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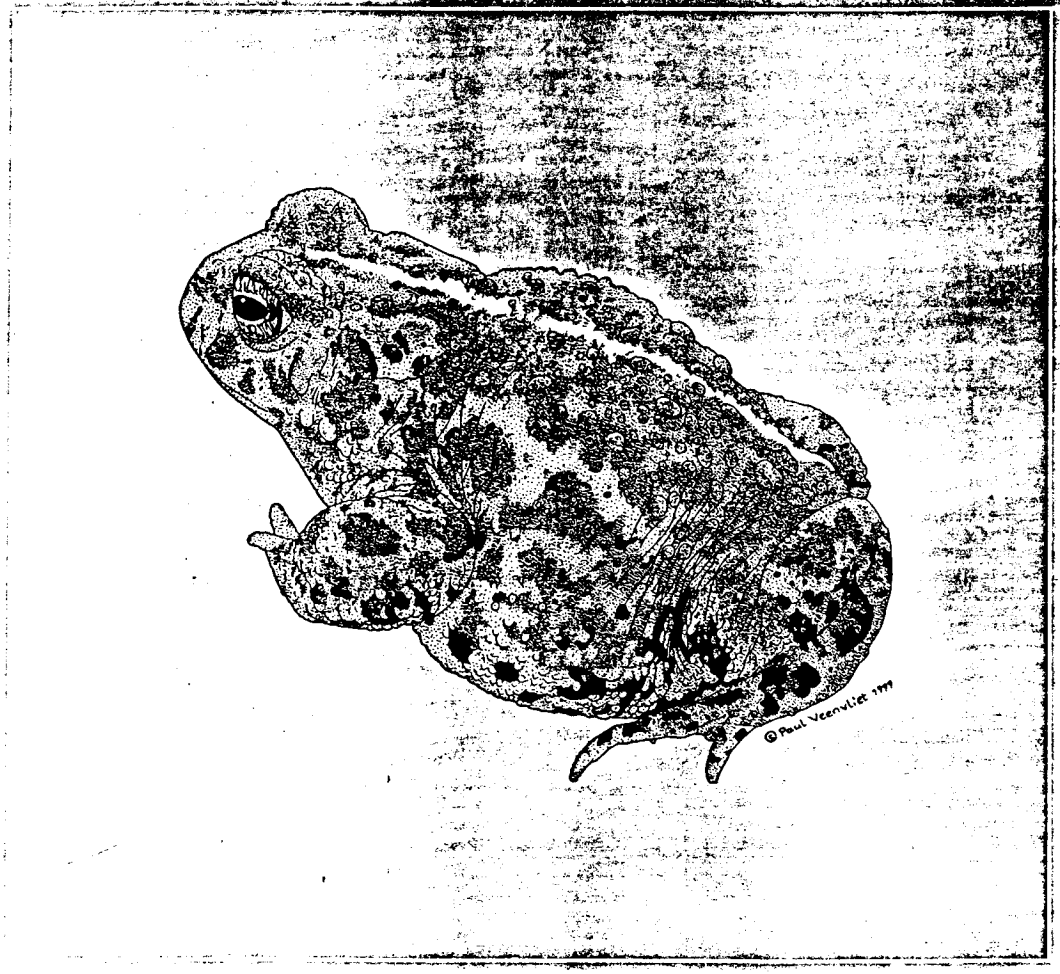

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Life History and Ecology of the Southern Redback Salamander, *Plethodon serratus*, in Missouri

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ABSTRACT.—**The life history and ecology of *Plethodon serratus* were studied in two populations in south-central and southeastern Missouri, USA. One population was located on private land in Perry County and the other was located in Mark Twain National Forest in Phelps County. Courtship and insemination probably occurred between December and March. Oviposition occurred during May or June and eggs hatched during July or August. Gravid females contained an average of 6.3 (range 4–10) enlarged ovarian follicles. We assume that reproduction among females is biennial on the basis of two distinct groups of mature females, those with enlarged, yolk-filled follicles and those with only small follicles. Hatchlings emerged in September and October and averaged 17 mm SVL (range 15–20 mm SVL). The growing season extended from September to May and little growth occurred during June to August. Growth during the first year after hatching averaged 10 mm. *Plethodon serratus* was most active on the forest surface between October and May in Phelps County and August and May in Perry County. The life-history pattern observed for *P. serratus* has characteristics of other small temperate plethodontid salamanders.**

