
FILLING GAPS IN LIFE-HISTORY DATA: CLUTCH SIZES FOR 21 SPECIES OF NORTH AMERICAN ANURANS

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Abstract.—Lack of demographic information on North American anurans weakens the ability of amphibian biologists to ask basic ecological and evolutionary questions about this declining group of vertebrates. Accurate data on clutch sizes are required for assessments of geographic variation in this life-history trait and an understanding of environmental (e.g., climate change) and genetic impacts on demography among populations. We quantified the number of eggs in 469 clutches for 21 of the 27 species of anurans that occur in Virginia. Clutch sizes ranged from 116 in *Pseudacris ocularis* to 16,536 in *Anaxyrus terrestris*. Maximum clutch sizes for 11 species exceeded the maximum number reported in the literature. Relationships of clutch size to maternal body size were not significant for seven species (*Gastrophryne carolinensis*, *Hyla cinerea*, *Hyla femoralis*, *Hyla squirella*, *Pseudacris brimleyi*, *Pseudacris crucifer*, *Pseudacris feriarum*), possibly because of small sample sizes, but correlations for *Anaxyrus americanus*, *A. terrestris*, and *Lithobates sylvaticus* were significantly positive. Maternal body size explained 41% to 73% of the variation in clutch size in these latter three species with positive correlations. Demographic data from several locations within the ranges of widespread North American anurans would allow assessment of sources of environmentally and genetically induced geographic variation in life-history traits, including clutch size. Studies of anuran natural life histories are urgently needed despite the fact that such studies are not in vogue or supported by most academic institutions and funding agencies.

Key Words.—demography; ecology; geographic variation; life history; Virginia

INTRODUCTION

Elucidation of life-history patterns requires information on traits such as clutch and egg size, annual clutch frequency, fecundity, age and size at maturity, age-specific reproductive effort, neonate size, and survivorship (Stearns 1976, 1977; Roff 1992). Variation in these traits for ectotherms is influenced strongly by geographic variation in environmental conditions. Amphibian populations at higher elevations and latitudes generally have shorter breeding seasons, longer larval periods, larger size at metamorphosis, relatively larger adults that reach reproductive maturity at older ages, produce smaller clutches relative to body size, and have larger eggs compared to populations at lower elevations and latitudes (Atkinson 1994; Berrigan and Charnov 1994; Morrison and Hero 2003). Life-history information on North American anurans is often inadequate or missing altogether, even for species considered common, to determine if such patterns can be considered generalizations (Dodd and Franz 1993; Lannoo 1998; Wells 2007). A review by Morrison and Hero (2003) included only 13 published studies comparing life-history traits in high and low elevation populations among amphibians worldwide. Only three species of anurans and two species of salamanders were

included from North America despite relatively high levels of diversity within these groups.

Dodd (2013:pp. xxv) noted that “the basis for many reported life-history traits rested on little empirical data.” Life-history traits have been documented in several locations for some widespread species such as *Lithobates catesbeianus*, *Lithobates sylvaticus*, and *Pseudacris crucifer*. However, little to no data are available for other widespread species such as *Acris crepitans* (Bayne 2004), *Spea multiplicata* (Woodward 1987), and *Lithobates blairi* (Dodd 2013). Clutch data for most species are included in fewer than five references. There is only one reference for each of 34 species and none for 15 species, representing almost half of the North American frog fauna (Crother 2012). Moreover, clutch data for some species may not be accurate due to geographic bias (Dodd 2013). Because geographic variation in anuran life-history attributes and varying techniques used to assess clutch size may introduce additional variation, amphibian ecologists are left with a limited understanding of the basic ecology and life-history evolution of these amphibians.

During our fieldwork on amphibians in Virginia in the 1970s and 1980s, we accumulated counts of the number of eggs in clutches oviposited by females of 21 species of anurans. The preliminary report of clutch sizes in nine Virginia anurans in Mitchell (1986) used approximated numbers based on some of the data in this

paper. We re-examined our field notes, and those of others available to us, for clutch data and where possible the sizes of the females that produced them. This paper summarizes our results on clutch size and relationships of clutch size to female body size for species with sample sizes greater than or equal to eight that include measurements of female body size. We briefly review the difficulties of obtaining clutch size data for some species and show that different techniques may yield different results that affect accurate assessments of geographic variation in this life-history trait.

