

- Evolution and Ecology of Unisexual Vertebrates. pp 49–71. New York State Museum, Albany.
- FROST, D. R., AND J. W. WRIGHT. 1988. The taxonomy of uniparental species with special reference to parthenogenetic *Cnemidophorus* (Sauria: Teiidae). *Syst. Zool.* 37:200–208.
- HUBBS, C. L., AND K. KURONUMA. 1942. Analysis of hybridization in nature between two species of Japanese flounders. *Pap. Michigan Acad. Sci., Arts Letters* 28:343–378.
- LEUCK, B. E., E. E. LEUCK, II, AND R. T. B. SHERWOOD. 1981. A new population of New Mexico whiptail lizards, *Cnemidophorus neomexicanus* (Teiidae). *Southwest. Natur.* 26:72–74.
- LOWE, C. H., AND J. W. WRIGHT. 1966. Evolution of parthenogenetic species of *Cnemidophorus* (whiptail lizards) in western North America. *J. Arizona Acad. Sci.* 4:81–87.
- _____, AND R. G. ZWEIFEL. 1952. A new species of whiptailed lizard (genus *Cnemidophorus*) from New Mexico. *Bull. Chicago Acad. Sci.* 9:229–247.
- MASLIN, T. P., R. G. BEIDLEMAN, AND C. H. LOWE, JR. 1958. The status of the lizard *Cnemidophorus perplexus* Baird and Girard (Teiidae). *Proc. U. S. Natl. Mus.* 108:331–345.
- MAYR, E. 1963. Names given to hybrids. *Bull. Zool. Nomenclature* 20:50–51.
- PARKER, E. D., JR., AND R. K. SELANDER. 1984. Low clonal diversity in the parthenogenetic lizard *Cnemidophorus neomexicanus* (Sauria: Teiidae). *Herpetologica* 40:245–252.
- TAYLOR, H. L., AND P. A. MEDICA. 1966. Natural hybridization of the bisexual teiid lizard *Cnemidophorus inornatus* and the unisexual *Cnemidophorus perplexus* in southern New Mexico. *Univ. Colorado Stud., Ser. Biol.* 22:1–9.
- _____, AND C. R. COOLEY. 1995. A multivariate analysis of morphological variation among parthenogenetic teiid lizards of the *Cnemidophorus cozumela* complex. *Herpetologica* 51:67–76.
- WALKER, J. W. 1986. The taxonomy of parthenogenetic species of hybrid origin: cloned hybrid populations of *Cnemidophorus* (Sauria: Teiidae). *Syst. Zool.* 35:427–440.
- _____, J. E. CORDES, AND M. A. PAULISSEN. 1989a. Hybrids of two parthenogenetic clonal complexes and a gonochoristic species of *Cnemidophorus*, and the relationship of hybridization to habitat characteristics. *J. Herpetol.* 23:119–130.
- _____, W. C. GUEST, J. E. CORDES, AND M. A. PAULISSEN. 1989b. Morphological and chromosomal evidence of hybridization between parthenogenetic *Cnemidophorus laredoensis* and gonochoristic *Cnemidophorus gularis*. *Copeia* 1989:1059–1064.
- _____, E. D. PARKER, JR., H. L. TAYLOR, J. E. CORDES, AND R. M. ABUHTIBA. 1990b. Hybridization between all-female *Cnemidophorus tessellatus* and gonochoristic *Cnemidophorus sexlineatus*. *J. Herpetol.* 24:388–396.
- _____, J. E. CORDES, AND R. M. ABUHTIBA. 1990a. Hybridization between all-female *Cnemidophorus neomexicanus* and gonochoristic *C. sexlineatus* (Sauria: Teiidae). *Amer. Midl. Natur.* 123:404–408.
- _____, R. M. ABUHTIBA, AND J. E. CORDES. 1991. Morphological and experimental verification of hybridization between all-female *Cnemidophorus laredoensis* B and gonochoristic *Cnemidophorus gularis* (Squamata: Teiidae). *Herpetologica* 47:152–164.
- _____, J. E. CORDES, AND J. M. WALKER, JR. 1992. Habitat preferences of a disjunct population of parthenogenetic *Cnemidophorus neomexicanus* (Sauria: Teiidae) in San Miguel Co., New Mexico. *Southwest. Natur.* 37:82–86.
- _____, H. L. TAYLOR, AND J. M. CORDES. 1994. Hybrid *Cnemidophorus* (Sauria: Teiidae) in Ninemile Valley of the Purgatoire River, Colorado. *Southwest. Natur.* 39:235–240.
- WRIGHT, J. W. 1969. Status of the name *Cnemidophorus perplexus* Baird and Girard (Teiidae). *Herpetologica* 25:67–69.
- _____, AND W. G. DEGENHARDT. 1962. The type locality of *Cnemidophorus perplexus*. *Copeia* 1962:210–211.
- _____, AND C. H. LOWE. 1967. Hybridization in nature of whiptail lizards (genus *Cnemidophorus*). *Amer. Mus. Novitat.* 2286:1–36.

