53	0.13-0.67	
	SE	0.35	0.22	0.06	0.06	0.06	0.01	0.02	0.02	
February	$\bar{x}$	46.3	10.9	1.60	2.00	1.80	0.31	0.37	0.45	24
	R	42.2-53.2	8.70-14.0	0.67-2.30	1.10-2.70	1.10-2.40	0.13-0.40	0.13-0.53	0.27-0.67	
	SE	0.64	0.29	0.09	0.08	0.07	0.02	0.02	0.03	
March	$\bar{x}$	46.6	10.4	1.60	2.10	1.70	0.28	0.34	0.39	22
	R	42.0-50.4	7.50-14.9	0.53-2.40	0.67-2.70	0.67-2.30	0.13-0.40	0.13-0.40	0.13-0.53	
	SE	0.52	0.40	0.09	0.10	0.08	0.02	0.02	0.02	
April	$\bar{x}$	44.4	10.7	1.90	2.20	1.90	0.28	0.34	0.37	33
	R	42.0-51.2	7.30-14.7	1.10-2.70	1.60-3.10	1.10-2.70	0.13-0.40	0.13-0.40	0.13-0.53	
	SE	0.41	0.25	0.08	0.06	0.07	0.01	0.01	0.02	
May	$\bar{x}$	45.2	10.1	1.80	2.20	2.00	0.25	0.29	0.35	8
	R	43.1-49.0	8.70-11.6	0.93-2.40	1.10-2.70	1.30-2.30	0.13-0.27	0.13-0.40	0.27-0.53	
	SE	0.75	0.37	0.18	0.22	0.14	0.02	0.03	0.03	



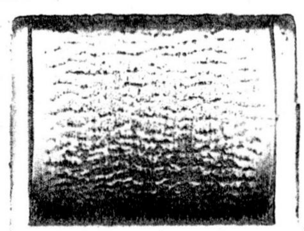


TABLE 2. Per cent of mature males with spermatoza in the testis and/or vas deferens.

Month	J	J	A	S	O	N	D	J	F	M	A	M
Sample Size	6	10	1	14	10	9	23	33	24	22	33	8
posterior testis	100	20	100	21	0	11	0	0	0	0	0	0
anterior testis	17	30	100	100	60	44	9	0	0	0	0	0
anterior vas deferens	0	30	0	100	100	100	100	85	75	64	74	50
posterior vas deferens	0	40	0	100	100	100	100	94	88	77	76	63

addition, paired adults were frequently found under surface objects during December and January.

FEMALE REPRODUCTIVE CYCLE

Subadult females (30 to 43 mm SVL) contain numerous, yolkless ova smaller than 0.9 mm diameter; and they have small (mean diameter 0.22 ± 0.01 mm), straight oviducts.

Two groups of adult females (44 to 58 mm SVL) can be recognized. Individuals of the first group contain relatively small, yolked, ovarian eggs ranging in diameter from 1.0 to 2.0 mm. Their oviducts are slightly convoluted and larger (mean diameter 0.84 ± 0.02 mm) than oviducts of subadult females. The second group is characterized by adult females with large, yolked, ovarian ova (3.0 to 4.3 mm diameter) and highly swollen (mean diameter 1.67 ± 0.06 mm) and convoluted oviducts. The mean SVL of the first group is 48.6 mm (n=104, se=0.35), and 49.5 mm (n=55, se=0.42) for the second group. The difference between these means (0.9 mm) is not significant at the 0.05 level.

Because the size distribution of ova in mature females is bimodal, a biennial breeding cycle is postulated for female *P. vehiculum.* Females of the first group would not have oviposited until the year after they were collected, while females of the second group were ready to oviposit the same year they were collected. Females in the first group probably consist of older, spent females and young females that have never oviposited. That this group is not composed entirely of young females that have yet to oviposit is shown by the lack of correlation between ovum diameter and SVL for this group (Fig. 2). A positive correlation is seen only in subadult females (Fig. 2). The difference in sample size between the two groups of females may reflect the facts that females about to oviposit are more difficult to find and that females with small ova include recruits from the subadult category.