METHODS

We obtained clutch sizes for 21 of the 27 species of anurans that occur in Virginia (Mitchell and Reay 1999; Beane et al. 2010) from a variety of locations east of the Blue Ridge Mountains between 1979 and 1986. We obtained clutch data for most species from locations in the Richmond area southeastward to the Atlantic Coast in the Coastal Plain Physiographic Province. Data for *Hyla versicolor* were obtained in Amherst County, Virginia, at the western edge of the Piedmont Physiographic Province, and for *Lithobates sylvaticus* in Prince William County in the northern part of the state at the eastern edge of the Piedmont. Except for the two species of *Acris* that were captured along lake margins, we obtained all clutches from anurans inhabiting ephemeral wetlands (e.g., vernal pools, road rut pools, road-side ditches). We captured pairs of males and females in amplexus or separately prior to oviposition and placed them in buckets or large (25 × 45 cm) individual plastic bags (when buckets were unavailable in the field) with a small amount of water from the original breeding pond following the technique pioneered by Collins (1975). We added twigs to buckets and bags for clutch attachment sites. Bags were left overnight while floating on the water or adjacent to the site on land during which time most of the pairs oviposited eggs. We used this technique for all but one species. We collected single clutches of *Lithobates sphenoccephalus* eggs within one to two days of oviposition from temporary ponds and pools. Egg counts in these egg masses should be accurate estimates of clutch size because female *L. sphenoccephalus* in Virginia lay their eggs in single, clear gelatinous masses often unattached to vegetation (pers. obs.). We never found smaller egg masses adjacent to the larger masses as was noted by Dodd (2013) for this species in some locations. We, therefore, assumed a single egg mass of this species represented the female's entire clutch in Virginia.

We counted the number of eggs in several of the clutches immediately following oviposition (*Anaxyrus terrestris*, *Pseudacris kalmi*, *Pseudacris ocularis*). However, we preserved clutches for 15 species (*Acris*

crepitans, *Acris gryllus*, *Anaxyrus fowleri*, *Gastrophryne carolinensis*, *Hyla chrysoscelis*, *Hyla cinerea*, *Hyla femoralis*, *Hyla gratiosa*, *Hyla squirella*, *Hyla versicolor*, *Lithobates palustris*, *Pseudacris brimleyi*, *Pseudacris crucifer*, *Pseudacris feriarum*, and *Scaphiopus holbrookii*) in 10% formalin and stored them for examination in the laboratory. We used both techniques to process clutches for three species (*Anaxyrus americanus*, *Lithobates sphenoccephalus*, *Lithobates sylvaticus*). We counted the total number of eggs in all clutches except for *A. terrestris*. We obtained the number of eggs for *A. terrestris* clutches by counting oviposited eggs in 10–15 ml of egg mass after straining to remove water and volumetrically estimating the number of remaining eggs. We measured snout-vent (SVL) lengths of some of the females of most species to the nearest mm. Measurements of the female parent were not available for seven species. Regression statistics follow Zar (2009) and we calculated them using SigmaPlot 12.3[®] (Systat Software, Inc., San Jose, California, USA). Significance-level was set at $\alpha = 0.05$.