Accepted: 3 October 1996.

Journal of Herpetology, Vol. 31, No. 1, pp. 107–110, 1997
Copyright 1997 Society for the Study of Amphibians and Reptiles

Reproductive Ecology of *Bombina variegata*: Development of Eggs and Larvae

JONAS BARANDUN AND HEINZ-ULRICH REYER,* *Zoological Institute, University of Zürich Winterthurerstrasse 190, 8057 Zürich Switzerland.*

Anuran life history typically involves an aquatic larval stage and an adult terrestrial stage. The larval habitat allows rapid growth and development, whereas the terrestrial life enables animals to disperse and escape from unfavorable local conditions (Wilbur, 1980). In most species, highest mortality occurs during the larval stage. Thus survival until metamorphosis is a critical determinant of population dynamics (Berven, 1990; Banks et al., 1993).

Important sources of larval mortality are predation, desiccation, and competition (Beebee and Beebee, 1978; Berven, 1990). The most important aquatic predators are fishes, salamanders, and predacious invertebrates (Smith, 1983; Werner, 1986). Predators can completely eliminate anuran larvae, while intra- and interspecific competition at high tadpole densities usually reduces survival and growth rates (Wilbur, 1980; Semlitsch and Reyer, 1992). Habitat stability can mediate both predation and competition. Predators are generally most abundant in permanent ponds or lakes, while larval density and competition can increase rapidly in drying ponds (Newman, 1987).

Rapid development and large size at metamorphosis improve juvenile survival and lead to earlier sexual maturity and higher life-time egg production (Riis, 1991). Under most conditions, however, metamorphosis at smaller than maximal size is necessary for survival (Werner, 1986). The trade-off between maximiz-

* To whom correspondence should be addressed.

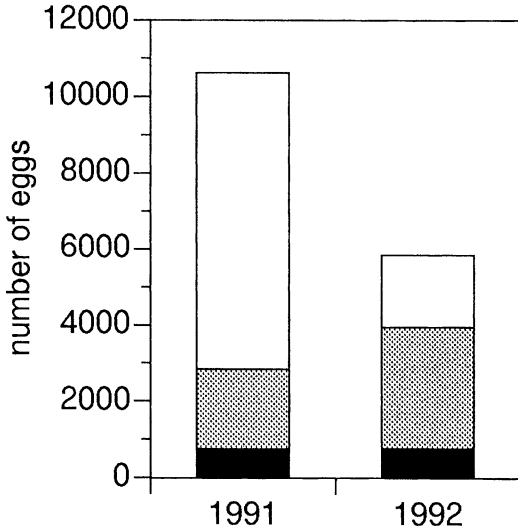


FIG. 1. Total egg number and survival in the population in 1991 ($N = 10624$) and 1992 ($N = 5853$). Black: survived until metamorphosis, gray: died before metamorphosis from unknown reasons, white: died from desiccation.

ing size at metamorphosis and minimizing risk of mortality during larval development is most pronounced in temporary ponds. Species breeding in temporary ponds are therefore expected to evolve developmental plasticity to maximize reproductive success under different conditions (Philippi and Seger, 1989).