The cloaca and adjacent tissue of 32 females of the first group were sectioned. None of the cloacae contained spermatophores, nor were spermatozoa present in any of the 32 spermathacae. Of 32 females of the second group, collected from October to April, 31 contained spermatozoa, either in the tubules or in the lower tract of the spermathecae. The one exception was the female caught earliest in the fall season (early October). Furthermore, the 13 females collected in December and January with spermatophores in their vents all contained large, yolky ova, and hence were females of the second group. These limited data suggest that only females ready to oviposit (second group females) will mate during a given mating season, and that spermatozoa are not retained in the spermathecae for any appreciable time after the eggs have been deposited. Sayler (1966) reported similar observations for *P. cinereus,* as did Reagan (1972) for *P. neomexicanus.*

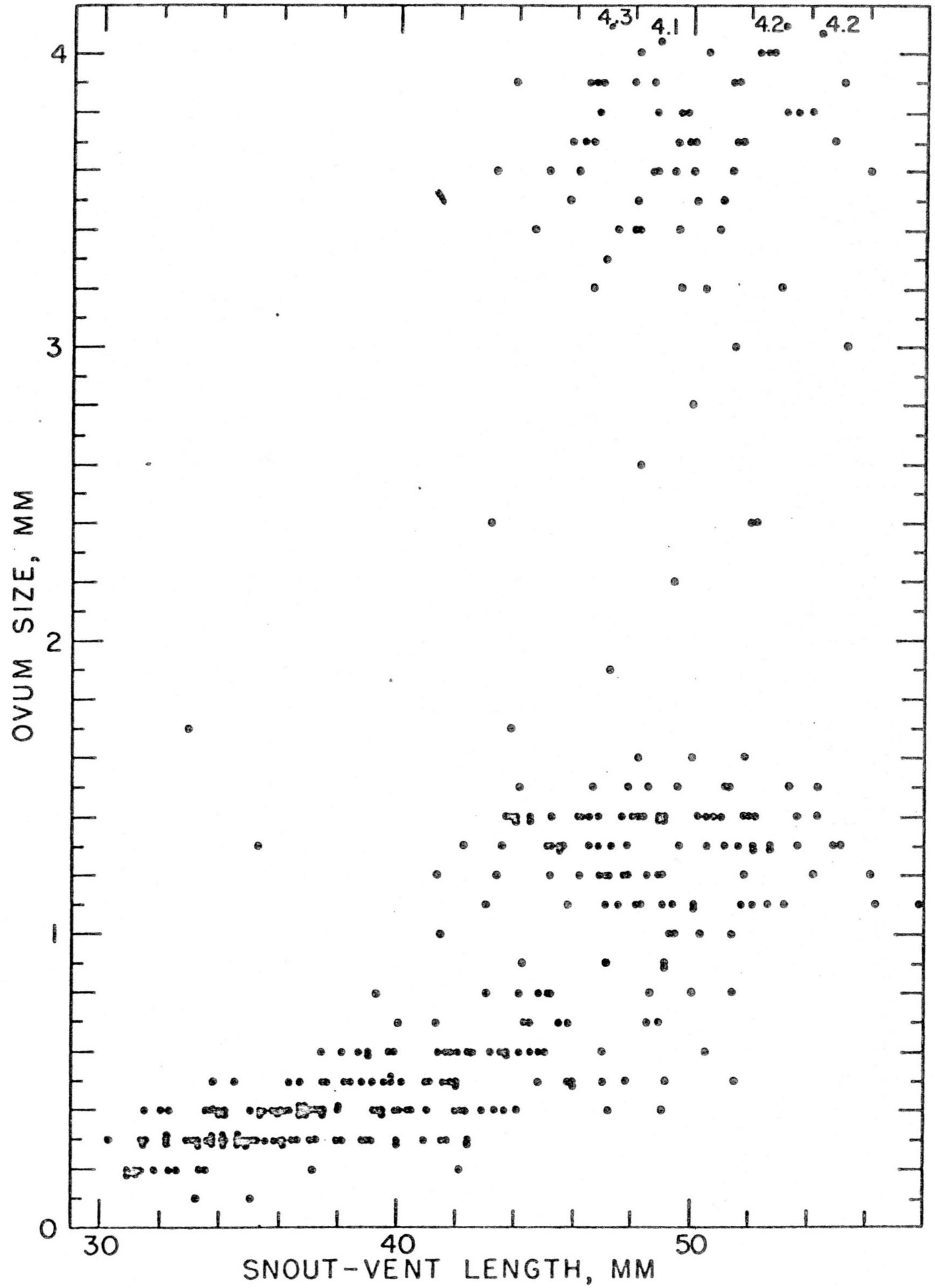


FIGURE 2. Size of ovarian ova as a function of snout-vent length in *P. vehiculum*. Three groups are recognized: subadults, and two groups of adults.

No clutches of eggs, recently spent females, nor females with oviducal eggs were found during this study. Therefore we can only deduce the time of oviposition and the length of the incubation period from indirect evidence. Since courtship activity is at a peak in December and January, egg-laying must occur sometime thereafter, in spring or early summer. No females with large ova were collected from May to August; presumably this is the period of incubation. Females probably remain with their clutches as do the females of most plethodontid species. The nest sites are obviously well-hidden, probably situated deep in talus or in cracks in solid rock. Deep-lying nest sites would not only protect the eggs from high temperatures and predators, but also prevent dessication of the embryos and hatchlings, an important consideration since summers are usually exceedingly dry in the Coast Range. The incubation period is probably 60 to 90 days, as for other plethodons with eggs of similar size. Observations on the closely related and sympatric *P. dunni* support these contentions. Dumas (1955) found recently deposited eggs and an attending female *P. dunni* on 6 July 1952, 15 inches back in a rock crevice. The eggs were incubated at 13 C in the laboratory (the temperature of the nest site) and were ready to hatch 70 days later in September.