Woodland salamanders are the dominant group of vertebrates inhabiting many forest ecosystems (Heatwole, 1962; Burton and Likens, 1975; Jaeger, 1980; Bury, 1983). These salamanders have ecological and physiological characteristics that make them particularly sensitive to large- and small-scale environmental changes. Trophic position, dense populations, and complex life histories provide these salamanders with the potential to be key ecological components of forest floor communities and serve as indicators of the effects of disturbance on the forest ecosystem (Pough et al., 1987; Petranka et al., 1994; Ash, 1996; Herbeck and Larsen, 1999). Determining life history and ecology of natural populations is fundamental for understanding conservation implications of management decisions on woodland salamanders.

Plethodon serratus, the southern redback salamander, has been recognized as a distinct species since 1976 (Highton and Webster, 1976). Its geographic range includes disjunct populations in Arkansas and Oklahoma, Louisiana, Missouri, and Tennessee and Georgia. *Plethodon serratus* is abundant in the oak-hickory and oak-pine forests of the Missouri Ozark Mountains (Johnson, 1992). The Missouri range is limited to the southeastern portion of the state extending from the Missouri River south to the Arkansas border excluding the "bootheel" (Johnson, 1992). Although common throughout its range, no complete studies have been conducted on its life history in Missouri. We document the life history and ecology of *P. serratus* in Missouri and make comparisons to other species in the small *Plethodon* group.

MATERIALS AND METHODS

Study Area.—Two locations in the Missouri Ozark Mountains were chosen as collection sites. The Ozark mountains are a peneplain with a maximum elevation of 540 m. The first collection site was located in the Inner Ozark Border region of Perry County (Nelson, 1987). The second site was located in the Gasconade River Hills of Phelps County (Nelson, 1987). The Perry County study area was on private land and the Phelps County study area was on Mark Twain National Forest. Both collection sites are located on north and east facing slopes comprised of mixed hardwoods dominated by white oak (*Quercus alba*) in the forest canopy. Soils are dry to xeric chert or limestone and well to excessively drained (Meinert et al., 1997). This region receives an average of 112 cm of precipitation annually and has a mean annual temperature of 13.5 C. The daily temperature during summer months (June, July, August) can reach a mean maximum of 32.5 C and during winter (December, January, February) can reach a mean minimum of 4.8 C (Missouri Department of Conservation weather station data).

We made monthly field collections from February 1996 through March 1997. Individuals were hand collected by turning logs, flipping rocks, and raking through leaf litter along logs and in leaf-filled pits left by fallen trees. A total of 545 *P. serratus* were collected; 371 from Perry County and 174 from Phelps County. Precise collecting time was recorded to calculate a standardized rate of capture for each month (i.e., numbers of salamanders/person/hour).

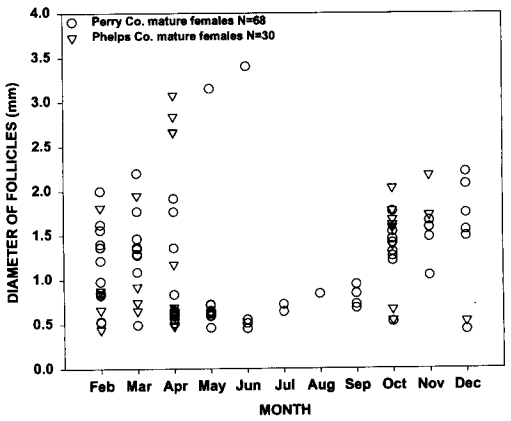

FIG. 1. Seasonal variation in right testis diameter of *Plethodon serratus* from Perry County and Phelps County, Missouri.

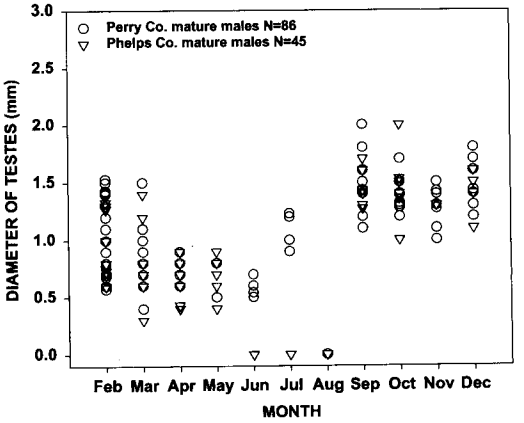

FIG. 2. Seasonal variation in diameter of ovarian follicles of *Plethodon serratus* from Perry County and Phelps County, Missouri.