Temporary ponds provide favorable food supplies and temperature conditions for tadpoles (Williams, 1987). Although predator abundance is generally low, desiccation is an important risk of mortality (Beebe and Beebe, 1978; Newman, 1987). Desiccation normally depends on weather and hydrology. When water level depends on rainfall, the patterns of filling and duration will vary irregularly among ponds depending on seasonal rainfall patterns. This raises the question of how reproductive success varies among different ponds and under different weather conditions.

The developmental and behavioral plasticity of the yellow-bellied toad, *Bombina variegata*, offers an opportunity for studying this question. Egg size and size at metamorphosis are variable (Rafinska, 1991). The species inhabits a wide range of variable habitats; typical spawning sites are small, sunny, shallow ponds (Bauer, 1987). The spawning period lasts for three months (Barandun, 1990), thus allowing not only the choice of the pond but also of a climatically suitable time.

We studied a population of *Bombina variegata* in a military training area near Kloten, northeast of Zürich, Switzerland, in 1991 (46 ponds) and 1992 (45 ponds). All spawning ponds were rain-filled depressions in clay soil created by vehicles. Pond characteristics varied with respect to duration, age, size, vegetation, and presence of aquatic predators. Some ponds changed dramatically during one season due to natural succession or disturbance. With four excep-

tions, all ponds dried out at some time during both years of study.

Bombina variegata lay their eggs in several masses of 1–60 connected eggs. Eggs of different pairs could only rarely be distinguished by direct observation. We counted eggs every 1–2 d during periods of spawning activity and may have underestimated the number of eggs in large or densely vegetated ponds where small egg masses were difficult to spot. In addition, the numbers of infected, damaged, or empty eggs were recorded in order to estimate mortality rate until hatching. Because damaged and infertile eggs were quickly infected by fungi, we did not distinguish between damaged, infertile, and infected eggs. Newts (*Triturus alpestris* and *T. vulgaris*) eat whole eggs or remove embryos out of the jelly of *Bombina* egg masses (unpubl. data). In the field, the direct influence of newts on egg mortality could only be estimated by counting opened, empty jellies. The frequency of empty eggs was therefore taken as a measure of newt predation.

In 22 cases, cohorts of spawn laid within 5 d could be distinguished until metamorphosis. In 12 of these cases, there was only one cohort present in a pond at all. In the other 10 cases, there was a time difference of more than 15 d between the spawning dates, and tadpoles could clearly be separated by two distinct size peaks as well as by the time of metamorphosis. Seven cohorts which could not clearly be separated were omitted from the analysis.

The duration of all available ponds was estimated each year. A pond was classified as dry only when no standing water remained. However, many tadpoles died before this time. Before pond desiccation, tadpoles aggregated in small areas within a pond for a few days and free swimming was restricted. This situation was classified as high density condition. The presence of potential competitors (tadpoles of *Bufo calamita*, *Hyla arborea*, and *Rana esculenta*) was also noted. Metamorphs were removed from the ponds every 1–2 d, counted, photographed, and their body size measured from pictures. The presence or absence of newts was recorded at every visit. Invertebrates were sampled with a dipnet on 15 May, 15 June, 30 July (1991), and on 3 June and 27 July (1992). Footprints of predacious birds around ponds were noted. Climatic data were received from a meteorological station 2 km from the study site (Swiss Meteorological Centre, Zürich). All statistics were performed after Sachs (1984).

