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Author(s): Clara A. Wheeler , Hartwell H. Welsh Jr. , and Lisa M. Ollivier
Source: Journal of Herpetology, 47(1):131-137. 2013.
Published By: The Society for the Study of Amphibians and Reptiles
DOI: http://dx.doi.org/10.1670/11-141
URL: http://www.bioone.org/doi/full/10.1670/11-141

Journal of Herpetology, Vol. 47, No. 1, 131–137, 2013

Reproductive Biology of the Del Norte Salamander (*Plethodon elongatus*)

Clara A. Wheeler,[1] Hartwell H. Welsh Jr., and Lisa M. Ollivier

USDA Forest Service, Pacific Southwest Research Station, Arcata, California 95521 USA

Abstract.—**We examined seasonal reproductive patterns of the Del Norte Salamander, *Plethodon elongatus*, in mixed conifer and hardwood forests of northwestern California and southwestern Oregon. Seasonal size differences in reproductive structures suggested that maximum spermatogenic activity occurred during the late summer, with spermatozoa transfer to the vasa deferentia occurring in the fall through spring. Maximum development of mature follicles occurred during the winter; however, follicular growth occurred year-round and was asynchronous among individuals. Courtship and mating probably occurred in late fall through early spring, with egg deposition from spring into early summer. Reproduction for females was not annual, and patterns suggested that the reproductive cycle was biennial or less frequent. In contrast, evidence indicated annual reproduction in males. Gravid females contained an average of 10 mature follicles.**

Plethodontid salamander reproductive patterns and cycles have been studied to a greater extent in the eastern United States than in the western United States, and studies have resulted in some generalizations. Eastern species tend to have annual reproduction in both sexes, whereas western species tend to exhibit biennial female reproduction and annual spermatogenesis. These patterns seem to differ primarily because of climate (Houck, 1977b). Eastern plethodontids are surface active during a prolonged warm season throughout which temperatures remain above freezing (roughly late March through October). During this period, courtship, mating, spermatogenesis, egg laying, and brooding activities occur. The surface activity of western plethodontids is associated with a brief rainy season that is interrupted by dry summer conditions in most areas. While western females are brooding egg clutches in refugia in the summer, the remainder of the population is restricted to subsurface refugia by high temperature and dry conditions at the ground surface (Houck, 1977b; Feder, 1983). In contrast, eastern plethodontids, with the exception of brooding females, remain surface active throughout the summer (Houck, 1977b; Taylor et al., 1990). The shorter window of surface activity in the west limits the time available to salamanders to acquire body mass and fat stores, because most feeding occurs at or near the surface (Maiorana, 1976; Stearns and Koella, 1986; Bernardo, 1994). These studies further state that factors that slow acquisition of body mass may lead to a delay in maturity, change in growth rates, reduced clutch sizes, and increased mortality rates. In addition, Houck (1977b) suggested that females may breed biennially as a consequence of their lengthy brooding period and concurrent inability to forage during the shortened annual activity period in the west.

The Del Norte Salamander, *Plethodon elongatus*, is a terrestrial salamander that occurs in mixed conifer and hardwood forests of southwestern Oregon and northwestern California. The distribution, habitat associations, and population ecology of this plethodontid have been studied comprehensively (Welsh and Lind, 1991, 1992, 1995; Diller and Wallace, 1994; Welsh et al., 2006). However, little is known about the life history of *P. elongatus* (but see Ollivier and Welsh, 2003; Wheeler et al., 2007), including its reproductive biology and ecology. Reproductive information is limited to a few descriptive studies and an observation of a nest that was attended by an adult female (Livezey, 1959). The account reported clutch size ($N = 10$), egg diameters, hatchling size, and nest location (Livezey, 1959) and both disagreed with and supported earlier accounts (Wood, 1934; Stebbins, 1954, respectively). Wood (1934) described a specimen and several small egg clusters that were presumably *P. elongatus*. The embryo sizes and egg diameters he reported were comparable to those in Livezey (1959), but his estimated clutch size of 100 was much larger than that reported for other plethodontids; the identification of these eggs may have been erroneous (Stebbins, 1962). Stebbins (1954) observed 10 and 11 ova in two dissected specimens, and ova diameters were similar to those observed by Livezey (1959). As a western plethodontid salamander, *P. elongatus* is predicted to exhibit an annual spermatogenic cycle in males and a biennial reproductive cycle in females, summer brooding of eggs, and fall courtship and mating (e.g., Peacock and Nussbaum, 1973; Herrington and Larsen, 1987; Ovaska and Gregory, 1989). The above-mentioned inferences are based on the habits and characteristics of other similarly sized congenerics; it is expected that different plethodontid species living under comparable conditions would show similar patterns of activity (Houck, 1977a). However, no formal investigation of the reproductive habits of *P. elongatus* has been conducted. We used the dissection of voucher specimens to address questions associated with the reproductive ecology and biology of this cryptic salamander from the western United States.