RESULTS

Clutch size of 469 clutches for the 21 species studied ranged from 116 in *Pseudacris ocularis* to 16,537 in *Anaxyrus terrestris* (Table 1). Twelve of the 21 species of anurans for which we had data on clutch size also had corresponding measurements of maternal body size for at least a portion of the sample. We used samples of ≥ 8 were available for nine species in the analyses, whereas we considered samples of ≤ 6 for three species too small. The relationship of clutch size to maternal SVL was not significant for *Gastrophryne carolinensis* ($F_{2,7} = 3.773$, $P = 0.093$, $n = 9$), *Hyla cinerea* ($F_{2,7} = 2.71$, $P = 0.131$, $n = 12$), *Hyla femoralis* ($F_{2,17} = 0.770$, $P = 0.394$, $n = 19$), *Hyla squirella* ($F_{2,4} = 0.640$, $P = 0.468$, $n = 9$), *Pseudacris brimleyi* ($F_{2,2} = 2.98$, $P = 0.481$, $n = 4$), *Pseudacris crucifer* ($F_{2,21} = 3.09$, $P = 0.093$, $n = 24$), and *Pseudacris feriarum* ($F_{2,6} = 1.29$, $P = 0.299$, $n = 8$). Relationships for three species were positive and significant (Fig. 1): *Anaxyrus americanus* ($F_{2,5} = 13.68$, $P = 0.014$, $n = 8$), *A. terrestris* ($F_{2,16} = 39.86$, $P < 0.001$, $n = 25$), and *Lithobates sylvaticus* ($F_{2,50} = 34.77$, $P < 0.001$, $n = 52$). Regression equations for *A. americanus* were clutch size = 249.8 SVL–15463.6, $r^2 = 0.73$, $n = 8$, for *A. terrestris* clutch size = 349.0 SVL–19579.9, $r^2 = 0.63$, $n = 25$, and for *L. sylvaticus* clutch size = 19.6 SVL–469.2, $r^2 = 0.41$, $n = 52$.

DISCUSSION

The 21 species with clutch data that we analyzed represent 78% of the entire Virginia frog fauna and 21% of the North American frog fauna (Mitchell and Reay 1999; Dodd 2013). We were unable to acquire clutch

TABLE 1. Female snout-vent length (SVL) and descriptive statistics of clutch size for 21 species of frogs in Virginia. Sample sizes (n) are followed by $\bar{x} \pm SE$ and range. Clutch data for *L. sphenoccephalus* represent egg mass counts.

Species	n	Female SVL	n	Clutch Size
<i>Acris crepitans</i>			2	188–196
<i>Acris gryllus</i>	6	24.40 ± 0.60, 22–26	9	170.33 ± 25.65, 109–340
<i>Anaxyrus americanus</i>	8	77.13 ± 1.70, 71–85	17	3,920.35 ± 319.16, 2,273–6,140
<i>Anaxyrus fowleri</i>	—		8	4,578 ± 614.50, 2,662–7,742
<i>Anaxyrus terrestris</i>	25	72.76 ± 1.68, 58–94	51	5,513.13 ± 484.30, 1,704–16,537
<i>Gastrophryne carolinensis</i>	9	28.83 ± 0.52, 27–31	35	820.74 ± 68.59, 208–1,614
<i>Hyla chrysoscelis</i>	—		30	1,916.07 ± 79.84, 832–2,667
<i>Hyla cinerea</i>	13	41.85 ± 1.45, 35–49	41	1,271.71 ± 55.07, 689–2,228
<i>Hyla femoralis</i>	19	34.88 ± 0.33, 32–37	65	1,289.66 ± 43.83, 701–2,086
<i>Hyla gratiosa</i>	3	62.33 ± 1.86, 60–66	4	2,728 ± 65.62, 2,646–2,923
<i>Hyla squirella</i>	9	32.12 ± 0.52, 29–34	8	1,076.38 ± 230.15, 392–2,081
<i>Hyla versicolor</i>	—		4	2,200.00 ± 22.75, 2,159–2,257
<i>Lithobates palustris</i>			1	1,413
<i>Lithobates sphenoccephalus</i>	—		35	1,766.07 ± 148.68, 898–3,509
<i>Lithobates sylvaticus</i>	52	57.66 ± 0.65, 44–67	56	658.04 ± 18.80, 333–929
<i>Pseudacris brimleyi</i>	5	27.92 ± 26.34, 25–31	5	245.20 ± 27.75, 170–324
<i>Pseudacris crucifer</i>	24	30.66 ± 0.57, 25–34	72	889.34 ± 38.23, 242–1,648
<i>Pseudacris feriarum</i>	8	31.80 ± 0.82, 28–34	12	441.314 ± 50.26, 197–835
<i>Pseudacris kalmi</i>	—		3	923.67 ± 182.60, 573–1,187
<i>Pseudacris ocularis</i>	—		1	116
<i>Scaphiopus holbrookii</i>	—		10	2,518.70 ± 374.00, 1,177–5,395