Egg development was studied in 160 clutches between 18 May and 5 August, 1991. Hatching occurred 4–10 d after spawning. The average time for development was significantly longer in May (mean = 8.0 d) than in June (mean = 7.4 d; $t = 5.0$; $P < 0.001$) or in July (mean = 5.2 d; $t = 7.4$; $P < 0.001$). The increase in developmental rate is paralleled by an increase in water temperature. Among 22 cohorts, time to metamorphosis, including egg development, ranged from 33–58 d in 1991 and 34–51 d in 1992. The majority of tadpoles developed within 38–45 d in both years. Size at metamorphosis ranged from 9.8–19.5 mm SVL and averaged 14.7 mm. Tadpoles which metamorphosed under high density conditions before pond desiccation were significantly smaller (mean = 13.4 mm) than tadpoles metamorphosing under more benign conditions (mean = 15.8 mm; $t = 5.5$; $P < 0.001$).

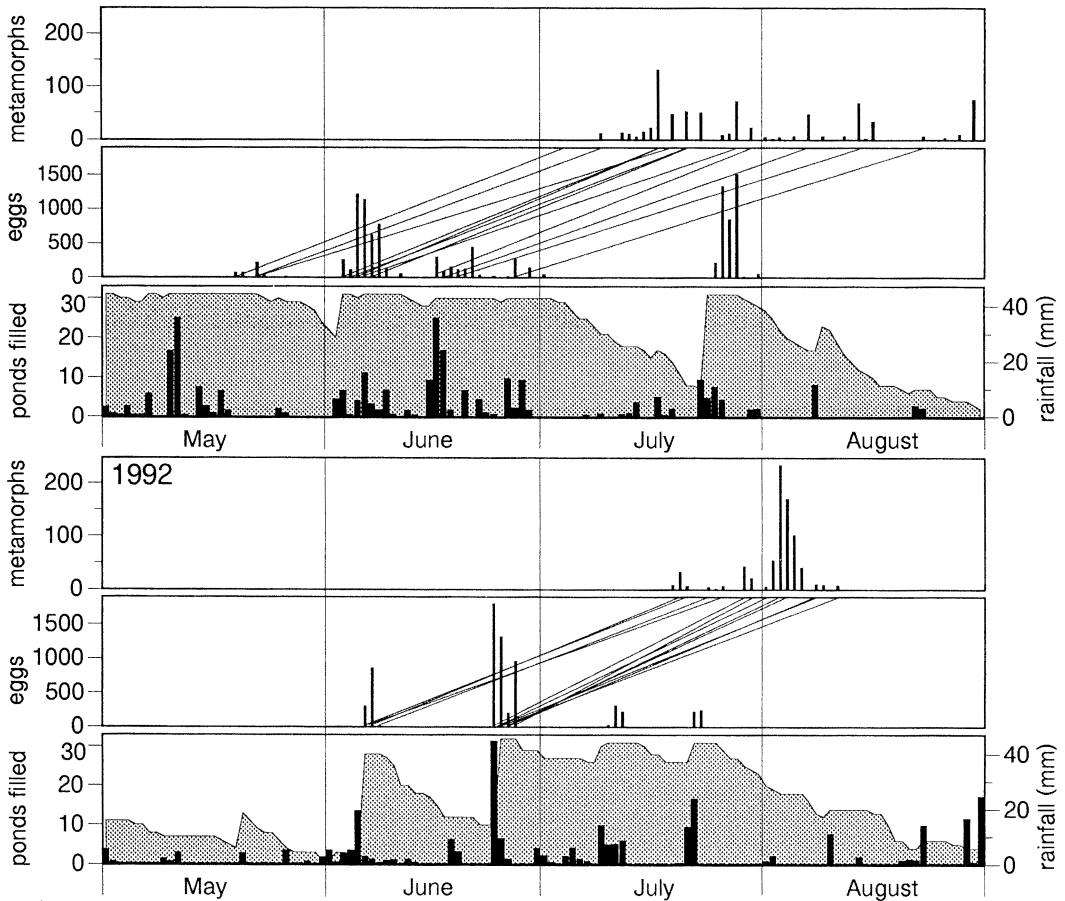


FIG. 2. Tadpole development in 1991 (top) and 1992 (bottom). The shaded areas indicate the number of ponds containing water. The black bars show the amount of daily rainfall. Tadpoles which could be followed until metamorphosis are shown by lines from date of spawning to date of metamorphosis.

