Journal of Herpetology, Vol. 41, No. 4, pp. 638–644, 2007

Green Salamander (*Aneides aeneus*) Growth and Age at Reproductive Maturity

JAYME L. WALDRON[1,2] AND THOMAS K. PAULEY

Department of Biological Sciences, Marshall University, Huntington, West Virginia 25755, USA

ABSTRACT.—**Growth and age at reproductive maturity are two life-history parameters that add an important temporal component to species conservation, yet such information is seldom available for plethodontid salamanders. We modeled growth and age at maturity for a northern West Virginia population of Green Salamanders, *Aneides aeneus*, using snout–vent length (SVL) growth intervals from a five-year mark-recapture study. Growth data were fit to the von Bertalanffy and logistic growth interval models and compared using the residual error mean square. The logistic model provided the best fit to the recapture data, indicating that Green Salamanders grow slowly for plethodontids and that it takes 7–8 yr to reach reproductive maturity. Our results revealed that Green Salamanders mature at a later age than most plethodontid species, indicating that the species might have greater generation time and longevity than previously suspected. Our data may offer insight into why the species is sensitive to population declines. Thus, we suggest that future research focus on Green Salamander longevity and generation time to provide a framework from which comparisons can be made across populations.**

The knowledge of a species' life history is vital for conservation and management. Information on growth patterns is particularly important because it can offer insight into age, longevity, and age-specific fecundity (Shine and Schwartzkopf, 1992). Species that grow slowly and have delayed maturation have ''slow'' life histories that can increase a species' vulnerability to extinction (MacArthur and Wilson, 1967; Webb et al., 2002), making knowledge of growth parameters an important temporal component to species conservation. Further, because growth is dependent on environmental conditions, such as food resources (Berven, 1982; Bernardo and Agosta, 2003), population density and competition (Licht, 1975; Kaplan, 1980), and habitat quality (Arntzen, 2000), growth models can be used to make comparisons among populations (Kunz, 1974; Schoener and Schoener, 1978; Gibbons et al., 1981); thus, potentially identifying populations at greatest risk of decline.

Unfortunately, information on growth and age at reproductive maturity is seldom available for plethodontid salamanders, and most studies have used skeletochronology rather than mark-recapture to describe plethodontid growth. Although mark-recapture is an effective way to estimate age, it is seldom used for plethodontids because it is labor intensive and requires several years of research to obtain reliable results (Halliday and Verrell, 1988). Of the few plethodontid studies that have used mark-recapture data to describe growth and estimate age at reproductive maturity, most have focused on semiaquatic species (e.g., Tilley, 1980; Marvin, 2001). Here, we present empirical data using the mark-recapture approach to determine growth and age at reproductive maturity for a highly terrestrial salamander, the Green Salamander (*Aneides aeneus*).

The Green Salamander is declining in some parts of its range, but the cause of such declines remains largely unknown (Corser, 2001). The species inhabits rock outcrops and arboreal habitat (Wilson, 2003; Waldron and Humphries, 2005) from southern Pennsylvania to northern Alabama and Mississippi (Petranka, 1998). Green Salamanders are quite mobile (Gordon, 1952; Williams and Gordon, 1961; W. J. Humphries and J. L. Waldron, unpubl. data) but are territorial of crevices and breeding habitat (Cupp, 1980). Aspects of the species' life history have been described from several parts of its range, including North Carolina (e.g., Gordon, 1952, Snyder, 1971), Mississippi (e.g., Woods, 1968), West Virginia (e.g., Canterbury, 1991; Waldron, 2000), and Kentucky (e.g., Cupp, 1991). Although some of the previous studies included mark-recapture analyses, there was no attempt to model Green Salamander growth patterns. Pauley and Watson (2005) speculated that Green Salamanders reach sexual maturity in three years based on size frequency distribu-

---

[1] Present address: Savannah River Ecology Laboratory, University of Georgia, Drawer E, Aiken, South Carolina 29802, USA.

[2] Corresponding Author: 106 Hayne Street, Walterboro, South Carolina 29488, USA; E-mail: waldron@srel.edu

tions in Mississippi (Woods, 1968) and West Virginia populations (Canterbury, 1991). However, size-frequency extrapolation can be problematic because of the assumption that age and size are statistically correlated and because it requires knowledge of adult growth rates and age-specific variation in body size (Gibbons, 1976; Halliday and Verrell, 1988). Thus, our objective was to model growth and estimate age at reproductive maturity for a high elevation, northern West Virginia population using mark-recapture data.

