NOTES

COMMUNITY LEVEL ANALYSIS OF OPPORTUNISTICALLY-BREEDING ANURANS IN WESTERN MÉXICO

Paulette L. Ford

Rocky Mountain Research Station, 333 Broadway SE, Suite 115,
Albuquerque, New Mexico 87102-3497, USA
Email: plford@fs.fed.us

Norman J. Scott, Jr.[1]

U.S. Geological Survey, Western Ecological Research Center,
Piedras Blancas Field Station, P.O. Box 70, San Simeon, CA 93452, USA
Email: reptile@tcsn.net

Tropical dry forests are among the most seasonal habitats in the world. They are most common in hot lowlands outside the equatorial rain forest zone, where rainfall is more seasonal and the dry season is most pronounced, lasting for several weeks or months (Brown and Lomolino 1998). They are also some of the most threatened of the major tropical forest types, largely because these forests can be cleared for pastures and fields and readily maintained by fire owing to the severe dry season (Janzen 1986). Anurans are among the many species that have evolved with the extreme seasonal variation of the dry tropics. Apparent adaptations to seasonality include opportunistic breeding and reproductive activity which are generally coordinated with rainfall patterns.

Many researchers have examined the forces molding communities of tadpoles in both experimental and natural sites (Alford 1999; Cortwright and Nelson 1990; Gascon 1991, 1992; Heyer 1976; Heyer et al. 1975; Morin 1983; Rowe and Dunson 1994; Toft 1985; Travis et al. 1985; Wilbur 1987). It is clear that a mixture of factors, including predation, competition, and history, function as the community structuring mechanisms. In order to gain additional insights into the factors affecting community structure, we examined spatial patterns of breeding site use of opportunistically-breeding anurans with tadpoles in a tropical deciduous forest at the start of the rainy season.

MATERIALS AND METHODS

Breeding activity was determined by sampling for tadpoles. Tadpole collection sites were located in forested and nonforested areas on the Estación de Biología "Chamela" of the Universidad Nacional Autónoma de Mèxico (UNAM), and in the nearby villages of Chamela and Emiliano Zapata, the Chamela and Cuitzmala rivers, and the Zarco Dam. Chamela is located in Jalisco State on the Pacific Coast of México (19°30' N, 105°03' W, elevation 200 m). The above sites were located within a 19 km radius. Elevations ranged from 20–500 m, and topography consisted primarily of low hills dissected by temporary watercourses. Small alluvial plains in the vicinity were mostly occupied by agricultural fields (Ceballos and Miranda 1987).

The climate is characterized by dry-wet seasonality. Mean precipitation is 748 mm/yr, with 80% occurring during July–October (Bullock 1986). Average monthly temperature is 25°C with little variation in monthly mean maxima

---

[1]Present address: PO Box 307, Creston, California 93423, USA.

(29–32°C), but greater seasonal changes in minima (15–23°C). The rainy season of 1991 started on 16 and 18 June with precipitation of 1 mm and 16 mm respectively, and it rained six times for a total of 114 mm of rainfall between the collection dates of 20 June and 13 July 1991.

Before tadpoles were collected at each visit we recorded 11 habitat variables for each body of water including characteristics of water (temperature, area, depth, turbidity measured with a Secchi disc), substrate (mud, stone or cement, sand), and vegetation type (algae, rotted leaves and vegetation, emergent grass and vegetation, zero vegetation). Tadpoles were collected with a dip net in and around the edges of the site with a large net (45 cm x 20 cm) for the larger bodies of water (e.g., rivers, canals), and with a smaller net (15 cm x 12 cm), in the smaller bodies of water (e.g., temporary ponds). Thirty-four potential aquatic breeding sites were surveyed, including rivers, temporary ponds, pools behind a dam, and an irrigation canal. For logistical reasons, breeding sites were sampled every 4–5 days to detect successional changes in species composition. A sample of the tadpoles from each collection locality was preserved right after capture in 5% formalin, whereas some individuals were reared through metamorphosis to insure a positive identification. The *Bufo* tadpoles were described, two (*B. marmoreus*, *B. mazatlanensis*) for the first time, in Ford and Scott (1996).

We compared the frequency distribution of the number of species per breeding site to a Poisson distribution using a *G*-test with William's correc-tion (Sokal and Rohlf 1981). Goodness-of-fit was calculated between the Poisson distribution and our observed counts. We also calculated expected frequencies assuming species occur independently (Sokal and Rohlf 1981). We performed a principal components analysis (on the correlation matrix) (SAS 1989) on the 34 breeding sites for the 11 measures of habitat variables.