Materials and Methods

Specimen Collection and Dissection.—We collected 356 *P. elongatus* by using pitfall trap and visual encounter methods (Heyer et al., 1994) from 1984 to 1988. We sampled mixed conifer and hardwood stands of the Klamath Mountains and Coast range of southwestern Oregon and northwestern California during the spring (March–May) and fall (October–November); however, not all these months were sampled every year. All salamanders were euthanized in chloretone, preserved in 10% formalin, and stored in 70% ethyl alcohol for later processing.

We examined specimens and recorded data in the laboratory between fall 1988 and spring 1989. We used calipers to measure the length from the snout to the anterior margin of the vent (SVL) and total length to the nearest 1 mm, and we measured mass to the nearest 0.1 g with a spring scale. Euthanized specimens were then dissected to determine life stage, sex, and reproductive condition. Juveniles ($N = 11$) lacked visible reproductive organs and were eliminated from the analyses. We determined life stage (subadult vs. adult) based on visual examination of reproductive organs (Ollivier and Welsh, 2003).

[1]Corresponding Author. E-mail: cawheeler@fs.fed.us
DOI: 10.1670/11-141

In males, small white testes, and straight, unpigmented, and narrow vasa deferentia were characteristic of subadults. Adult males possessed enlarged, darkly pigmented testes and wide, convoluted vasa. We measured testes lengths, testes diameters (anterior, middle, and posterior), three diameters of each vas deferens (anterior, middle, and posterior), and lengths and widths of the fat bodies of each individual by using an ocular micrometer in a × 10 dissecting microscope. We used the formula for the volume of a cylinder ($\pi r^2 h$) to calculate testicular size (radius [r] was half the averaged diameters of the testis; height [h] was the length of the testis). In other studies, seasonal variation in testes size has revealed patterns in the timing of spermatogenetic activity (Semlitsch and West, 1983); testicular swelling occurs during spermatogenesis (Sayler, 1966), and shrinking indicates sperm evacuation from the testes to vasa deferentia (Wilkinson et al., 1993; Herbeck and Semlitsch, 2000). We calculated fat body volume ($\pi r^2 h$), where r was half the width of the fat body and h was fat body length, and we used this latter variable as a measure of size. We could not confirm reproductive maturity, verify presence of sperm in testes or vasa deferentia, or determine the stage of spermatogenesis of individual males with certainty because we did not prepare histological slides.

In females, we classified life stages based on visual examination of reproductive structures rather than by using frequency distributions of SVLs to establish size cutoffs. The presence of small ovaries lacking developing follicles and straight, narrow oviducts were characteristic of subadults. Adult females possessed developing ovarian follicles and enlarged, convoluted oviducts. We measured ovary lengths, ovary diameters (anterior, middle, and posterior), three diameters of each oviduct (anterior, middle, and posterior), and lengths and widths of fat bodies. We used the formula for the volume of a cylinder ($\pi r^2 h$) to calculate ovary size (r was half the averaged diameters of the ovary; h was the length of the ovary). Female fat body volume ($\pi r^2 h$) was calculated for each individual. We recorded the number of follicles in the largest set and measured the diameters of follicles.

Analyses.—We measured structures from both left and right reproductive tracts for females and males, but we used measurements from just the right side to simplify analyses, except for follicle counts; they were total counts. Multiple measurements of vasa deferentia diameters, and also of oviduct diameters, were highly correlated so we reduced these variables, by using only the middle diameter measurements for analyses. For adult females, we created frequency histograms to examine the distribution of mean follicle sizes for each month sampled. We used Spearman's correlation analyses to examine associations between SVLs and reproductive structure sizes and the relationship between the number of mature follicles and follicle sizes.