MATERIALS AND METHODS

Study Area.—The study area was located in the Mead Westvaco Wildlife and Ecosystem Research Forest in Randolph County, West Virginia, at an elevation of 880 m. The study site consisted of several emergent rocks scattered along a west-facing, forested slope. Timber bordering the study site was selectively harvested during the summer of 2002. Prior to logging, the forest canopy was closed, leaving the rocks well shaded and allowing minimal light to penetrate to the forest floor. The dominant tree species in the area included tulip poplar (*Liriodendron tulipifera*), black birch (*Betula lenta*), American beech (*Fagus grandifolia*), red maple (*Acer rubrum*), and eastern hemlock (*Tsuga canadensis*). The sparse understory consisted of greenbrier species (*Smilax* sp.), black cohash (*Cimicifuga racemosa*), and saplings of the dominant tree species. The area receives the greatest annual average precipitation (approximately 170 cm per year) in West Virginia.

Salamander Capture and Measurement.—We conducted Green Salamander mark-recapture surveys at the study area between 1999 and 2003. We visually surveyed the study area yearly using both diurnal and nocturnal surveys. When salamanders were captured, they were measured for snout–vent length (SVL) to the nearest 0.1 mm. Sex was determined based on the presence of mental glands in males and eggs in gravid females; however, sex could not be determined when sexually dimorphic characters were absent outside of the breeding season. When neither mental glands nor eggs were observed in adults during the breeding season, we assumed they were nongravid females. Between 1999 and 2001, we marked Green Salamanders with visual implant elastomers (Northwest Marine Technologies, Inc., Shaw Island, Washington). However, because of problems with tag loss (unpubl. data), we used digital photography to identify the dorsal pattern of each salamander (e.g., Doody, 1995; Grant and Nanjappa, 2006), which allowed for individual salamander recognition. A portfolio of dorsal photographs was carried in the field so salamanders could be identified and released immediately following capture. Recaptures were verified in at least one of two ways: (1) a second person compared the dorsal pattern of the salamander with the photograph; and (2) a second photograph was taken and compared with the original photograph in the laboratory.

Growth.—Growth rates were calculated as the percent change in SVL, divided by the time interval between captures. We used growing seasons (March–November) as time intervals to control for inactivity during winter months when it was assumed the salamanders did not grow. Because they do not require knowledge of age (Fabens, 1965; Frazer and Ehrhart, 1985; Frazer et al., 1990), we used the growth interval forms of the von Bertalanffy and logistic equations to model Green Salamander growth.

The von Bertalanffy growth interval equation,

$$L_2 = a - (a - L_1)e^{-rd}, \tag{1}$$

and the logistic growth interval equation,

$$L_2 = a\,L_1 / \left[L_1 + (a - L_1)e^{-rd}\right], \tag{2}$$

were used, where L_1 is the length at first capture, L_2 is the length at recapture, d is the time between capture and recapture (i.e., number of growing seasons), e is the base of the natural logarithms, a is the asymptotic size, and r is the characteristic growth parameter (Fabens, 1965; Schoener and Schoener, 1978; Frazer and Ehrhart, 1985; Aresco and Guyer, 1999). We used nonlinear least squares regression with the Marquardt algorithm (PROC NLIN; SAS vers. 9.1, SAS Institute, Inc., Cary, North Carolina, 2002) to fit the recapture data to equations 1 and 2, and to estimate asymptotic SVL (a) and the characteristic growth parameter (r). The residual error mean square (REMS) was used to compare the two growth models, where the model with the lowest REMS (Schoener and Schoener, 1978), and the most biologically appropriate estimate of a (Frazer et al., 1990) was considered the best fit to the recapture data (Aresco and Guyer, 1999). According to Frazer et al. (1990), the estimate of a should be slightly larger than the average size of the largest individuals in the population. The average SVL of the largest reproductively mature individuals in our study population ($N = 16$), that is, those with SVL > 55.8 (males, $N = 4$; females, $N = 12$), was 59.7 (SE = 0.8; 95% CI = 58.0–61.5). We used SVL = 55.8 as our cut off for this value because we marked 33 reproductively mature adults and used SVL measurements taken upon first capture of the largest 50% to determine the average size of the largest individuals.