data for six species that occur in the state: *Anaxyrus quercicus*, *Lithobates clamitans*, *L. catesbeianus*, *L. virgatipes*, *Pseudacris brachyphona*, and *P. nigrita* (Mitchell and Reay 1999; Beane et al. 2010). Maximum clutch sizes we report for 11 species from Virginia (*Acris gryllus*, *Anaxyrus terrestris*, *Gastrophryne carolinensis*, *Hyla cinerea*, *H. femoralis*, *H. squirella*, *Pseudacris brimleyi*, *P. crucifer*, *P. feriarum*, *P. kalmi*, *Scaphiopus holbrookii*) exceed the maximum number reported in the literature (Mitchell 1986; Dodd 2013 and references therein). We report the first known clutch size for *P. ocularis*. The only clutch size reported in the literature for *A. terrestris* (2,888; Wright 1932) is slightly higher than the minimum reported here. The maximum clutch size for *A. terrestris* in Virginia (16,537) is comparable to reported maximum counts for two other similar-sized bufonids that occur in the state: *A. americanus* (15,835; Miller 1909) and *A. fowleri* (15,618; Trauth et al. 1990). Maximum clutch sizes known for *A. americanus* and *A. fowleri* in Virginia are half of the reported maxima in Arkansas and Massachusetts (Miller 1909, Trauth et al. 1990). Maximum number of eggs in post-oviposition egg masses for *L. sphenoccephalus* is larger than the

maximum number for egg masses in Arkansas (Trauth et al. 1990). The range of clutch sizes for *L. sylvaticus* in Virginia are within published ranges for Alaska, Arkansas, and Colorado, but the maximum is larger than those reported for Alabama, Georgia, Illinois, and Tennessee (Dodd 2013 and references therein). Clutch sizes for Virginia *A. crepitans*, *H. chrysoscelis*, *H. gratiosa*, *H. versicolor*, and *L. palustris* are within published data (Dodd 2013).

The relationship of clutch size to female body size was significantly positive for *A. americanus*, *A. terrestris*, and *L. sylvaticus*. Of the species included in this paper, positive correlations of clutch size to maternal body size has been reported for *A. americanus*, *A. fowleri*, *H. chrysoscelis*, *L. palustris*, *L. sphenoccephalus*, *P. crucifer*, and *P. feriarum* (Oplinger 1966, Clarke 1974, Howard 1988, Ritke et al. 1990, Trauth et al. 1990). Lack of positive correlations have been documented for *H. femoralis* in Florida (Delis 2001), and *G. carolinensis*, *H. femoralis* and *P. crucifer* in Arkansas (Trauth et al. 1990). We found no positive correlations for these species in Virginia. Detection of a positive relationship between clutch size and female body size is influenced by female size and age, health, genetics, environmental