All salamanders were killed in chloretone, preserved in 10% formalin, and stored in 60% ethyl alcohol. Measurements were taken on specimens preserved for at least 30 d. Snout–vent length (SVL) was measured from the snout to the anterior end of the vent. Specimens were dissected to determine sex and reproductive condition. Number of ovarian follicles, follicle diameter, and oviduct diameter were measured on females. The largest set of ovarian follicles containing yolk from each individual female was counted to determine potential clutch size. We measured the diameter of anterior, middle and posterior portions of the right testis, and diameter of vas deferens of males. Condition of vas deferens and color of testes and vas deferens were noted. Measurements were made using a dissecting microscope and ocular micrometer. Data on other small *Plethodon* were summarized from the literature for comparison.

RESULTS

Reproductive Cycle.—Testes of 128 mature male *P. serratus* having enlarged and darkly pigmented testes and vas deferens indicated seasonal size variation (Fig. 1). The diameter of the anterior portion of the testes attained maximum size in September (mean = 1.48 ± 1 SE) following emergence from underground summer retreats. The anterior portion of the testes began decreasing in diameter in November and reached minimum size (mean = 0.68 ± 0.04 mm) and black coloration during April. Because enlargement of the testes indicates active spermatogenesis (Sayler, 1966; Angle, 1969), maximum spermatogenic activity most likely occurs during late summer. As spermatozoa were evacuated from the testes the vas deferens became swollen. The vas deferens increased in size from the smallest diameters in June (mean = 0.14 ± 0.02 mm) to the largest diameters in November through February (mean = 0.30 ± 0.01 mm).

Ovarian follicles of 98 mature female *P. serratus* indicated seasonal size variation (Fig. 2). Smallest follicle diameter occurred in September (mean = 0.79 ± 0.06 mm) after emerging from underground summer retreats, and follicles increased to a maximum diameter (mean = 2.03 ± 0.27 mm) by April or May after accumulating yolk over winter. The oviducts were also large (0.9 mm in diameter) and convoluted in April and May. In studies of northern populations of *P. cinereus*, egg clutches have been found in June (Blanchard, 1928; Burger, 1935; Test, 1955; Werner, 1971). Sayler (1966) suggested oviposition occurred in June for populations of *P. cinereus* in Maryland based on the assumption of a 12-week period from initial egg deposition to the first appearance of hatchlings in September. *Plethodon serratus* hatchlings in Missouri were first found in September; therefore, we suggest that oviposition probably occurs in late May or June.

Mature *P. serratus* females collected in the spring were placed in two classes: (1) those with yellow, yolk-filled ovarian eggs 2.0–4.0 mm in diameter and large, convoluted oviducts (65%); and (2) females of equal SVL with whitish follicles <1.0 mm in diameter and nearly straight oviducts (35%) (Fig. 2). Thus, we assume that reproduction among females was not annual or was approximately biennial based on the presence of a large group of non-reproductive mature females in the spring of the year.

Fecundity.—Of 98 mature females collected throughout the year, 58 were collected between February and May and had enlarged follicles allowing us to estimate clutch size. The mean

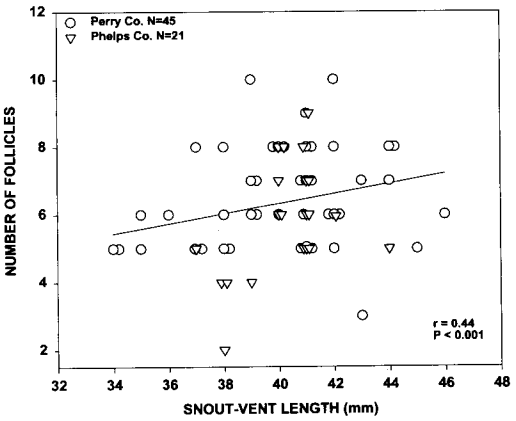

FIG. 3. Relationship between number of enlarged ovarian follicles and snout–vent length for *Plethodon serratus* from Perry County and Phelps County, Missouri.