It was often difficult to determine the sex of captured individuals; therefore, growth was not modeled separately for males and females. When we recaptured salamanders more than one time, we used the growth interval between the first and last capture in analyses. Measurements from 19 salamanders, including six males, six females, and seven individuals with unknown sex, provided 19 growth intervals. We compared the average SVL of marked adult males ($N = 14$) and females ($N = 19$) using a t-test for equal variance.

Age at Maturity.—We estimated mean age at reproductive maturity using modeling procedures outlined by Frazer and Ehrhart (1985), which included the general von Bertalanffy equation and the general logistic equation models. The general von Bertalanffy equation used was:

$$L = a\left(1 - be^{-rt}\right), \tag{3}$$

where t is age, a is the asymptotic size, r is the characteristic growth parameter, and e is the base of the natural logarithms. The general logistic equation model used was:

$$L = a/\left(1 + be^{-rt}\right), \tag{4}$$

with parameters defined in Equation 3. Since models 3 and 4 require knowledge of age, we solved for t by calculating parameter b using the estimates of a and r obtained from equations 1 and 2 (Frazer and Ehrhart, 1985). Mean hatchling SVL (h) of Green Salamanders was 14.9 (SD = 0.6), which was based on the measurements of newly hatched individuals ($N = 14$) from two clutches found within the study area. Thus, for the von Bertalanffy growth model (equation 3), we solved for b using the following equation:

$$b = 1 - (h/a)$$
$$b = 1 - (14.9/71.08),$$

where h is the average SVL for hatchlings. For the logistic model (equation 4), we solved for b using the following equation:

$$b = (a/h) - 1$$
$$b = (63.56/14.9) - 1.$$

Thus, the von Bertalanffy model we used was:

$$L = 71.08\left(1 - 0.79e^{-0.15t}\right), \tag{5}$$

and the logistic equation we used was:

$$L = 62.33/\left(1 + 3.26e^{-0.33t}\right). \tag{6}$$

We solved for t at given values of $L = L_m$, that is, an estimate of the mean size at reproductive maturity (Frazer and Ehrhart, 1985), in which the average SVL of the adult males and females in the population (i.e., $\bar{x} = 55.3$, SE = 0.94) was used as the upper limit for L_m, and the smallest recorded SVL of a salamander with sexually dimorphic characters (i.e., 46.0) was used as the lower limit for L_m.

RESULTS

Our recapture data included juvenile, subadult, and adult salamanders, which is required for generating reliable parameter estimates using the growth models (Frazer et al., 1990; Aresco and Guyer, 1999). Females ($\bar{x} = 57.1 \pm 1.1$, range = 46.8–66.5) were larger than males ($\bar{x} = 52.8 \pm 1.4$, range = 46.0–62.7; t-test, $t_{31} = 2.36$, $P < 0.05$), and growth rates slowed in older, reproductively mature individuals (Fig. 1). The von Bertalanffy and logistic growth interval equations (equations 1 and 2; Fig. 2) fit the growth data well; however, the logistic model had slightly lower REMS than the von Bertalanffy model and had a more biologically relevant (Frazer et al., 1990) estimate of a (Table 1). Thus, the logistic model provided the more appropriate growth parameters for our study population.

Estimates from the general von Bertalanffy and logistic models (equations 3 and 4, respectively) of average age at maturity were similar (Table 1). However, the von Bertalanffy model estimated a younger age at maturity than the logistic model, and the 95% confidence intervals for each equation did not overlap (Table 1). Because the logistic growth model gave a more reliable growth estimate, we concluded that it takes approximately 7.5–8 yr (i.e., growing seasons) for Green Salamanders to reach reproductive maturity. We observed eggs in female body cavities between November and May, and Green Salamanders breed in spring and fall in northern West Virginia (Canterbury and Pauley, 1994). Females at our study site did not oviposit until May (Waldron, 2000), and hatchlings first emerged in late August and early September (Waldron, 2000). Thus, our estimates of age at reproductive maturity indicate that females do not nest until their ninth year of life at our study site.