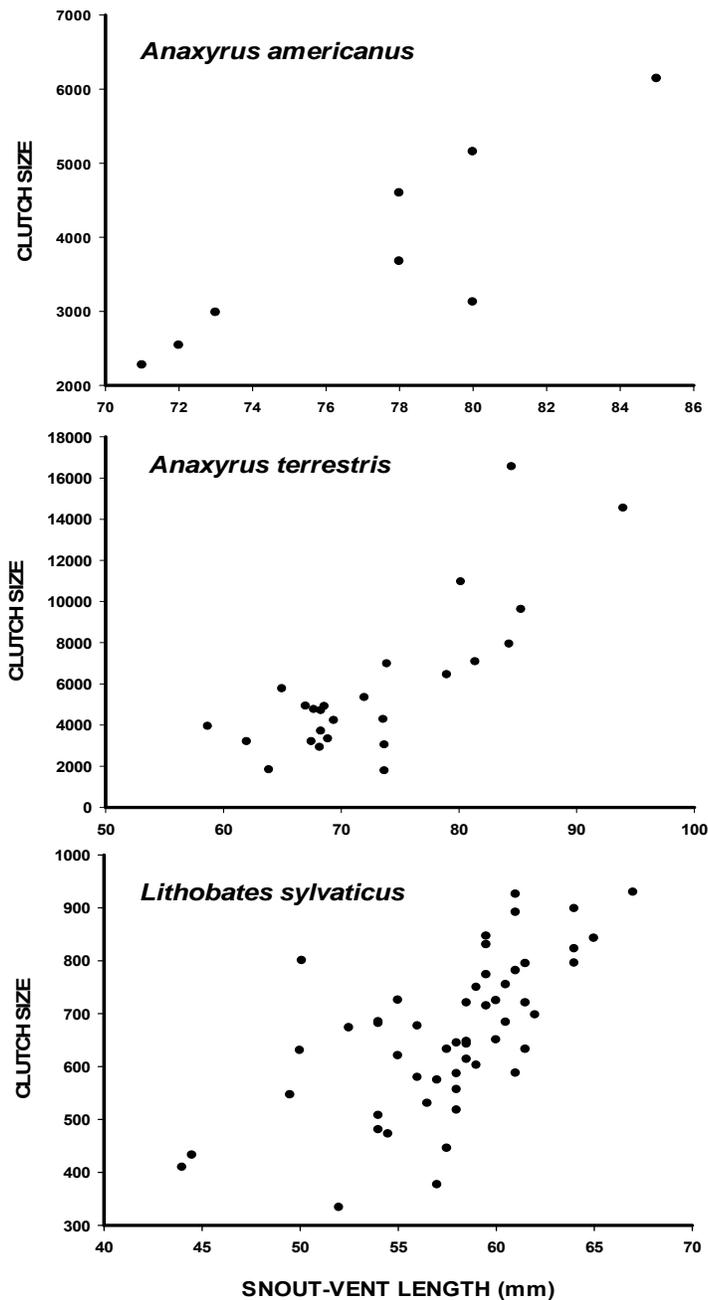


FIGURE 1. Relationship of clutch size and maternal body size for *Anaxyrus americanus*, *Anaxyrus terrestris*, and *Lithobates sylvaticus* from Virginia, USA. See results for statistical analysis.

factors, and sample size (Perrill and Daniel 1983; Wells 2007). Our sample sizes for three species with corresponding female body sizes (*A. gryllus*, *H. gratiosa*, *P. brimleyi*) may have been too small to detect positive relationships (but see Wood et al. 2014).

Accurate clutch sizes may be difficult to obtain in the field for some species because of sensitive behavioral

and physiological characteristics (e.g., *Lithobates catesbeianus*, *Lithobates clamitans*) or the technique used (Collins 1975; Dodd 2013). Because counting hundreds or thousands of eggs in a single clutch is tedious and time consuming, some researchers have counted a sample of enlarged ovarian eggs in museum specimens or eggs in ovulated clutches and then

extrapolated the number for the entire clutch by mass or volumetric displacement (e.g., Barbour and Walters 1941; Gosner and Rossman 1959; Brugger 1984; Woodward 1987; Trauth 1989). Others have caught amplexant pairs in the field and allowed them to oviposit in a bucket (Gunzberger 2006) or mated field-caught individuals in the laboratory and counted the eggs (Collins 1975; Berven 1982, 2009). Clutches obtained from pairs already in amplexus when captured may not represent the entire complement because some eggs may have already been deposited. This is especially true of hylids and the one microhylid that lay eggs singly or in small clusters (e.g., *H. femoralis*, Altig 1972; *P. brachyphona*, Barbour and Walters 1941; Mitchell and Pauley 2005; *P. crucifer*, Minton 2001; Klemens 1993). The lowest counts for *G. carolinensis* and *H. squirella* reported in this paper may be inaccurate for this reason.

Complete counts of eggs in oviposited clutches, rather than counts based on extrapolations or the number of enlarged ovarian eggs in preserved specimens, increases the accuracy of clutch size data. Counts of enlarged follicles in specimens may overestimate clutch size if some of the eggs are retained or ovulated in a second clutch (Wells 1976; Perrill and Daniel 1983). The ecologically relevant clutch size is the number actually oviposited. Accurate clutch size data provide a crucial element for calculation of age-specific reproductive effort, correlations with maternal age and size, and elucidation of geographic patterns in life histories. Because of the questionable accuracy of the counts in some anuran clutches, the conclusions by Wells (2007) about relationships of clutch size with body size among species in different reproductive modes would have been more robust if accurate counts based on adequate sample sizes in multiple populations had been available.