Results

Reproductive Biology of Males.—We observed 34 subadult males and 141 adult males. Subadult males (range, 28.5–48.0 mm SVL) were smaller than adult males (range, 43.0–67.0 mm); however, there was some overlap. Mental gland presence or absence was not a clear indicator of sexual maturity in males. Six percent of subadults and 71% of adults possessed visible mental glands. Furthermore, males with prominent mental glands were observed during each month sampled. The relationship between testes size and SVL was exponential, and variance in testis size increased with SVL (Fig. 1A). Subadults had small testes (0.86 ± 0.13 mm^3 [mean ± SE]), narrow vasa deferentia (0.11 ± 0.01 mm), and small fat bodies (0.13 ± 0.06 mm^3). Adults had larger testes (8.09 ± 0.41 mm^3), wider vasa deferentia (0.31 ± 0.01 mm), and larger fat bodies (1.17 ± 0.21 mm^3).

Variability in the size of adult male reproductive structures revealed seasonal variation in spermatogenesis. Testicular size of adult males was larger during the fall than the spring (Fig. 2A); testes were largest in October (10.17 ± 0.64 mm^3) and smallest in March (4.31 ± 0.83 mm^3). Vasa deferentia were generally larger in the spring than the fall; vasa deferentia were smallest in November (0.27 ± 0.01 mm) and largest in May (0.39 ± 0.03 mm). The decrease in testes size from October to November, along with small testes and large vasa deferentia during the spring, indicated that sperm evacuation occurs from fall through spring. Fat body size exhibited a seasonal pattern similar to that in testes size (larger in the fall). The size of testes ($R = 0.64$, $P < 0.0001$, $N = 141$), vasa deferentia ($R = 0.57$, $P < 0.0001$, $N = 141$), and fat bodies ($R = 0.28$, $P < 0.001$, $N = 137$) was correlated positively with SVL for adult males.

Reproductive Biology of Females.—We collected 44 subadult and 126 adult females. The relationship between follicle size and SVL was exponential, and variance in follicle size increased with SVL (Fig. 1B). Subadults (range, 29.0–49.1 mm SVL) were generally smaller than adults (range, 41.5–67.0 mm) but with considerable overlap. Subadults possessed nonvisible, or numerous previtellogenic (≤0.5 mm) follicles (0.20 ± 0.01 mm), small ovaries (0.67 ± 0.08 mm^3), and narrow and generally straight oviducts (0.11 ± 0.01 mm), and they lacked or had small fat bodies (0.48 ± 0.19 mm^3). Adult females had large ovaries (26.85 ± 3.91 mm^3), wide oviducts (0.77 ± 0.07 mm), and large fat bodies (5.87 ± 0.75 mm^3). Adults contained follicles of varying sizes (1.02 ± 0.07 mm; range, 0.2–4.44 mm). Frequency histograms of follicle sizes revealed a bimodal distribution for March, May, and November (Fig. 3), suggesting two reproductive states within the sample of adult females. One group contained previtellogenic (≤0.5 mm, $N = 44$) or small vitellogenic (0.6–1.4 mm, $N = 54$) follicles, and the other group contained large mature follicles (≥1.5 mm, $N = 28$; these females were classified as "gravid"). Follicles ≥1.5 mm observed in fall captures contained yolk (dark yellow) and were considered large enough to attain sufficient size (increasing in size in November and the winter) to be oviposited the following spring. Many adult females with vitellogenic and mature follicles also possessed a set of previtellogenic follicles embedded between larger follicles; however, only the largest sets of follicles were counted and measured, and these data are presented here.

For adult females, follicle sizes indicated seasonal variation (Fig. 2B). During the fall, follicle sizes were highly variable, whereas in the spring most follicles were previtellogenic or small vitellogenic, with the exception of a few spring captures that contained very large mature follicles. In nongravid adult females, follicle sizes were similar during October, November, and March; mean follicle diameter was largest in March (0.72 ± 0.13 mm) and smallest in May (0.37 ± 0.12 mm). Oviduct and fat body sizes had similar seasonal variation. Ovaries were large during the fall and small during the spring; ovary sizes were highest in November (9.35 ± 2.14 mm^3) and smallest in May (3.41 ± 2.39 mm^3). In nongravid adult females, the number of follicles was positively correlated with SVL ($R = 0.34$, $P < 0.001$). In gravid females, follicle sizes were smallest in October (2.27 ± 0.11 mm), increased in November, reached maximum diameters in March (4.17 ± 0.32 mm), and then decreased in May. The largest follicles (3.28, 3.89, and 4.44 mm) were observed in March and May captures. Ovary and oviduct sizes