RESULTS

Thirty-two of the 34 sites contained eggs and larvae of six species (*Bufo marinus*, *B. marmoreus*, *B. mazatlanensis*, *Hypopachus variolosus*, *Leptodactylus melanonotus*, *Smilisca baudinii*). The majority of potential breeding sites (65%) contained only tadpoles of a single species; 29% had two species and 6% had no tadpoles (Table 1, Fig. 1). The frequency distribution of the number of species per site was significantly different ($G = 24.5$, $P < 0.01$) from a Poisson curve, the distribution expected if species occurred at random among sites. The difference between the two distributions was due to a larger number of single-species communities and a lower number of sites containing no or multiple species than expected based on the Poisson. The significance level for goodness-of-fit between the Poisson distribution and our observed counts was $\chi^2 = 14.48$, $P < 0.001$. The null hypotheses of species occurring independently of other breeding anurans was rejected ($\chi^2 = 6.7$, $P < 0.05$) for *L. melanonotus*, *B. mazatlanensis*, and *B. marinus,* but not for *S. bau-*

TABLE 1. Summary of 34 potential anuran breeding sites and larval occurrences, in Chamela, Jalisco, México, during June–July 1991. Species abbreviations are *Bufo marinus* (Bma), *B. mazatlanensis* (Bmz), *B. marmoreus* (Bmm), *Hypopachus variolosus* (Hv), *Smilisca baudinii* (Sb), *Leptodactylus melanonotus* (Lm).

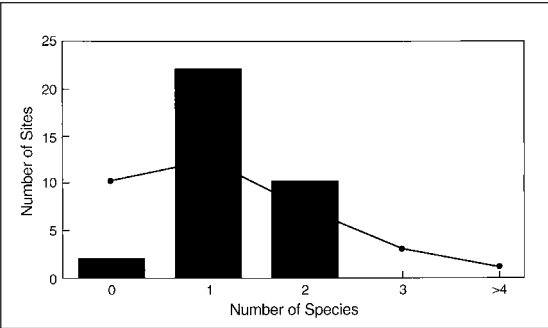| Breeding Sites	Species					
	Bma	**Bmz**	**Bmm**	**Hv**	**Sb**	**Lm**
Nonforested—15/34 (44%)						
Rivers (2)	1	0	0	0	0	1
Riverside Pools (3)	2	0	0	0	0	0
Canals (2)	0	2	0	0	0	0
Pig Wallow (1)	0	0	1	0	1	0
Arroyo Temporary Pools (4)	0	0	4	0	2	0
Dam Pools (3)	0	0	3	0	2	0
Forested—19/34 (56%)						
Temporary Ponds (17)	0	0	0	8	13	0
Concrete Deer Troughs (2)	0	0	0	0	2	0
Totals $n = 34$	$n = 3$	$n = 2$	$n = 8$	$n = 8$	$n = 20$	$n = 1$

Figure 1. The frequency distribution of the number of species per breeding site (bar) compared to a Poisson distribution (line). Adjusted $G = 24.5$, ($P < 0.001$).

dinii, *H. variolosus*, and *B. marmoreus* ($\chi^2 = 0.123$, $P = 0.95$). These results suggest that the tadpole communities of opportunistic breeders at the start of the rainy season were more dispersed with less sharing of breeding sites than expected by chance.

Principal component analysis (PCA) showed that the first three components account for 70% of the variation in the data (Table 2). Subsequent components contribute less than 7.2% each. Principal component (PC) 1 represents a gradient from small, temporary, relatively cool breeding sites to permanent, large breeding sites with high temperatures. PC 2 is related to amount and type of vegetation, substrate type, and depth of water in the breeding sites. PC 3 represents a turbidity gradient from high

TABLE 2. Values of 11 habitat variables from a principal component analysis (PC) of 34 sites.