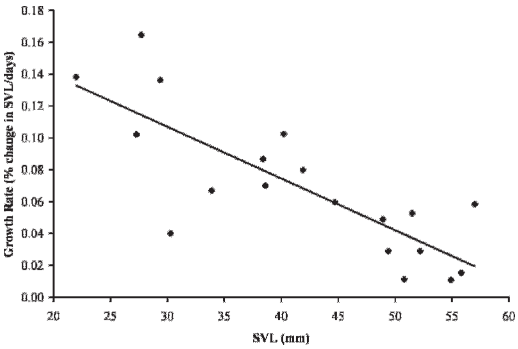

FIG. 1. Growth rate plotted against initial Green Salamander (*Aneides aeneus*) snout to vent length (SVL) for a northern West Virginia population. Growth rates were calculated as the percent change in SVL (mm), divided by the time interval between captures. We used growing season (March-November) days as time intervals to control for inactivity during winter months when it was assumed the salamanders did not grow.

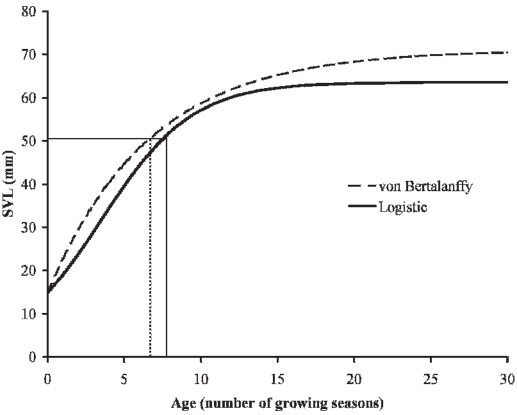

FIG. 2. Predicted curves for growth in snout to vent length (SVL) for a West Virginia population of Green Salamanders (*Aneides aeneus*) from non-linear regression of von Bertalanffy (dashed curve) and logistic (solid curve) growth interval equations. Vertical lines correspond to age at maturity estimates from the von Bertalanffy model (dotted vertical line) and logistic model (solid vertical line).

DISCUSSION

Growth parameters observed in this study indicate that Green Salamanders exhibit indeterminate growth (i.e., continue to grow beyond the size at which they reach reproductive maturity [Table 2]). The smallest reproductively mature individual in the study population was 46.0 mm SVL, yet according to the logistic growth model, growth in the study population did not asymptote until individuals reached 63.5 mm. Although some plethodontids reach maturity at greater ages (e.g., Houck, 1982; Bruce et al., 2002), our estimates of age at reproductive maturity are much greater than previous reports for Green Salamanders and those reported for many other plethodontid salamanders (e.g., Houck, 1982). Reports of age at maturity within *Aneides* vary, ranging from two to four years (Pauley and Watson, 2005; Ramotnik, 2005; Staub and Wake, 2005a,b,c). The discrepancy between our estimated age at maturity and those reported by others might reflect interspecific or regional intraspecific variation in the species' life history, or is a consequence of methodology. Other researchers used size frequency histograms to estimate age at maturity for *Aneides*, which can be unreliable because variance in body size within a particular age class can be high (Halliday and Verrell, 1988).

In many plethodontid species, females reproduce initially at larger body sizes and greater ages than males and grow larger than males (Marvin, 1996). Similar to other reports of Green Salamander size (i.e., Gordon, 1952; Canterbury, 1991), females were larger than males in this study. Because we were unable to separate males and females in our analyses, we likely underestimated the age and size at which females first reproduce, while simultaneously overestimating the same parameters for males. Because Green Salamanders have reproductive strategies similar to most other plethodontids (e.g., females spend approximately three months guarding eggs and breed biennially [Canterbury and Pauley, 1994]), growth may differ between the sexes following maturation. Regardless of our inability to quantify intrapopulation variation in growth patterns, our results revealed that Green Salamanders reach reproductive maturity at a greater age than previously suspected, which has profound implications for conservation strategies aimed at protecting the species and its habitat.