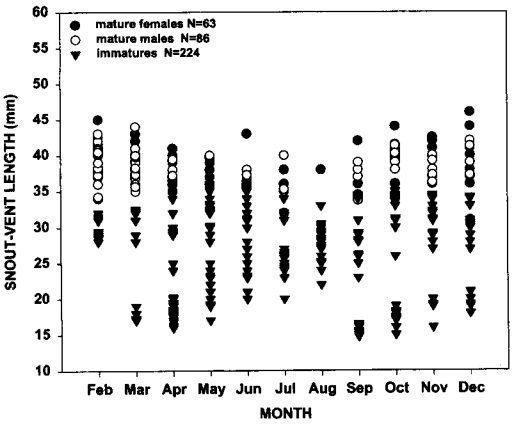

FIG. 4. Snout–vent length distribution in relation to collection date of *Plethodon serratus* from Perry County, Missouri.

number of enlarged ovarian follicles was 6.3 (range 4–10). We found that the number of enlarged ovarian follicles increased significantly with SVL ($r = 0.44$, $P < 0.001$; Fig. 3). However, SVL explained 20% of the variation in the number of ovarian follicles ($r^2 = 0.20$).

Growth, Size, and Maturity.—The smallest individuals collected averaged 17 mm SVL (range 15–20 mm SVL) from both Perry and Phelps counties in September 1995. These juveniles possibly represented newly emerging young of the year. If newly emerging juveniles collected in September were estimated to be approximately three months old, by May of their second year (24 mo old) immatures are indistinguishable in SVL from older, mature individuals. In September (27 mo old) all individuals >35 mm SVL are sexually mature. Therefore, we suggest that males and females reach reproductive maturity during the summer at age 24–27 months. Because *P. serratus* likely breed between December and March, we speculate that newly mature males and females first court between 31–33 mo old. Females likely deposit their first clutch of eggs the following May or June at 35–36 mo.

The growing season extends from September to May with little growth occurring during the summer months (June–August). Plots of SVL by month of capture (Figs. 4, 5) indicate distinct size classes that correspond to age classes. Based on these distributions we estimated that growth averaged 10 mm during the first year after hatching, 8.8 mm during the second year, and decreased to 2.6 mm in their third year upon reaching maturity. Thus growth rates appear to be highest during the first and second years and become considerably lower when reproductive maturity is reached.

The smallest mature female was 34 mm SVL from Perry County and 36 mm SVL from Phelps County. The average mature female SVL was 38.9 ± 0.36 mm (range 34–46 mm) from Perry County. The average mature female SVL was 39.7 ± 0.34 mm (range 36–44 mm) from Phelps County. There was no significant difference in average SVL of mature females from Perry and Phelps counties ($t = -1.52$, $df = 82.7$, $P > 0.133$).

The smallest mature male was 31 mm SVL from Perry County and 32 mm from Phelps County. The average mature male SVL was 38 ± 0.27 mm (range 31–44 mm) from Perry County. The average mature male SVL was 37.9 ± 0.39 mm (range 32–43 mm) from Phelps County. No significant difference occurred in average SVL of mature males from Perry and Phelps counties ($t = 0.15$, $df = 126$, $P > 0.881$).

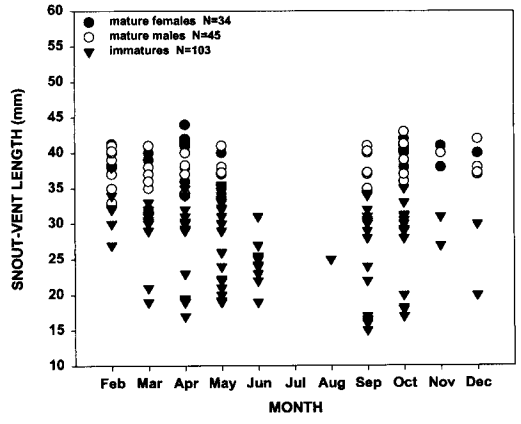

FIG. 5. Snout–vent length distribution in relation to collection date of *Plethodon serratus* from Phelps County, Missouri.