	PC 1	PC 2	PC 3
Proportion of Total Variance	28%	22%	20%
Water temperature	0.42	0.07	–0.20
Breeding site area	0.33	–0.05	0.31
Breeding site depth	0.14	0.39	0.42
Breeding site turbidity	0.02	0.18	0.56
Substrate			
Mud	0.28	0.22	–0.46
Stone or cement	–0.37	0.35	0.09
Sand	0.08	–0.39	0.34
Vegetation			
Algae	0.30	–0.28	–0.09
Rotted leaves and vegetation	–0.44	–0.29	–0.05
Emergent grass and vegetation	0.44	–0.21	0.14
Zero vegetation	0.14	0.52	–0.08

to low. A plot of species along PC 1 and PC 2 reveals some segregation of species along habitat parameters (Table 2, Fig. 2).

Fifty-six percent of all breeding sites were located in the forested hills and lowlands of the field station, and 44% were in the nonforested villages and surrounding areas. The 13 breeding sites occupied by the three *Bufo* species and *L. melanonotus* were all in nonforested areas. *Hypopachus variolosus* always bred in forested sites ($n = 8$). *Smilisca baudinii* bred 75% of the time in forested areas and 25% in nonforested areas ($n = 15$). *Leptodactylus melanonotus*, *B. mazatlanensis*, and *B. marinus* did not share breeding sites with other species. If two species were found breeding at the same site, *S. baudinii* was one of them. It bred with both *H. variolosus* and *B. marmoreus*, but *H. variolosus* and *B. marmoreus* did not share sites. No successional changes in species composition were detected.

The adults encountered at the breeding sites commonly did not correspond to the larvae in them, a phenomenon also noted by Dixon and Heyer (1968). *Leptodactylus melanonotus* adults were collected in and around several temporary and semi-permanent ponds and rivers but only bred at the Río Chamela. Adult *B. marinus*, *B. marmoreus*, and *B. mazatlanensis* were collected together around many of the same sites, but their tadpoles did not share them. Adult *S. baudinii* usually were collected in the vicinity of their breeding sites, except for the adults collected at the rivers. No adult *H. variolosus* were collected, nor were their calls able to be distinguished among the loud calling of *Bufo*, *Smilisca*, *Rana* and other species.

DISCUSSION

Fifteen species of aquatic-breeding anurans are known to occur in Chamela and the surrounding area (García and Ceballos 1994; Ramírez-Bautista 1994), but eggs and larvae of only six species (40%) were found in aquatic breeding sites surveyed during the month after the first annual rains. The early-breeding species were *Smilisca baudinii*, *Leptodactylus melanonotus*, *Hypopachus variolosus*, *Bufo marmoreus*, *B. mazatlanensis*, and *B. marinus*. *Smilisca baudinii* usually bred in temporary rain pools formed during the first part of the rainy season. The temporary pools ranged in size from shallow, puddles to extensive ditches or large flooded areas. In the more xeric portions of its range

Figure 2. Principal component analysis of 11 habitat variables from 34 breeding sites (two obs hidden). Numerals denote *Bufo marinus* (1), *B. mazatlanensis* (2), *B. marmoreus* (3), *Hypopachus variolosus* (4), *Smilisca baudinii* (5), *Leptodactylus. melanonotus* (6), *S. baudinii + H. variolosus* (7), *S. baudinii + B. marmoreus* (8), no species present = 0.

Leptodactylus melanonotus is found only in association with permanent bodies of water, such as persistent springs or irrigation water (Heyer 1970). In more mesic areas it is often associated with temporary bodies of water, such as rain-filled ditches along roadsides (Heyer 1970). In our area, it bred only in the permanent water of the Río Chamela. *Hypopachus variolosus* typically occurs in both forested and more open situations. Individuals are commonly found in breeding congregations, at temporary bodies of water (Lee 1996). In this study, *H.*

variolosus tadpoles were found in shallow leaf- and water-filled pools in forested areas. All three *Bufo* species can breed in temporary or permanent streams, rivers, and ponds. In our study, *B. marinus* and *B. mazatlanensis* bred in permanent rivers and canals, but *B. marmoreus* tadpoles were found in sites where the water was more temporary.

It appeared that many of the opportunistic breeders in our study were spatially partitioning the habitat by breeding in either forested or nonforested habitats. In addition, they may have been avoiding the sharing

of breeding sites as long as unoccupied sites were available. Half of the species in our study shared breeding sites. Duellman and Trueb (1966) reported that *Smilisca baudinii* has a tendency to breed alone, but it is known to share breeding sites with all of the species in this study. We found *Smilisca baudinii* tadpoles sharing nonforested ponds with *Bufo marmoreus* and forest ponds with *Hypopachus variolosus*. Dixon and Heyer (1968) in an early rainy season study in Colima, Mexico, reported *S. baudinii*, *B. marmoreus*, *H. variolosus*, and *L. labialis* all sharing a breeding pond at the same time.