Amphibian body size and age at reproductive maturity are life-history traits that vary among populations along environmental gradients (Hemelaar, 1988; Miaud et al. 2001; Ashton, 2002; Morrison and Hero, 2003). Because salamanders largely follow Bergman's rule (Ashton, 2002), and our study area was located at a high elevation in the northern extent of the species' range, the study population may represent extreme growth and age at reproductive maturity in the species. Amphibians at higher latitudes or altitudes typically have shorter growing seasons and are larger and older at reproductive maturity (Berven, 1982; Hemelaar, 1988; Ryser, 1996; Morrison and Hero, 2003). Canterbury and Pauley (1994) described Green Salamander growing and reproductive seasons that were shorter in West Virginia relative to

TABLE 1. Comparison of von Bertalanffy and logistic growth interval models for Green Salamanders (*Aneides aeneus*) from a northern West Virginia population, 1999–2003. The models estimated asymptotic SVL (*a*) and the growth parameter (*r*), and were compared using the residual error mean square (REMS), where the model that best fit the data had the lowest REMS value. Estimates of Green Salamander age at reproductive maturity were based on general von Bertalanffy and logistic growth models of growth intervals ($N = 19$). The models estimated age at reproductive maturity (*t*) in number of growing seasons (i.e., March–November). Ninety-five percent confidence intervals are shown in brackets, and standard errors are shown in parentheses.

Model	Asymptotic SVL (*a*)	Growth parameter (*r*)	REMS	Age at maturity (t)
von Bertalanffy	71.08 (7.20) [55.87–86.29]	0.15 (0.04) [0.05–0.24]	13.82	6.87 (0.14) [6.58–7.16]
Logistic	63.56 (3.09) [57.04–70.09]	0.33 (0.05) [0.22–0.45]	13.01	7.72 (0.12) [7.46–7.98]

populations in the southern portion of the species' range. Thus, it is likely that Green Salamanders show altitudinal and elevational variation similar to other amphibian species.

Potential benefits of later maturation include higher fecundity through extended growth and larger female size and lower instantaneous juvenile death rates (Stearns, 1992). Green Salamanders in West Virginia are larger than those in the southern extent of their range (Canterbury, 1991), and northern populations likely have slower growth and delayed maturation as compared to southern populations. Delayed maturation is expected to result in an increase in generation time (Stearns and Crandall, 1984), which could have important conservation implications for this species.

TABLE 2. Green Salamander (*Aneides aeneus*) snout–vent length (SVL) measurements taken during a mark-recapture study of a West Virginia population, 1999–2003. An asterisk indicates that the sex of the individual was identified. ''Days'' refers to the number of days since last capture, excluding the hibernation season (i.e., December–February).

	SVL (mm)		
Salamander No.	Capture 1	Capture 2 (days)	Capture 3 (days)
Males			
1	51.5*	56.3 (538)*	67.4 (405)
2	38.6	47.7 (605)	53.9 (225)*
3	50.8*	52.3 (513)*	-
4	54.9*	56.5 (98)	56.6 (460)*
5	29.4	31.9 (155)	46.0 (384)*
6	48.9*	49.6 (79)	-
Females			
1	38.4	46.8 (380)*	-
2	52.2	60.6 (938)*	-
3	41.9	55.8 (667)*	-
4	40.2	52.4 (437)*	55.1 (98)
5	57.0*	58.6 (128)	-
6	55.8*	58.5 (637)	-
Unknown Sex			
1	33.9	41.2 (538)	-
2	49.4	49.8 (76)	-
3	27.7	47.4 (504)	-
4	44.7	53.3 (555)	-
5	30.3	31.1 (125)	-
6	22.0	26.2 (225)	-
7	27.3	36.9 (511)	-