Seasonal Activity.—The number of individuals collected each month varied during the year. *Plethodon serratus* were relatively abundant in the leaf litter late August through December and February through May for Perry County, and September through October and February through May for Phelps County. No salamanders were found in January. Adults began disappearing from the leaf litter late May for both Perry and Phelps counties. However, younger age classes did not disappear until July in Perry County and June in Phelps County. Salamanders seemingly remained underground through the summer (June–August) possibly to avoid high temperatures and desiccation (Taub, 1961; Spotila, 1972) because none or relatively few individuals were found during these months despite intensive searching. Individuals representing all age classes were first collected in September, as they emerged from underground retreats.

Seasonal activity patterns for *P. serratus* are related to night air temperatures and soil moisture (Spotila, 1972). Salamanders respond behaviorally to fluctuations in moisture and temperature resulting in use of various microhabitats (Heatwole, 1960, 1962). Sixty-two percent of captured *P. serratus* were located primarily within the leaf litter and were associated with down wood from April to June when the relative humidity was high (maximum mean relative humidity from April through June was 96.2%) and night air temperature was cool (minimum mean temperature from April through June was 12 C). From September to March, 85% of captured individuals were primarily located under rocks. Individual captures per person per hour decreased during July and August (8.3 salamanders/person/hour) from the previous spring capture rate (14.3 salamanders/person/hour).

Discussion

Life-history characteristics of *P. serratus* in the Ozark Mountains of Missouri appeared similar to those of other small *Plethodon* species in North America (Table 1). All salamanders of the genus *Plethodon* have highly seasonal reproductive cycles, in which female *P. dorsalis* and *P. websteri* breed annually (Semlitsch and West, 1983; Meshaka and Trauth, 1995) and female *P. hoffmani, P. larselli, P. neomexicanus, P. richmoni,* and *P. vehiculum* breed biennially (Angle, 1969; Reagan, 1972; Peacock and Nussbaum, 1973; Williams, 1978; Nagel, 1979; Herrington and Larsen, 1987; Ovaska and Gregory, 1989; Marvin, 1996; Table 1). We found that female *P. serratus* in Missouri bred biennially. These results contrast reports of female *P. serratus* in Georgia (Camp, 1988) and Arkansas (Taylor et al., 1990) that indicated annual reproductive cycles. Populations of *P. serratus* in Georgia and Arkansas may have a longer continuous activity period in which to forage than do populations in Missouri. Biennial female reproductive cycles have been observed for populations of small *Plethodon* in Maryland, New Mexico, Ohio, Oregon, Pennsylvania, Tennessee, Washington, and British Columbia (Table 1). Sayler (1966) concluded that *P. cinereus* in Maryland would not reproduce the spring following a breeding year but would require an additional year to mature a second clutch of eggs. Highton (1956) observed *P. glutinosus* in Florida that develop egg clutches annually compared to *P. glutinosus* in Maryland, which develop egg clutches biennially. Populations of *Plethodon* in southern regions have a longer continuous activity period than species in northern regions, resulting in greater energy intake thereby allowing southern species to develop egg clutches annually (Organ, 1961; Highton, 1962; Semlitsch and West, 1983). Females need to accumulate sufficient energy reserves for producing and brooding eggs (Fitzpatrick, 1973; Houck, 1977). Foraging time and, therefore, reproductive cycles of *Plethodon* species may be determined by regional microclimatic factors such as temperature and rainfall, as well as by prey availability and quality for species in which females defend territories.

Oviposition occurred during late May or June for *P. serratus* populations in Missouri and clutches of 4–10 eggs developed between June, July, and August, which is similar to reports from populations of *P. serratus* in Arkansas (Taylor et al., 1990) and Georgia (Camp, 1988; Table 1). We found the number of ovarian follicles increased as SVL increased for *P. serratus* in Missouri. Taylor et al. (1990) observed a significant linear relationship between the number of enlarged ovarian follicles and SVL of *P. serratus* in Arkansas ($r^2 = 0.39$, $P < 0.001$); however, a nonsignificant relationship was found in Georgia ($r = 0.37$, $P > 0.1$; Camp, 1988).