Total mortality from spawning to metamorphosis averaged 93% in 1991 and 87% in 1992 (Fig. 1). Total egg mortality of a sample of 3087 eggs was 9% in 1991. Only 2.8% of eggs were infertile or infected, with one infertile clutch comprising >50% of these eggs. Offspring recruitment was concentrated in a few ponds: In both years, more than two thirds came from only three out of 15 successful ponds. These ponds differed between years.

Pond desiccation was responsible for at least 79% of premetamorphic mortality in 1991 and 37% in 1992 (Fig. 1). An additional 7% (1991) and 33% (1992) of tadpoles died in ponds which partially dried out. Other reasons of mortality could not be quantified but were clearly less important in both years. Three different groups of predators were observed: adult newts (*Triturus alpestris* and *T. vulgaris*) eating eggs and small tadpoles, invertebrates (*Libellulidae*, *Aeshmidae*, *Hydrophilidae*, *Notonectidae*, and *Nepidae*) eating tadpoles, and birds (*Ardea cinerea*, *Corvus corone*, and *Larus ridibundus*) eating large tadpoles and metamorphs. Birds were particularly observed at shallow, poorly vegetated ponds which were free of aquatic predators. However, bird occurrence was not recorded system-

atically and the effect of avian predation on larval and postmetamorphic mortality could not be quantified. Tadpoles of *Bombina variegata* and *Bufo calamita* were never observed eating eggs of the same or the other species.

Adult newts, the only observed egg predators, were present in ponds from April to around mid June. In June 1991, 9.8% of 1797 eggs that were scored were empty compared to only 0.9% of 1290 eggs in July after newts left the ponds. Newts and invertebrate predators were mostly absent in new or quickly drying ponds. These ephemeral ponds—although often used for spawning in the two years of the study—were never successful. As a consequence, larval survival was higher in ponds also containing aquatic predators ($X^2 = 24.8$; [df = 1;] $P < 0.001$).

Spawning activity occurred after the onset of high rainfall (Fig. 2). Metamorphs emerged over a period of 56 d in 1991, but only over 23 d in 1992. The peak of metamorph numbers in August 1992 reflects a mass escape from drying ponds. In both years, all offspring laid after 30 June dried during droughts in August. In other years, metamorphs were observed to emerge until mid September (unpubl. data). So, both the time of

spawning and metamorphosis were strongly determined by weather conditions.

The spawning ponds in the study area were temporary and dependent on rain for filling. Single rain events refilled ponds and extended their duration up to three weeks. Larval survival was critically dependent on pond duration, and thus on the unpredictable patterns of rainfall, irrespective of other pond qualities. The dominant importance of climatic conditions for juvenile recruitment is characteristic for many amphibians spawning into temporary ponds and responsible for marked fluctuations in survival rates among years (Banks et al., 1993; Dodd, 1993).

The droughts in August of both study years were unusual compared with the long-term average. Consequently, egg and larval mortality due to desiccation was probably unusually high. Casual observations in 1993 and 1994 suggest that metamorphs were distinctly more numerous although no quantitative data are available. Compared with desiccation, predation was a minor cause of mortality. In a climatically favorable year with little mortality through pond desiccation, the relative importance of predation may be higher, but the loss to predators is unlikely to be as significant as the loss to desiccation in dry years. Aquatic predators were most likely to co-occur with tadpoles in ponds that produced metamorphs. The occurrence of predacious birds at ponds lacking aquatic predators can counterbalance the absence of aquatic predators in these ponds. So neither desiccation nor predation could be avoided with certainty.

Both larval development rate and size at metamorphosis varied by a factor of two, which is among the broadest recorded ranges of plasticity in anurans (Duellman and Trueb, 1986). Plasticity in metamorphic size allows exploitation of various aquatic habitats because it enables animals to escape early at a small size under risky conditions, or metamorphose later at a larger size under favourable conditions (Kaplan and Cooper, 1984).