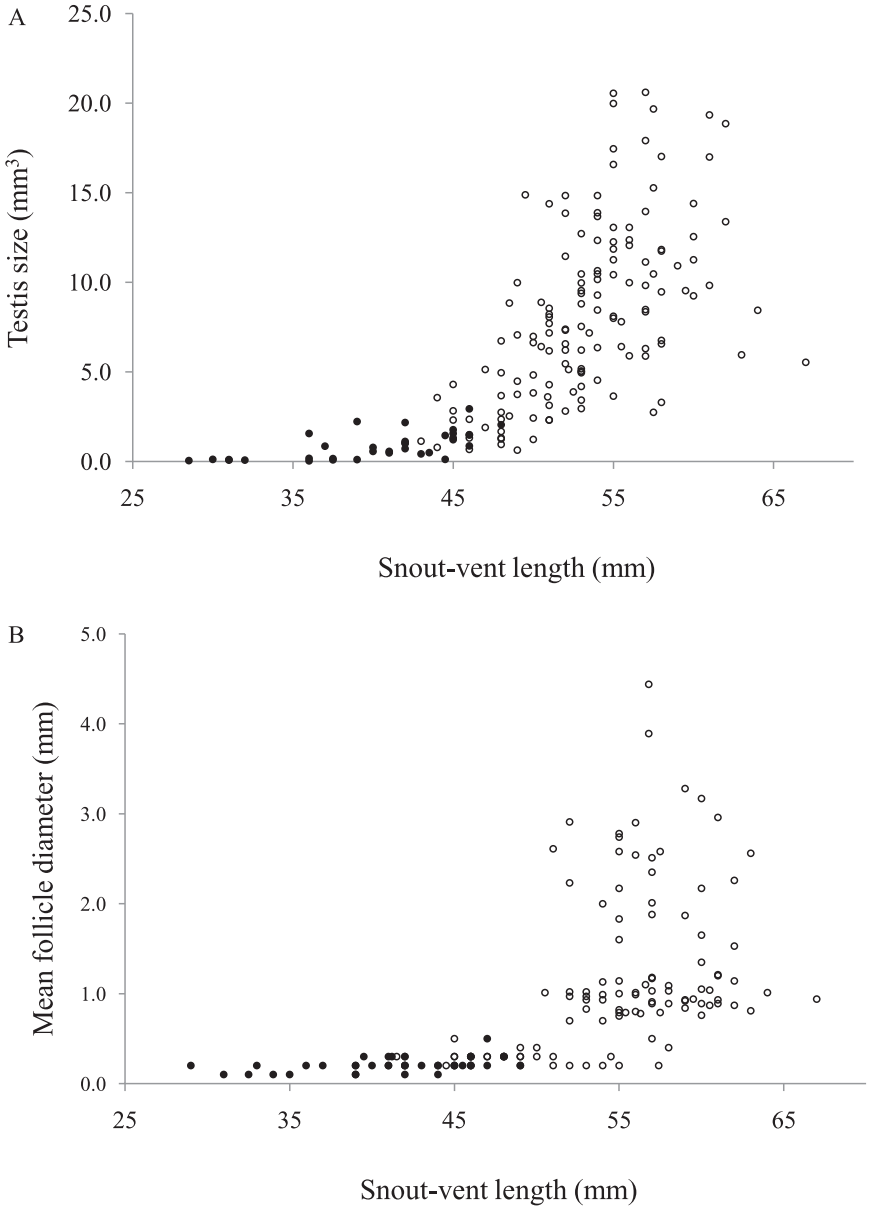

FIG. 1. Relationship between snout–vent length and (A) testis and (B) follicle sizes for *Plethodon elongatus*. Closed symbols represent subadults and open symbols represent adults.

had a similar seasonal pattern. In contrast, fat bodies were largest in November (11.94 ± 6.85 mm^3) and smallest in May (2.14 mm^3, $N = 1$). In gravid females, the total number of follicles was negatively associated with mean egg diameter ($R = -0.82$, $P < 0.00001$). Mean clutch size was 10.00 (SE = 0.47; range, 4–16) ova, based on the number of mature follicles (≥1.5 mm) observed in gravid females. Clutch size was correlated with SVL ($R = 0.45$, $P = 0.02$). SVL explained 20% of clutch size variation ($R^2 = 0.20$). The size of ovaries ($R = 0.72$, $P < 0.0001$, $N = 124$), oviducts ($R = 0.61$, $P < 0.0001$, $N = 126$), and fat bodies ($R = 0.30$, $P < 0.001$, $N = 122$) were positively correlated with SVL for adult females.