FECUNDITY

In 65 females with eggs 3.0 mm in diameter and larger, the mean number of eggs in the left ovary was 4.97 (s.e.=0.224) and the mean number for the right ovary was 5.46 (s.e.=0.251). The difference is not significant at this sampling intensity at the 0.05 level. Freiburg (1954) reported an average of 3.6 eggs/ovary for females from the same general area.

There is a significant, positive correlation between egg number and SVL (Fig. 3), but the relationship is probably exponential rather than linear. More data are needed for exceptionally large females in order to answer this question.

POPULATION STRUCTURE, GROWTH, AND SIZE

There is no direct evidence for the size of *P. vehiculum* at hatching. Individuals 16 mm SVL are common, and we have collected a few which were 15 mm SVL. Brodie (1970) reported one specimen 13 mm SVL. Based on known sizes at hatching for other plethodons with eggs of similar size, we believe that hatching normally occurs at about 15 mm SVL. There is probably enough yolk left at the time of hatching to allow for an additional 1 to 3 mm increase in SVL before feeding becomes necessary.

Hatchlings are not abundantly collected until late fall or early winter when the ground is soaked with rain. The modal SVL of this zero-age-class for December and January is 17 mm SVL. Peak hatching occurs a few months earlier, probably in August or September. Upon hatching, the young are likely to remain in the vicinity of the nest for up to one month as reported for *P. cinereus* (Burger, 1935; Piersol, 1910; Test, 1955). During this period, most of the remaining yolk is absorbed, and with the advent of the late fall and early winter rains, the hatchlings are ready to disperse and feed.

Figure 4 illustrates a cross-section of the population in January. Two size-classes of juveniles are evident: one with a modal SVL of 17 mm (zero-age-class) and another with a modal SVL of 27 mm (first year age-class). A group of subadult females is distinguishable in the histogram. These females average 37.4 mm SVL and are in the second year age-class. Mature females (third year age-class and older) are represented by the fourth peak on the upper side of the histogram (mean SVL=49.1 mm). This fourth group of females is heterogeneous in that different age-classes are represented. Younger, mature females have caught up in size with older, mature females in which growth has slowed, so that a "piling up" of age-classes has occurred.