Longevity is based on survivorship, but no information is currently available on the longevity of Green Salamanders. Staub and Wake (2005d) reported that Black Salamanders, *Aneides flavipunctatus*, can live up to 20 yr in captivity, but additional information on longevity within the genus is lacking. Green Salamander mark-recapture intervals have been as great as 13 yr in Kentucky (P. Cupp, pers. comm.). *Plethodon kentucki* and *Ensatina eschscholtzii* reach sexual maturity at three years but are known to live as long as 15 yr (Staub et al., 1995; Marvin, 1996, 2001). Some studies have reported observations on the longevity of other plethodontids (e.g., 6–15 yr for *Desmognathus quadramaculatus*, Castanet et al., 1996; Bruce et al., 2002; 5–11 yr for *Desmognathus ochrophaeus*, Houck and Francillon-Vieillot, 1988; 3–10 yr for *Plethodon metcalfi*, Ash et al., 2003). Whether Green Salamanders have longevities similar to other plethodontids or if any relationship between age at maturity and longevity is a consistent life-history trait within the taxon is unknown. Female Green Salamanders in northern West Virginia have a biennial reproductive cycle (Canterbury and Pauley, 1994); thus, assuming an average female lives long enough to reproduce twice, a very conservative life expectancy would be 11 yr (i.e., females nest in their ninth year plus two years of reproduction). However, given that Green Salamanders continue to grow well beyond the size at which they reach reproductive maturity, we speculate that Green Salamanders can live much longer.

Our study revealed that Green Salamanders reach reproductive maturity at a greater age than has been reported for most plethodontid salamanders. The identification of life-history attributes that may contribute to a species' sensitivity to regional decline is important in helping land managers and biologists recognize vulnerable populations and develop appropriate conservation priorities and management strategies. These results, combined with the unique habitat associations of Green Salamanders (e.g., Wilson, 2003; Waldron and Humphries, 2005), might offer insight into why the species is sensitive to population declines in some parts of its range, but not necessarily in others. We suggest that future research focus further on the species' life history to identify attributes that could make populations susceptible to decline, and to quantify any intrapopulation variation in growth patterns. Knowledge of Green Salamander survivorship and longevity, in particular, would greatly enhance our understanding of the species vulnerability in some parts of its range, and provide a framework from which comparisons could be made across populations.

Acknowledgments.—We thank Mead Westvaco, the West Virginia Division of Natural Resources Natural Heritage Program, and the Marshall University Graduate School for financial support of this research. We thank A. Johnson, J. Wykle, W. J. Humphries, E. Waldron, H. Waldron Jr., J. D. Leach, A. Longenecker, and Z. Felix for field assistance. This manuscript was improved by helpful reviews by S. Welch and J. W. Gibbons.

LITERATURE CITED

ARESCO, M. J., AND C. GUYER. 1999. Growth of the tortoise *Gopherus polyphemus* in Slash Pine plantations of southcentral Alabama. Herpetologica 55:499–506.

ARNTZEN, J. W. 2000. A growth curve for the newt *Triturus cristatus*. Journal of Herpetology 34:227–232.

ASH, A. N., R. C. BRUCE, J. CASTANET, AND H. FRANCILLON-VIEILLOT. 2003. Population parameters of *Plethodon metcalfi* on a 10-year-old clearcut and in nearby forest in the southern Blue Ridge Mountains. Journal of Herpetology 37:445–452.

ASHTON, K. G. 2002. Do amphibians follow Bergmann's rule? Canadian Journal of Zoology 80: 708–716.

BERNARDO, J., AND S. J. AGOSTA. 2003. Determinants of clinal variation in life history of Dusky Salamanders (*Desmognathus ocoee*): prey abundance and ecological limits on foraging time restrict opportunities for larval growth. Journal of Zoology 259:411–421.

BERVEN, K. A. 1982. The genetic basis of altitudinal variation in the Wood Frog, *Rana sylvatica*. An experimental analysis of life history traits. Evolution 36:962–983.

BRUCE, R. C., J. CASTANET, AND H. FRANCILLON-VIEILLOT. 2002. Skeletochronological analysis of variation in age structure, body size, and life history in three species of Desmognathine salamanders. Herpetologica 58:181–193.

CANTERBURY, R. A. 1991. Ecology of the Green Salamander, *Aneides aeneus* (Cope and Packard), in West Virginia. Unpubl. master's thesis. Marshall University, Huntington, WV.

CANTERBURY, R. A., AND T. K. PAULEY. 1994. Time of mating and egg deposition of West Virginia populations of the salamander *Aneides aeneus*. Journal of Herpetology 28:431–434.

CASTANET, J., H. FRANCILLON-VIEILLOT, AND R. C. BRUCE. 1996. Age estimates in desmognathine salamanders assessed by skeletochronology. Herpetologica 52:160–171.