DISCUSSION

Insight into the reproductive cycle of this species was limited by the fact that we sampled only during 2–3 mo each spring and fall. The initial objectives for specimen collection as part of a larger study did not include reproductive ecology; hence, our data set is incomplete. However, we had sufficient data to make reasonable inferences regarding seasonal variation in the reproductive activity of *Plethodon elongatus*. Based on the information we gathered, male and female *P. elongatus* have distinct reproductive cycles. Female reproduction may be biennial, less frequent, or irregular, whereas male *P. elongatus*, like males of other plethodontids (Sayler, 1966; Herrington and Larsen, 1987; Marvin, 1996; Herbeck and Semlitsch, 2000), undergo seasonal, annual spermatogenesis.

Testes and fat bodies of adult *P. elongatus* males were largest during the fall, and vasa deferentia were largest during the spring. Spermatogenesis likely occurred during the summer and fall, whereas sperm evacuation to the vasa deferentia, courtship, and mating probably occurred from fall through spring. In a more comprehensive study of the eastern plethodontid *Plethodon websteri* (Semlitsch and West, 1983), a species with seasonal activity similar to that of western plethodontids (sampled

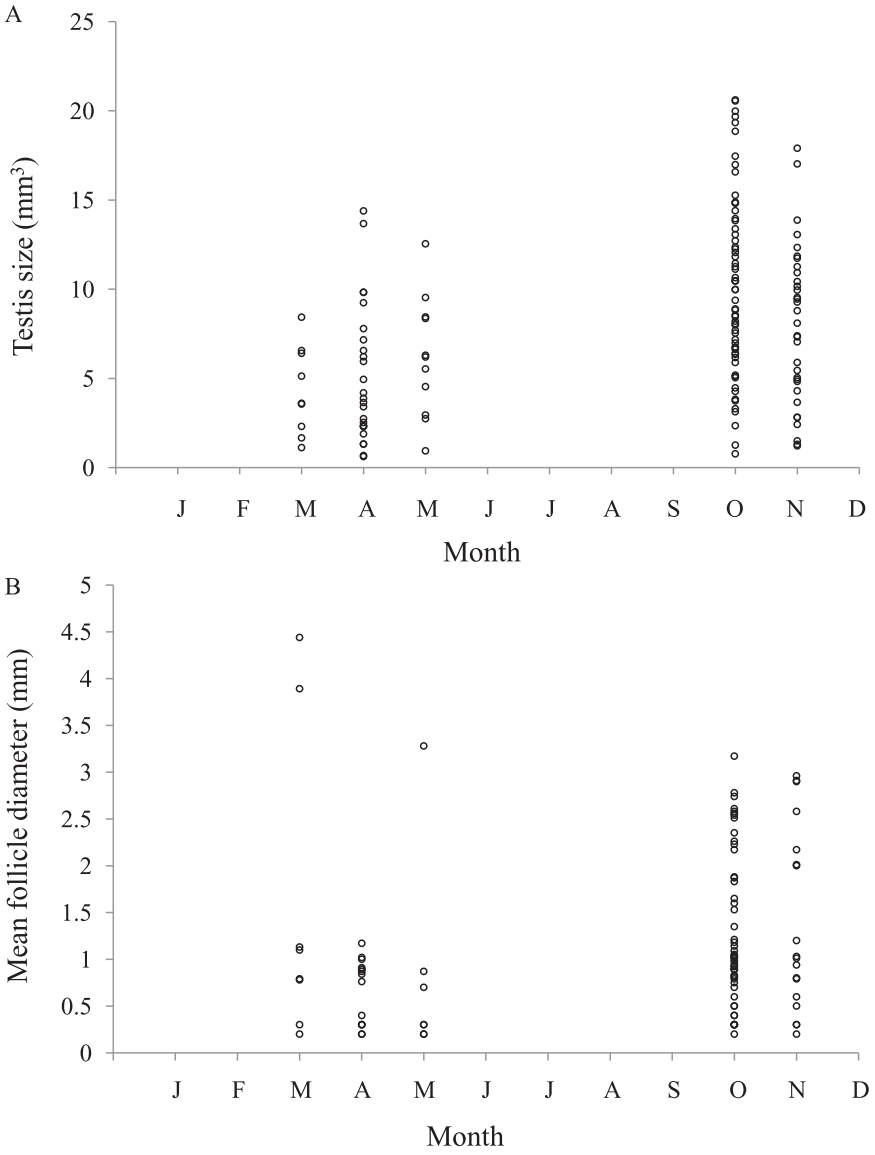

FIG. 2. Seasonal variation in (A) testis and (B) follicle sizes for adult *Plethodon elongatus*.