The histogram of Figure 4 does not distinguish a well-defined third and fourth group of males. However, the indistinct peak at 38 mm may represent the second year age-class of

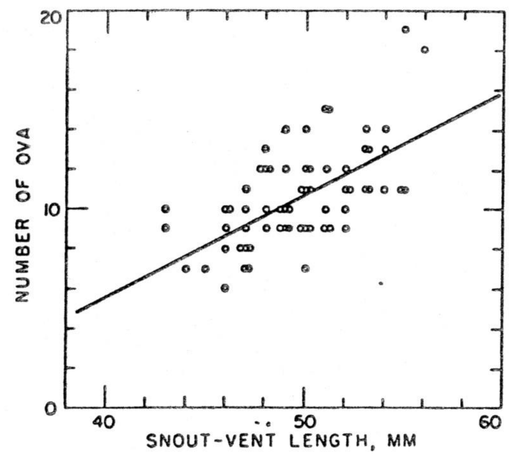


FIGURE 3. Ovarian egg number in relation to snout-vent length. Least squares fit. a=–14.94 se=4.38; b=0.51, se=0.09; r=0.59.

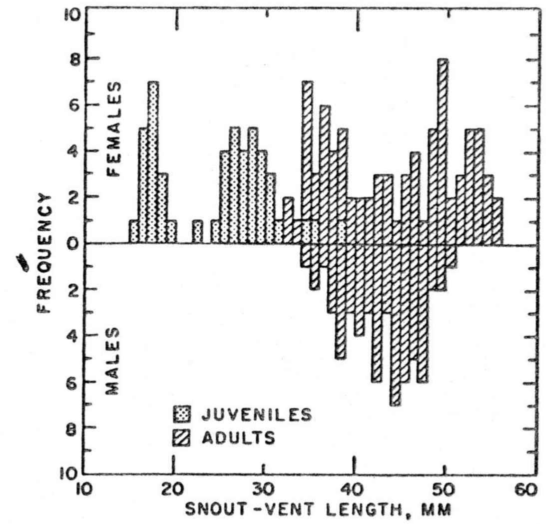


FIGURE 4. Frequency distribution of snout-vent lengths of all *P. vehiculum* collected in January, 1970.

subadult males. From these data, the growth rate of both sexes for the first 3 years can be estimated at 10 mm SVL/year.

Freiburg (1954) stated that there is no sexual dimorphism in size of *P. vehiculum.* However, our data show that mature females are on the average larger than mature males. Mature males range from 42 to 53 mm SVL ($\overline{X}$ = 45.7), whereas mature females range from 44 to 58 mm SVL ($\overline{X}$ = 49.1).

DISCUSSION

Table 3, adapted in part from Angle (1969), summarizes and compares life history information for 5 species of *Plethodon.* These data are only approximate and will pertain only to particular populations at particular times. Highton (1962b) and Angle (1969) indicated some of the population characteristics which vary geographically for *P. glutinosus* and *P. richmondi* respectively; and we are aware of at least size variation in *P. vehiculum.*

Table 3 shows that the life histories of the 5 species are similar, differing only in details. *P. glutinosus* is the most distinctive due to its larger average size, more rapid growth in the first year, later age at maturity, and higher fecundity. Generalizations that appear for the genus are that: 1) females have biennial cycles and males annual cycles; 2) oviposition occurs in the spring and incubation (± 60 days) is in the summer months with hatching in the fall; 3) spermatogenesis begins in spring and continues through the summer; 4) males mature at smaller size than females; 5) mature females average 2-5 mm SVL larger than mature males; 6) growth rates are 10-15 mm SVL/year for the first three years; 7) maturity occurs 2-3 years after hatching.