Analyses of geographic variation in life-history traits provide important information relevant to questions about such topics as environmental or genetic adaptations to local environments, effect of shorter growth seasons in northern populations compared to southern populations, energetic allocation to clutch and egg size, fecundity versus growth, and how climate change may affect anuran demography. Lack of demographic information on most North American anurans, as revealed by the paucity of accurate clutch size data (Dodd 2013), weakens our ability to ask basic evolutionary, adaptation, and conservation questions about this declining group of vertebrates. Lizard ecologists are far ahead of amphibian ecologists on this topic. For example, demographic studies of 14 populations of the Eastern Fence Lizard (*Sceloporus undulatus*) throughout its range (e.g., Gillis and Ballenger 1992; Niewiarowski 1994) revealed environmental and genetic sources of variation in growth rates, age at maturity, body size, fecundity, and other life-history traits. Northern populations are

characterized by delayed maturity, large adult body size, larger clutches, and higher longevity, whereas early maturity, small adult body size, smaller clutches, and short longevity characterized southern populations (Niewiarowski 1994). The contrasting characteristics described by Atkinson (1994), Berrigan and Charnov (1994), and Morrison and Hero (2003) for anurans at high and low elevations based on small numbers of studies appear to follow the same pattern. Very few studies exist, however, on the influence of latitude on clutch size in North American anurans. Morrison and Hero (2003) included one study of one Australian anuran (*Geocrinia victoriana*) that reported a decrease in clutch size with increasing latitude (Gollman and Gollman 1996). Larger clutches in high elevation populations of *Pseudacris triseriata* have been reported by Pettus and Angleton (1967) and for *L. sylvaticus* by Berven (1982) and Berven and Gill (1983). In contrast, clutch sizes were the same for *R. pretiosa* populations at high and low elevations (Licht 1975). The results for studies of clutch size and other life-history characters at different elevations in North America are mixed and require further study.

Demographic data from several locations at different elevations and latitudes in the ranges of widespread North American anurans would allow assessments of sources of environmentally and genetically induced geographic variation in life-history traits, including clutch size. Basic life-history data are essential for documentation and elucidation of the effects of climate change on anurans, especially at northern latitudes. Reproductive data may be particularly strong indicators of climate change for some widespread species (e.g., *Hyla versicolor*, *Lithobates sylvaticus*, *Pseudacris crucifer*), as is calling phenology for these species (Gibbs and Breisch 2001). Studies of anuran natural histories from many geographic locations are urgently needed despite the fact that such studies are not in vogue or supported by most academic institutions and government agencies (Greene 1994, 2005; Pauley 2005; Dodd 2013). Most publications containing clutch size data on the 21 species we studied were conducted before 2000, suggesting this negative view of natural history research remains prevalent among many amphibian biologists.