With pond duration being the most critical factor, spawning immediately after heavy rain provides the best chances to maximize reproductive success. Where climatic conditions are unpredictable, a long spawning period, plasticity in larval development, and the use of different incidents of heavy rainfall will improve reproductive success (Philippi and Seger, 1989). Our results imply that small changes in the pattern of rainfall can render reproduction more risky in rain dependent ponds, and thus may critically reduce juvenile recruitment in populations spawning in temporary, rain-filled ponds.

Acknowledgments.—We thank the many students and friends for their help in the field and B. Anholt, G. Guex, and R. D. Semlitsch for helpful comments on the manuscript.

LITERATURE CITED

- BANKS, B., T. J. C. BEEBEE, AND J. S. DENTON. 1993. Long-term management of a natterjack toad (*Bufo calamita*) population in southern Britain. *Amphibia-Reptilia* 14:155–168.
- BARANDUN, J. 1990. Reproduction of yellow-bellied toads *Bombina variegata* in a man-made habitat. *Amphibia-Reptilia* 11:277–284.
- BAUER, S. 1987. Verbreitung und Situation der Amphibien und Reptilien in Baden-Württemberg. *Beih. Veröff. Naturschutz Landschaftspflege Baden Württemberg* 41:71–157.
- BEEBEE, T. J. C., AND M. L. BEEBEE. 1978. A quantitative study of metamorphosis in the natterjack toad *Bufo calamita*. *Brit. J. Herpetol.* 5:689–693.
- BERVEN, K. A. 1990. Factors affecting population fluctuations in larval and adult stages of the wood frog (*Rana sylvatica*). *Ecology* 71:1599–1608.
- DODD, C. K. 1993. Cost of living in an unpredictable environment: the ecology of striped newts *Notophthalmus perstriatus* during a prolonged drought. *Copeia* 1993:605–614.
- DUELLMAN, W. E., AND L. TRUEB. 1986. *Biology of Amphibians*. McGraw-Hill Book Co., New York.
- KAPLAN, R. H., AND W. S. COOPER. 1984. The evolution of developmental plasticity in reproductive characteristics: an application of the “adaptive coin-flipping” principle. *Amer. Natur.* 123:393–410.
- NEWMAN, R. A. 1987. Effects of density and predation on *Scaphiopus couchii* tadpoles in desert ponds. *Oecologia* 71:301–307.
- PHILIPPI, T., AND J. SEGER. 1989. Hedging one’s evolutionary bets, revisited. *TREE* 4:41–44.
- RAFINSKA, A. 1991. Reproductive biology of the fire-bellied toads, *Bombina bombina* and *B. variegata* (Anura: Discoglossidae): egg size, clutch size and larval period length differences. *Biol. J. Linn. Soc.* 43:197–210.
- RIIS, N. 1991. A field study of survival, growth, biomass and temperature dependence of *Rana dalmanina* and *Rana temporaria* larvae. *Amphibia-Reptilia* 12:229–243.
- SACHS, L. 1984. *Angewandte Statistik*. Springer.
- SEMLITSCH, R. D., AND H. U. REYER. 1992. Performance of tadpoles from the hybridogenetic *Rana esculenta* complex: interactions with pond drying and interspecific competition. *Evolution* 46:665–676.
- SMITH, D. C. 1983. Factors controlling tadpole populations of the chorus frog (*Pseudacris triseriata*) on Isle Royale, Michigan. *Ecology* 64:905–911.
- WERNER, E. E. 1986. Amphibian metamorphosis: growth rate, predation risk, and the optimal size at transformation. *Amer. Natur.* 128:319–341.
- WILBUR, H. M. 1980. Complex life cycles. *Ann. Rev. Ecol. Syst.* 11:67–93.
- WILLIAMS, D. D. 1987. *The Ecology of Temporary Waters*. Timber Press, Portland, Oregon.

Accepted: 8 October 1996.