CORSER, J. D. 2001. Decline of disjunct Green Salamander (*Aneides aeneus*) populations in the southern Appalachians. Biological Conservation 97:119–126.

CUPP, P. V. 1980. Territoriality in the Green Salamander, *Aneides aeneus*. Copeia 1980:463–468.

———. 1991. Aspects of the life history and ecology of the Green Salamander, *Aneides aeneus*, in Kentucky. Journal of the Tennessee Academy of Science 66:171–174.

DOODY, J. S. 1995. A photographic mark-recapture method of patterned amphibians. Herpetological Review 35:38–41.

FABENS, A. J. 1965. Properties and fitting of the von Bertalanffy growth curve. Growth 29:265–289.

FRAZER, N. B., AND L. M. EHRHART. 1985. Preliminary growth models for Green, *Chelonia mydas*, and Loggerhead, *Caretta*, Turtles in the wild. Copeia 1985:73–79.

FRAZER, N. B., J. W. GIBBONS, AND J. L. GREENE. 1990. Exploring Fabens' growth interval model with data on a long-lived vertebrate, *Trachemys scripta* (Reptilia: Testudinata). Copeia 1990:112–118.

GIBBONS, J. W. 1976. Aging phenomena in reptiles. *In* M. F. Elias, B. E. Eleftheriou, and P. K. Elias (eds.), Experimental Aging Research, pp. 454–475. Bar Harbor, ME.

GIBBONS, J. W., R. D. SEMLITSCH, J. L. GREENE, AND J. P. SCHUBAUER. 1981. Variation in age and size at maturity of the Slider Turtle (*Pseudemys scripta*). American Naturalist 117:841–845.

GORDON, R. E. 1952. A contribution to the life history and ecology of the plethodontid salamander *Aneides aeneus* (Cope and Packard). American Midland Naturalist 47:666–701.

GRANT, E. H. C., AND P. NANJAPPA. 2006. Addressing error in identification of *Ambystoma maculatum* (Spotted Salamanders) using spot patterns. Herpetological Review 37:57–60.

HALLIDAY, T. R., AND P. A. VERRELL. 1988. Body size and age in amphibians and reptiles. Journal of Herpetology 22:253–265.

HEMELAAR, H. 1988. Age, growth, and other population characteristics of *Bufo bufo* from different latitudes and altitudes. Journal of Herpetology 22:369–388.

HOUCK, L. D. 1982. Growth rates and age at maturity for the plethodontid salamander *Bolitoglossa subpalmata*. Copeia 1982:474–478.

HOUCK, L. D., AND H. FRANCILLON-VIEILLOT. 1988. Tests for age and site effects on male mating success in a plethodontid salamander. Amphibia-Reptilia 9:135–144.

Kaplan, R. H. 1980. The implications of ovum size variability for offspring fitness and clutch size within several populations of salamanders (*Ambystoma*). Evolution 34:51–64.

Kunz, T. H. 1974. Reproduction, growth and mortality of the vespertilionid bat, *Eptesicus fuscus*, in Kansas. Journal of Mammalogy 55:1–13.

Licht, L. E. 1975. Comparative life history features of the Western Spotted Frog, *Rana pretiosa*, from low- and high-elevation populations. Canadian Journal of Zoology 53:1254–1258.

MacArthur, R. H., and W. E. Wilson. 1967. The Equilibrium Theory of Island Biogeography. Princeton University Press, Princeton, NJ.

Marvin, G. A. 1996. Life history and population characteristics of the salamander *Plethodon kentucki* with a review of *Plethodon* life histories. American Midland Naturalist 136:385–400.

———. 2001. Age, growth, and long-term site fidelity in the terrestrial plethodontid salamander *Plethodon kentucki*. Copeia 2001:108–117.

Miaud, C., F. Andreone, A. Riberon, S. De Michelis, V. Clima, J. Castanet, H. Francillon-Vieillot, and R. Guyetant. 2001. Differences in age, size at maturity and gestation duration among two neighbouring populations of the Alpine Salamander *Salamandra lanzai*. Journal of Zoology 254:251–260.

Morrison, C., and J. M. Hero. 2003. Geographic variation in life-history characteristics of amphibians: a review. Journal of Animal Ecology 72:270–279.