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LITERATURE CITED

- Altig, R. 1972. Notes on the larvae of premetamorphic tadpoles of four *Hyla* and three *Rana* with notes on tadpole color patterns. *Journal of the Elisha Mitchell Scientific Society* 88:113–119.
- Atkinson, D. 1994. Temperature and organism size – a biological law for ectotherms? *Advances in Ecological Research* 25:1–58.
- Bayne, K.A. 2004. The natural history and morphology of the Eastern Cricket Frog, *Acris crepitans crepitans*, in West Virginia. M.Sc. Thesis, Marshall University, Huntington, West Virginia, USA. 103 p.
- Barbour, R.W., and E.P. Walters. 1941. Notes on the breeding habits of *Pseudacris brachyphona*. *Copeia* 1941:116.
- Beane, J.C., A.L. Braswell, J.C. Mitchell, W.M. Palmer, and J.R. Harrison, Jr. 2010. *Amphibians and Reptiles of the Carolinas and Virginia*. University North Carolina Press, Chapel Hill, North Carolina, USA.
- Berrigan, D., and E.L. Charnov. 1994. Reaction norms for age and size at maturity in response to temperature: a puzzle for life historians. *Oikos* 70:474–478.
- Berven, K.A. 1982. The genetic basis of altitudinal variation in the Wood Frog *Rana sylvatica*. I. An experimental analysis of life history traits. *Evolution* 36:962–983.
- Berven, K.A. 2009. Density dependence in the terrestrial stage of Wood Frogs: evidence from a 21–year study. *Copeia* 2009:328–338.
- Berven, K.A., and D.E. Gill. 1983. Interpreting geographic variation in life-history traits. *American Zoologist* 23:85–97.
- Brugger, K.E. 1984. Aspects of reproduction in the Squirrel Treefrog (*Hyla squirella*). M.Sc. Thesis, University of Florida, Gainesville, Florida, USA. 85 p.
- Clarke, R.D. 1974. Activity and movement patterns in a population of Fowler’s Toad, *Bufo woodhousei fowleri*. *American Midland Naturalist* 92:257–274.
- Collins, J.P. 1975. A comparative study of the life history strategies in a community of frogs. Ph.D. Dissertation, University of Michigan, Ann Arbor, Michigan, USA. 148 p.
- Crother, B.I. (Ed.). 2012. *Scientific and standard English names of amphibians and reptiles of North America North of Mexico, with comments regarding confidence in our understanding*. 7th Edition. SSAR Herpetological Circular 39:1–92.
- Delis, P.R. 2001. Effects of urbanization on the community of anurans of a pine flatwood habitat in west central Florida. M.Sc. Thesis, University of South Florida, Tampa, Florida, USA. 253 p.
- Dodd, C.K., Jr. 2013. *Frogs of the United States and Canada*. 2 volumes. Johns Hopkins University Press, Baltimore, Maryland, USA.
- Dodd, C.K., Jr., and R. Franz. 1993. The need for status information on common herpetological species. *Herpetological Review* 24:27–50.
- Gibbs, J.P., and A.R. Breisch. 2001. Climate warming and calling phenology for frogs near Ithaca, New York, 1900–1999. *Conservation Biology* 15:1175–1178.
- Gillis, R., and R.E. Ballenger. 1992. Reproductive ecology of Red-chinned Lizards (*Sceloporus undulatus erythrocheilus*) in southcentral Colorado: comparisons with other populations of a wide-ranging species. *Oecologia* 89:236–243.
- Gollman, B., and G. Gollman. 1996. Geographic variation of larval traits in the Australian frog *Geocrinia victoriana*. *Herpetologica* 52:181–187.
- Gosner, K.L., and D.A. Rossman. 1959. Observations on the reproductive cycle of the Swamp Chorus Frog, *Pseudacris nigrita*. *Copeia* 1959:263–266.
- Greene, H.W. 1994. Systematics and natural history, foundations for understanding and conserving biodiversity. *American Zoologist* 34:48–56.
- Greene, H.W. 2005. Organisms in nature as a central focus for biology. *Trends in Ecology and Evolution* 20:23–27.
- Gunzberger, M.S. 2006. Reproductive ecology of the Green Treefrog (*Hyla cinerea*) in northwestern Florida. *American Midland Naturalist* 155:321–328.
- Howard, R.D. 1988. Sexual selection on male body size and mating behavior in American Toads, *Bufo americanus*. *Animal Behaviour* 36:1796–1808.
- Klemens, M.W. 1993. *Amphibians and Reptiles of Connecticut and Adjacent Regions*. Bulletin 112, State Geological and Natural History Survey of Connecticut, Hartford, Connecticut, USA.
- Lannoo, M.J. 1998. Conclusions. Pp. 429–431 *In Amphibian Declines: The Conservation Status of United States Species*. Lannoo, M. (Ed.). University of California Press, Berkeley, California, USA.
- 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.
- Miller, N. 1909. The American Toad (*Bufo lentiginos americanus*, LeConte) a study in dynamic biology. *American Naturalist* 43:641–668.
- Minton, S.A., Jr. 2001. *Amphibians and Reptiles of Indiana*. Indiana Academy of Science, Indianapolis, Indiana, USA.
- Mitchell, J.C. 1986. Life history patterns in a central Virginia frog community. *Virginia Journal of Science* 37:262–271.
- Mitchell, J.C., and T.K. Pauley. 2005. *Pseudacris brachyphona* (Cope. 1889). Pp. 465–467 *In*