January 1980 through May 1981, with no salamanders found from June through September), testes were largest in October, decreased in size in December, and were smallest in April. Semlitsch and West (1983) suggested that maximum spermatogenic activity likely occurred in late summer. Similarly, we suspect that maximum testicular swelling of breeding *P. elongatus* males occurred during the late summer when we did not sample; the October sample may represent already reduced testes after the evacuation of sperm to the vasa deferentia.

The presence of mental glands (external examination) was not a definitive indicator of sexual maturity or breeding activity; male *P. elongatus* exhibit less conspicuous mental glands than many eastern plethodontids, and we did not perform dissections of the lower jaw to examine gland clusters (Brodie, 1968). In a study of western plethodontids, Brodie (1968) concluded that mental gland development in *P. elongatus* corresponded with ontogenetic maturity and associated characteristics such as pigmented testes, and he did not find any indication of seasonal variation. In our study, some adult males possessed visible mental glands during all months sampled, further supporting Brodie's (1968) supposition.

A bimodal size distribution of the largest ovarian follicles during the prebreeding season has been perceived as evidence for a biennial reproductive pattern in many plethodontid studies; females with larger follicles would presumably reproduce during the next breeding season and those with smaller follicles forgo breeding until the following season (Jørgensen, 1992). Our data indicated asynchronous follicular development, with multiple stages represented throughout the sampling period. Females containing previtellogenic or small vitellogenic follicles may represent multiple reproductive conditions such as younger animals (first-time reproducers) and/or reproductively capable adults with follicles that would not become mature until a later oviposition season. Females with mature follicles likely represented fall captures that would have laid their eggs during the forthcoming spring, and spring captures that would have oviposited during that spring. Using follicle size distribution, however, to establish the frequency of reproduction may be inconclusive and the breeding period, as well as vitellogenic growth rate, should be known before drawing conclusions