Data for other species of *Plethodon* are scattered and meager. Pope (1950) and Pope and Pope (1951) provided useful information for *P. yonahlossee* and *P. ouachitae* respectively. Both of these eastern large plethodons apparently have life histories similar to *P. glutinosus.* Although the Popes did not have extensive data on size distribution of ova in mature females, their findings could be interpreted to indicate a biennial cycle for females of both *P. yonahlossee* and *P. ouachitae,* rather than to indicate an extended laying season as they suggested. Pauley and England (1969) reported that another eastern large plethodon, *P. wehrlei,* mates and oviposites in March and April. They did not suggest a biennial cycle for females, even though they

TABLE 3. Summary of life history data for five species of *Plethodon* (sources cited in text).

	glutinosus	*cinereus*	*richmondi*	*vehiculum*	*neomexicanus*
mating	spring and fall	Oct. to April	spring (and fall?)	Nov.-Jan.	spring-early summer
female cycle	biennial	biennial	biennial	biennial	biennial
male cycle	annual	annual	annual	annual	annual
oviposition	late spring	June	May-June	April-May	July-early August
size of mature ova (mm)	4.0-4.5	3.0-4.0	3.0-4.0	3.2-4.3	3.4-3.8
number of mature ova	16.7-26.1 (range of means)	9 (mode)	4.7-9.0 (range of means)	10.4 (mean)	7.7 (mean)
incubation period	± 60 days	± 56 days	61 days (18°C)	± 60 days	?
hatching	late summer	August	late Aug.-Sept.	probably Sept.	probably Sept.-Oct.
SV of hatchlings (mm)	13.7 (mean)	14-15	14-15	13-15	?
appearance of hatchlings	April of year after hatching	Sept.	March of year after hatching	Sept.	?
growth rate first year	15 mm SVL	11 mm SVL	10 mm SVL	10 mm SVL	?
size at maturity (mm)					
males	50	38	38	42	51
females	58	40	39	44	56
age at maturity (years)					
males	3+	2	2	2-1/2	?
females	3+	2	2-1/2	2-1/2	?
average adult size (mm SVL)					
males	61	42.0	45.6	45.7	57.9
females	66	44.8	47.1	49.1	60.5
onset of spermatogenesis	April	March	May	early June	June
sperm in vas deferens	Sept.	Aug.	Sept.	Sept.	?

reported two types of mature females present in October and January: those with large yolky ova, and those with ova less than one mm in diameter. Organ (1960) stated that *P. welleri*, an eastern small plethodon, courts in fall and broods in the summer; and that hatchlings vary from 12.0 to 15.0 mm SVL. Thurow (1963) reported additional life history information for *P. welleri*. He confirmed Organ's observations and wrote that males mature at 3 years, and females at slightly over 3 years. Thurow used body length rather than SVL, but reported that males matured at a smaller size (31 mm) than females (35 mm). He indicated a growth rate of 8-9 mm body length/year. These and other data for species of the genus *Plethodon* presented by Bishop (1943), Brooks (1948), Duellman (1954), Dunn (1926), Mohr (1952), and Wallace and Barbour (1957) suggest that the information in Table 3 may extend generally to most species of *Plethodon*.

It is difficult to derive taxonomic conclusions from these observations. Further studies, including analysis of both inter- and intraspecific variation in reproductive patterns, are needed to determine the taxonomic value of life history data in *Plethodon*. Especially valuable would be information on the life history of a large western plethodon (e.g. *P. dunni*). At least for the present, our observations on *P. vehiculum* suggest a general conformity of reproductive patterns across the genus *Plethodon*, and that no subgeneric designations are warranted.

ACKNOWLEDGMENTS

We thank Dr. Robert M. Storm for reading the manuscript and for advice. This research was supported in part by National Science Foundation grant no. GB-20963 to the Coniferous Forest Biome, U. S. Analysis of Ecosystems, International Biological Program. This is Contribution no. 3 from the Coniferous Forest Biome.

LITERATURE CITED

Angle, J. P. 1969. The reproductive cycle of the northern ravine salamander, *Plethodon richmondi richmondi*, in the valley and ridge province of Pennsylvania and Maryland. J. Washington Acad. Sci. 59(7-9):192-202.

Bishop, S. C. 1943. Handbook of salamanders. Comstock Publishing Co., Ithaca.