Herpetological Conservation and Biology

- Amphibian Declines: The Conservation Status of United States Species. Lannoo, M. (Ed.). University of California Press, Berkeley, California, USA
- Mitchell, J.C., and K.K. Reay. 1999. Atlas of Amphibians and Reptiles in Virginia. Special Publication Number 1, Virginia Department Game and Inland Fisheries, Richmond, Virginia, USA.
- Morrison, C., and J.-M. Hero. 2003. Geographic variation in life-history characteristics of amphibians: a review. *Journal of Animal Ecology* 72:270–279.
- Niewiarowski, P.H. 1994. Understanding geographic life-history variation in lizards. Pp. 31–49 *In* Lizard Ecology, Historical and Experimental Perspectives. Vitt, L.J., and E.R. Pianka (Eds.). Princeton University Press, Princeton, New Jersey, USA.
- Oplinger, C.S. 1966. Sex ratio, reproductive cycles, and time of ovulation in *Hyla crucifer crucifer*. *Herpetologica* 22:276–283.
- Pauley, T.R. 2005. Reflections upon amphibian conservation. Pp. 277–281 *In* Amphibian Declines, The Conservation Status of United States Species. Lannoo, M. (Ed.). University of California Press, Berkeley, California, USA.
- Perrill, S.A., and R.E. Daniel. 1983. Multiple egg clutches in *Hyla regilla*, *H. cinerea*, and *H. gratiosa*. *Copeia* 1963:513–516.
- Pettus, D., and G.M. Angleton. 1967. Comparative reproductive biology of montane and Piedmont chorus frogs. *Evolution* 21:500–507.
- Ritke, M.E., J.G. Rabb, and M.K. Ritke. 1990. Life history of the Gray Treefrog (*Hyla chrysoscelis*) in western Tennessee. *Journal of Herpetology* 24:135–141.
- Roff, D.A. 1992. The Evolution of Life Histories. Chapman and Hall, New York, New York, USA.
- Stearns, S.C. 1976. Life history tactics: a review of the idea. *Quarterly Review of Biology* 51:3–47.
- Stearns, S.C. 1977. The evolution of life history traits: a critique of the theory and a review of the data. *Annual Review of Ecology and Systematics* 8:145–171.
- Trauth, S.E. 1989. Female reproductive traits of the Southern Leopard Frog, *Rana sphenoccephala* (Anura: Ranidae) from Arkansas. *Proceedings of the Arkansas Academy of Science* 43:105–108.
- Trauth S.E., R.L. Cox, B.P. Butterfield, D.A. Saugey, and W.E. Meshaka. 1990. Reproductive phenophases and clutch characteristics of selected Arkansas amphibians. *Proceedings of the Arkansas Academy of Science* 44:107–113.
- Wells, K.D. 1976. Multiple clutches in the Green Frog (*Rana clamitans*). *Herpetologica* 32:85–87.
- Wells, K.D. 2007. The Ecology and Behavior of Amphibians. University of Chicago Press, Chicago, Illinois, USA.
- Wood, J., N. Freemantle, M. King, and I. Nazareth. 2014. Trap of trends to statistical significance: likelihood of near significant P value becoming more significant with extra data. *British Medical Journal* 348:g2215. doi:10.1136/BMJ.g2215.
- Woodward, B.D. 1987. Clutch parameters and pond use in some Chihuahuan desert anurans. *Southwestern Naturalist* 32:13–19.
- Wright, A.H. 1932. Life Histories of the Frogs of the Okefinokee Swamp, Georgia. North American Salientia (Anura) 2. Macmillan Press, New York, New York, USA.
- Zar, J.H. 2009. Biostatistical Analysis. 5th Edition. Prentice Hall, Upper Saddle River, New Jersey, USA.



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