Pauley, T. K., and M. B. Watson. 2005. *Aneides aeneus* (Cope and Packard, 1881). *In* M. Lannoo (ed.), Amphibian Declines, The Conservation Status of United States Species, pp. 656–658. University of California Press, Berkeley.

Petranka, J. W. 1998. Salamanders of the United States and Canada. Smithsonian Institution Press, Washington DC.

Ramotnik, C. 2005. *Aneides hardii* (Taylor, 1941) Sacramento Mountain Salamander. *In* M. Lannoo (ed.), Amphibian Declines, The Conservation Status of United States Species, pp. 661–662. University of California Press, Berkeley.

Ryser, J. 1996. Comparative life histories of a low-and a high-elevation population of the Common Frog *Rana temporaria*. Amphibia-Reptilia 17:183–195.

Schoener, T. W., and A. Schoener. 1978. Estimating and interpreting body-size growth in some *Anolis* lizards. Copeia 1978:390–405.

Shine, R., and L. Schwartzkopf. 1992. The evolution of reproductive effort in lizards and snakes. Evolution 46:62–75.

Snyder, D. H. 1971. The Function of Brooding Behavior in the Plethodontid Salamander, *Aneides aeneus*: A Field Study. Unpubl. Ph.D. diss., University of Notre Dame, South Bend, IN.

Staub, N. L., and D. B. Wake. 2005a. *Aneides ferreus* Cope, 1869 Clouded Salamander. *In* M. Lannoo (ed.), Amphibian Declines, The Conservation Status of United States Species, pp. 658–660. University of California Press, Berkeley.

———. 2005b. *Aneides lugubris* Hallowell, 1949 Arboreal Salamander. *In* M. Lannoo (ed.), Amphibian Declines, The Conservation Status of United States Species, pp. 662–664. University of California Press, Berkeley.

———. 2005c. *Aneides vagrans* Wake and Jackman, 1999 Wandering Salamander. *In* M. Lannoo (ed.), Amphibian Declines, The Conservation Status of United States Species, pp. 664–666. University of California Press, Berkeley.

———. 2005d. *Aneides flavipunctatus* (Strauch, 1870) Black Salamander. *In* M. Lannoo (ed.), Amphibian Declines, The Conservation Status of United States Species, pp. 660–661. University of California Press, Berkeley.

Staub, N. L., C. W. Brown, and D. B. Wake. 1995. Patterns of growth and movements in a population of *Ensatina eschscholtzii platensis* (Caudata: Plethodontidae) in the Sierra Nevada, California. Journal of Herpetology 29:593–599.

Stearns, S. C. 1992. The Evolution of Life Histories. Oxford University Press Inc., New York.

Stearns, S. C., and R. E. Crandall. 1984. Plasticity for age and size at sexual maturity: a life-history adaptation to unavoidable stress. *In* G. Potts and R. Wootton (eds.), Fish Reproduction, pp. 13–33. Academic Press, New York.

Tilley, S. G. 1980. Life histories and comparative demography of two salamander populations. Copeia 1980:806–821.

Waldron, J. L. 2000. Ecology and Sympatric Relations of Crevice Salamanders in Randolph County, West Virginia. Unpubl. master's thesis. Marshall University, Huntington, WV.

Waldron, J. L., and W. J. Humphries. 2005. Arboreal habitat use by the Green Salamander, *Aneides aeneus*, in South Carolina. Journal of Herpetology 39:486–492.

Webb, J. K., B. W. Brook, and R. Shine. 2002. What makes a species vulnerable to extinction? Comparative life-history traits of two sympatric snakes. Ecological Research 17:59–67.

Williams, K. L., and R. E. Gordon. 1961. Natural dispersal of the salamander *Aneides aeneus*. Copeia 1961:353.

Wilson, C. R. 2003. Woody and arboreal habits of the Green Salamander (*Aneides aeneus*) in the Blue Ridge Mountains. Contemporary Herpetology 13:http://www.selu.edu/journals/ContemporaryHerpetology/ch/2003/2/index.htm

Woods, J. E. 1968. The Ecology and Natural History of Mississippi Populations of *Aneides aeneus* and Associated Salamanders. Unpubl. Ph.D. diss., University of Southern Mississippi, Hattiesburg.

Accepted: 5 June 2007.