Brodie, E. D., Jr. 1970. Western salamanders of the genus *Plethodon:* systematics and geographic variation. Herpetologica 26(4):468-516.

Brooks, M. 1948. Notes of the Cheat Mountain salamander. Copeia 1948(4):239-244.

Burger, J. W. 1935. *Plethodon cinereus* (Green) in eastern Pennsylvania and New Jersey. Amer. Nat. 69:578-586.

Duellman, W. E. 1954. The salamander *Plethodon richmondi* in southwestern Ohio. Copeia 1954(1):40-45.

Dumas, P. C. 1953. The ecological sympatric relations of *Plethodon dunni* and *Plethodon vehiculum*. Ph.D. Thesis, Oregon State University, Corvallis, 48 p.

———. 1955. Eggs of the salamander *Plethodon dunni* in nature. Copeia 1955(1):65.

Dunn, E. R. 1926. The salamanders of the family Plethodontidae. Smith College Anniv. Publ. 441 p.

Freiburg, R. E. 1954. Studies on the biology of two ambystomid and five plethodontid salamanders of western Oregon. Ph.D. Thesis, Oregon State University, Corvallis, 66 p.

Galigher, A. E. and E. N. Kozloff. 1964. Essentials of practical microtechnique. Lea and Febiger, Philadelphia.

Grobman, A. B. 1944. The distribution of the salamanders of the genus *Plethodon* in eastern United States and Canada. Ann. New York Acad. Sci. 45(7):261-316.

Highton, R. 1956. The life history of the slimy salamander, *Plethodon glutinosus*, in Florida. Copeia 1956(2):75-93.

———. 1962a. Revision of the North American salamanders of the genus *Plethodon*. Bull. Florida State Mus. 6(3):235-367.

———. 1962b. Geographic variation in the life history of the slimy salamander. Copeia 1962(3):597-613.

Mohr, C. E. 1952. The eggs of the zig-zag salamander, *Plethodon cinereus dorsalis*. Amer. Caver Bull. 14:59-60.

Organ, J. A. 1960. Studies on the life history of the salamander, *Plethodon welleri*. Copeia 1960(4):287-297.

Pauley, T. K. and W. H. England, 1969. Time of mating and egg deposition in the salamander, *Plethodon wehrlei* Fowler and Dunn, in West Virginia. Proc. West Virginia Acad. Sci. 41:155-160.

Piersol, W. H. 1910. The habits and larval state of *Plethodon cinereus erythronotus.* Trans. Can. Inst. 8:469-492.

Pope, C. H. 1950. A statistical and ecological study of the salamander *Plethodon yonahlossee.* Bull. Chicago Acad. Sci. 9(5):79-106.

——— and S. H. Pope. 1949. Notes on growth and reproduction of the slimy salamander *Plethodon glutinosus.* Fieldiana 31(29):251-261.

——— and ———. 1951. A study of the salamander *Plethodon ouachitae* and the description of an allied form. Bull. Chicago Acad. Sci. 9(8):129-152.

Reagan, D. P. 1972. Ecology and distribution of the Jemez Mountains salamander, *Plethodon neomexicanus.* Copeia 1972(3):486-492.

Sayler, A. 1966. The reproductive ecology of the red-backed salamander, *Plethodon cinereus,* in Maryland. Copeia 1966(2):183-193.

Stebbins, R. C. 1951. Amphibians of western North America. University of California Press, Berkeley and Los Angeles.

Test, F. H. 1955. Seasonal differences in populations of the redbacked salamander in southeastern Michigan. Pap. Michigan Acad. Sci. Arts Letters 40:137-153.

Thurow, G. R. 1963. Taxonomic and ecological notes on the salamander *Plethodon welleri.* Univ. Kansas Sci. Bull. 44(5):87-108.

Wallace, J. T. and R. W. Barbour. 1957. Observations on the eggs and young of *Plethodon richmondi.* Copeia 1957(1):48.

Werner, J. K. 1971. Notes on the reproductive cycle of *Plethodon cinereus* in Michigan. Copeia 1971(1):161-162.

O