Young of the year hatched in July and emerged from underground brooding sites in September. These characteristics are similar for other small *Plethodon* species except *P. hoffmani* and *P. richmondi* juveniles, which emerge in early spring approximately six months after hatching (Angle, 1969; Nagel, 1979; Table 1). Growth during the first year for *P. serratus* averaged 10 mm and decreased to 2.6 mm for adults in their third year. Mean growth during the first year for *P. serratus* is within the range of growth rates reported for other small *Plethodon* (Houck, 1977) and is similar to that observed for *P. dorsalis, P. websteri, P. kentucki,* and *P. vehiculum* (Semlitsch and West, 1983; Ovaska and Gregory, 1989; Meshaka and Trauth, 1995; Marvin, 1996). No clear growth rate trend is apparent for small *Pletho-*

TABLE 1. Life history characteristics for 10 species of small *Plethodon*. Sources: (1) Sayler 1966, (2) Blanchard 1928, (3) Werner 1971, (4) Nagel 1977, (5) Wilkinson et al. 1993, (6) Meshaka and Trauth 1995, (7) Angle 1969, (8) Herrington and Larsen 1987, (9) Reagan 1972, (10) Williams 1978, (11) Duellman 1954, (12) Nagel 1979, (13) Camp 1988, (14) Peacock and Nussbaum 1973, (15) Ovaska and Gregory 1989, (16) Semlitsch and West 1983, (17) Organ 1960, (18) Thurow 1963.

Species	Location	Time of oviposition	Time of hatching	Juvenile emergence	Age at first reproduction (months)	SVL at maturity (mm)		Mean fecundity (eggs)	Female reproductive cycle	Reference
						Males	Females			
P. cinereus	Maryland	June	August	September	24–36	34	34	?	Biennial	1
P. cinereus	Tennessee, Michigan	June	?	September	36	38–39		8.4	Annual	2, 3, 4
P. dorsalis	Arkansas	May–June	August	September	24–36	30–34	30–34	5.3	Annual	5, 6
P. hoffmani	Pennsylvania, Maryland	Late May–June	Late August–September	March	36	38–42	39–43	4.7	Biennial	7
P. larselli	Washington, Oregon	March–April	August	October–November	48	39–42	44	7.3	Biennial	8
P. neomexicanus	New Mexico	July–August	September–October	?	?	51	56	7.7	Biennial	9, 10
P. richmondi	Tennessee, Ohio	Late May–June	August–September	March–April	36–48	38	39	8.3	Biennial	11, 12
P. serratus	Missouri	May–June	July	September	24–36	31	34	6.3	Biennial	Present study
P. serratus	Georgia	July	September	October	?	30–34	32–34	5.5	Annual	13
P. vehiculum	Oregon, British Columbia	Spring–early summer	August–September	Late fall–early winter	36–48	38–42	42–44	5.5	Biennial and triennial	14, 15
P. websteri	South Carolina	June–July	August–September	October–November	24–36	29–30	27–31	5.8	Annual	16
P. welleri	Virginia, Tennessee	July–August	August–September	?	36–48	32	34	6.9	?	17, 18

don from northern or southern regions of North America. Reproductive maturity occurs 24–27 mo after hatching when individual *P. serratus* are greater than 35 mm SVL. For most other small *Plethodon*, reproductive maturity can occur between 24 and 48 mo after hatching (Table 1) and between 30 and 44 mm SVL.

Temperature and moisture regimes of the forest floor will determine the microclimate (Gieger, 1965; Chen et al., 1997) and, subsequently, microhabitats available for woodland salamanders (Spotila, 1972). From April to June 62% of captured *P. serratus* were located within the leaf litter and down wood and from September to March 85% were located under rocks. Few *P. serratus* were captured during June, July, and August because the majority of individuals move to the subterranean habitat. These observations indicate that *P. serratus* utilize a variety of microhabitats and shift their use seasonally because of changes in soil moisture and ambient temperature conditions.

Environmental changes that subsequently modify temperature and moisture regimes of the forest floor will determine microhabitats available for woodland salamanders. *Plethodon serratus* are completely terrestrial and have direct development; therefore, the forest must provide microhabitats for all stages of the life history of this species to maintain viable populations. This study documents the life history characteristics of *P. serratus* from two populations in Missouri. This information can be used to define habitat requirements for *P. serratus*. Land managers can be more effective when managing forest ecosystems for species diversity and economic yields when provided with information on life history, and therefore habitat requirements, of species that are integral components of the ecosystem. Because the physiology and life history of *P. serratus* make them excellent indicators of ecosystem health, these studies can be utilized to determine the impact from environmental changes.

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