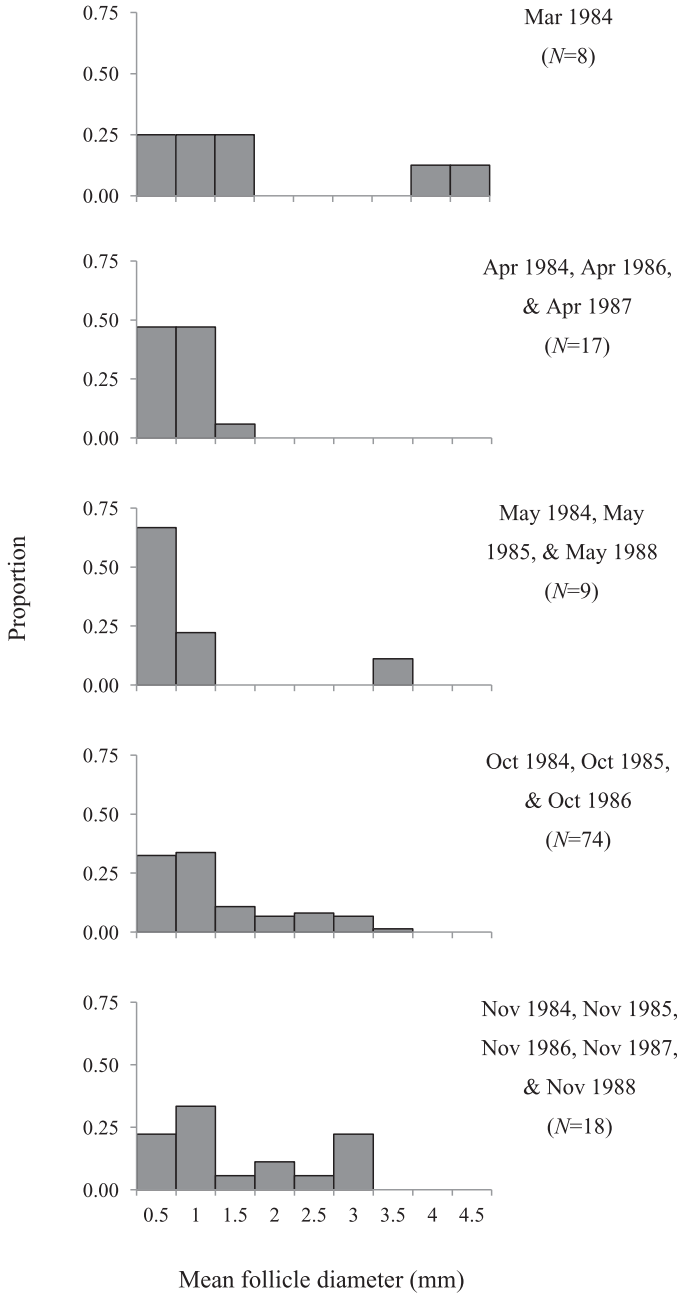

FIG. 3. Distribution of follicle diameter for adult female *Plethodon elongatus* for each month sampled.

based on this method (Jørgensen, 1992). The proportion of adult females containing mature follicles was highest during November; however, the largest follicles (3.28, 3.89, and 4.44 mm) were observed in spring captures (Figs. 2B and 3). Vitellogenic growth of *P. elongatus* follicles likely continues during the winter as seen in other plethodontid salamander species (*Plethodon hoffmani*, formerly identified as *Plethodon richmondi*, Angle, 1969; *Plethodon jordani*, Hairston, 1983). During winter and spring, large vitellogenic follicles (≥1.5 mm) probably become ripe for oviposition, although we do not know the rate of follicular development and whether it is possible for small vitellogenic follicles (0.6–1.4 mm) to advance to maturity before the following spring.

A *P. elongatus* nest observation during late July (Livezey, 1959) and timing of oviposition of other western plethodontids in the spring (*Plethodon larselli*, Herrington and Larsen, 1987) and spring–early summer (*Plethodon vehiculum*, Peacock and Nussbaum, 1973; Ovaska and Gregory, 1989) are consistent with our conclusions. Few gravid females were observed in the spring likely because they retreat to underground oviposition sites during this period. In contrast, females with previtellogenic or small vitellogenic follicles were observed more frequently during the spring. Similarly, Peacock and Nussbaum (1973) did not observe gravid females of *P. vehiculum* from May through August and suggested their absence was due to incubation and attachment to their clutches; this hypothesis was further supported by an observation of two nests that were attended by adult salamanders during May (Hanlin et al., 1979).

Females captured in the fall that contained mature follicles were presumably individuals receptive to courtship and mating. In addition, we observed spermatophores in females captured in October ($N = 1$) and November ($N = 2$), all with large mean follicle diameters (>2.5 mm), further indicating that courtship and mating occur in the fall. Based on the sizes of testes and vasa deferentia, courtship and mating likely continue through the winter and spring, although we do not have a sufficient time series in our sample to support this interpretation. Like other plethodontids, females may be capable of storing sperm and delaying fertilization (Houck et al., 1985). Females captured in the fall, including those containing previtellogenic or small vitellogenic follicles (<1.5 mm), may be mating and storing sperm to use during a later laying season.

Information from a mark–recapture study of *P. elongatus* (Welsh and Lind, 1992) corroborates our suggestion that females do not reproduce annually and revealed a biennial female reproductive cycle. Of seven adult females that were captured twice (captured and recaptured during the same season over consecutive years), four were gravid 1 yr and not the previous or next year, and three were not gravid during either year (Welsh and Lind, unpubl. data). In addition, of two adult females that were captured and then recaptured 2 yr later during the same season (i.e., captured initially in November 1986, recaptured in November 1988), one female was gravid during both years and the other female was not gravid in either year (Welsh and Lind, unpubl. data). Data from the mark–recapture study indicated that only 23% (74/320) of mature females captured had ova visible through the abdominal wall (Welsh and Lind, unpubl. data); this proportion corresponded to this study where we classified 22% (28/126) of adult females as gravid. This finding suggests that the reproductive cycle of females may be even less frequent than biennial, assuming a more equal ratio (i.e., 1 : 1) of gravid to nongravid adult females would be expected in a population that reproduces every other year. Marvin (1996) similarly concluded that female *Plethodon kentucki* reproduce biennially or less frequently based on a mark–recapture study.

We observed a mean of 10 mature follicles in gravid females though actual clutch sizes (number of eggs oviposited) may be smaller (Hairston, 1983). Furthermore, the number of maturing follicles decreased as the follicle diameters increased in the spring and the two gravid females captured in the spring that were nearing oviposition had 7 and 8 mature follicles. We did observe atretic follicles in several gravid females that suggested that some follicles were resorbed as the process of vitellogenesis progressed; this explains the negative relationship between the number of mature follicles and follicle size. It is also possible

that not all maturing follicles are deposited; however, our estimated clutch size based on the number of mature follicles compares to other *P. elongatus* specimens containing 10–11 eggs (Stebbins, 1954) and a clutch containing 10 eggs (Livezey, 1959). Estimated and actual clutch sizes of other western *Plethodon* species were also comparable: *P. vehiculum* had a mean of 10.4, *P. larselli* had 7.3, and *Plethodon vandykei* had 5.5 enlarged follicles (as summarized by Marvin 1996); and two *P. vehiculum* nests in Oregon contained eight and nine eggs (Hanlin et al., 1979).

The relationship between fat bodies and amphibian gonads is still uncertain and contentious (Jørgensen, 1992). In adult males, we found that fat bodies were largest in the fall when testes were swollen and smallest in the spring when vasa deferentia were distended and presumably packed with sperm. In gravid females, fat bodies were largest in the fall during the period of yolk deposition and were reduced (possibly depleted) in the spring when follicles were ready for oviposition. This relationship is similar to that of other amphibian studies where fat bodies were largest when reproductive females underwent early vitellogenesis and decreased in size as follicles developed; studies have shown that fat body size decreases before and during breeding (see Jørgensen, 1992). However, the role of the fat bodies in salamander reproduction is not clear; furthermore, the tail in plethodontid salamanders (especially in females) is the predominant fat storage structure (Fitzpatrick, 1976). We did not collect tail mass data to examine differences by season and reproductive condition, or relationship with reproductive structures. In addition, if the population overwintered, depletion of fat stores may have been a result of reduced or arrested foraging rather than energetically demanding reproductive activities, or perhaps a consequence of both factors.

As we expected, based on a few studies of other western plethodontids, courtship and mating likely occur primarily in the fall and winter, oviposition in the spring, and brooding occurs during the summer. However, compared with eastern species, less is known about the life histories of western plethodontids. Further research is needed to better understand seasonal patterns and reproductive cycles of eastern and western species, specifically factors that create differences (regional, inter- and intraspecific). Seasonal variation in microclimate affects surface activity and habitat suitability for life-history activities such as courtship, mating, and oviposition; these reproductive activities seem to be influenced largely by climatic factors such as precipitation. For example, some southeastern plethodontids that live in climates comparable with temperate western forests (mild, wet winters and hot, dry summers) had similar seasonal reproductive patterns to those of temperate western plethodontids (Semlitsch and West, 1983; Wilkinson et al., 1993; Herbeck and Semlitsch, 2000).

Like other western plethodontids, *P. elongatus* females do not reproduce every year and have a biennial or less frequent reproductive cycle, whereas males reproduce annually. Predicting the reproductive cycle of a species, and determining the factors influencing an individual's capacity to breed within a given year is challenging. Reproductive cycles are not necessarily species specific; several studies have found contrasting results that are better explained by differences in activity periods of populations (*Plethodon glutinosus*, Highton, 1956, 1962; *Plethodon cinereus*, Nagel, 1977; *Plethodon serratus*, Herbeck and Semlitsch, 2000). Limitations of surface activity affect foraging time and consequently the amount of energy accumulated by individuals. Sufficient energy reserves are required by female salamanders to produce and brood eggs (Fitzpatrick, 1973; Houck, 1977b) and thus directly influence the reproductive cycle.

Additional study of species with extensive and varying geographic ranges would help to identify factors that influence reproductive cycles and therefore reproductive output. We suspect that coastal *P. elongatus* females, that experience long, mild winters and humid summers, and lower elevation populations, that undergo longer periods of surface activity, may reproduce more frequently. Considerable geographic variation in the range of *P. elongatus*, specifically longitudinal (coastal vs. inland) and elevational gradients (sea level, 1,700 m), makes it a promising species for further investigating the environmental and evolutionary factors that influence variation in plethodontid reproductive cycles.

Acknowledgments.—We thank G. McLaughlin for involving us in such an intriguing series of questions and for early guidance in the data collection process. We also extend a special thanks to L. Houck for insight and suggestions in interpreting our results.

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Accepted: 19 January 2012.