Spatially, not only were there different tadpole assemblages in forested and nonforested sites, but there was also segregation of species along breeding site habitat parameters within each type. In the forested sites, *S. baudinii* occurred by itself only in the smallest, coolest, detritus-filled ponds, whereas *Hypopachus variolosus* was alone only in the largest, warmest forest ponds with emergent vegetation. In intermediate-type ponds, these two species tended to occur together. In the unforested areas, *B. marinus* and *B. mazatlanensis* bred in the warmest, largest bodies of water, and *B. marmoreus* was found in smaller, cooler sites. However, in general, the three species of *Bufo*, like most toads, bred in more permanent waters in the warmer half of the habitat spectrum (Fig. 2).

The hyper-dispersion or avoidance of breeding in occupied ponds that we observed is probably temporary. Previous natural history observations indicate that many of the species that we observed are able to breed in the same sites. It is probable that they do so as patterns of breeding behavior change during the rainy season. As more rain falls, more water accumulates, and more species breed, breeding site selection and criteria may also change.

Our data suggest that at our study site anuran breeding dynamics occur on at least two levels. In a coarse-grain analysis, most anuran species appeared to be temporally and spatially partitioning their habitat by breeding early or late and breeding almost exclusively in either forested or nonforested habitats. In a fine-grain analysis, the early-breeders were hyper-dispersed among the breeding sites, and being the only species at a breeding site was common.

LITERATURE CITED

Alford, R.A. 1999. Ecology, resource use, competition and predation. In: R.W. McDiarmid and R. Altig (eds.), *Tadpoles: the Biology of Anuran Larvae*, pp. 240—278. University of Chicago Press, Chicago, Illinois, USA.

Brown, J.H. and M.V. Lomolino. 1998. *Biogeography. Second Edition*. Sinauer Associates, Sunderland, Massachusetts, USA.

Bullock, S.H. 1986. Climate of Chamela, Jalisco, and trends in the south coastal region of México. File for Meteorology, Geophysics and Bioclimatology, Series B 36:297–316.

Ceballos, G. and A. Miranda. 1987. *Los Mamíferos de Chamela, Jalisco*. Instituto de Biología, Universidad Nacional Autónomo de México, México D.F.

Cortwright, S.A. and C.E. Nelson. 1990. An examination of multiple factors affecting community structure in an aquatic amphibian community. Oecologia 83:123–131.

Dixon, J.R. and W.R. Heyer. 1968. Anuran succession in a temporary pond in Colima, México. Bulletin of the Southern California Academy of Sciences 67:129–137.

Duellman, W.E. and L. Trueb. 1966. Neotropical hylid frogs, genus *Smilisca*. University of Kansas, Publications of the Museum of Natural History 17:281–375.

Ford, P.L. and N.J. Scott, Jr. 1996. Descriptions of *Bufo* tadpoles from the southwestern coast of Jalisco, México. Journal of Herpetology 30:253–257.

García, A. and G. Ceballos. 1994. *Guía de Campo de los Reptiles y Anfibios de la Costa de Jalisco, México. Field Guide to the Reptiles and Amphibians of the Jalisco Coast, Mexico.* Fundación Ecológica de Cuixmala, A.C., Instituto de Biología, Universidad Nacional Autónoma de México, México D.F.

Gascon, C. 1991. Population-and community-level analyses of species occurrences of central Amazonian rainforest tadpoles. Ecology 72:1731–1746.

Gascon, C. 1992. Aquatic predators and tadpole prey in central Amazonia: field data and experimental

manipulations. Ecology 73:971–980.

Heyer, W.R. 1970. Studies on the frogs of the genus *Leptodactylus* (Amphibia: Leptodactylidae). VI. Biosystematics of the Melanonotus group. Los Angeles County Museum of Natural History, Contributions in Science 191:1–48.

Heyer, W.R. 1976. Studies in larval amphibian habitat partitioning. Smithsonian Contributions to Zoology 242:1–27.

Heyer, W.R., R.W. McDiarmid, and D.L. Weigmann. 1975. Tadpoles, predation and pond habitats in the tropics. Biotropica 7:100–111.

Janzen, D.H. 1986. The external threat. In: M.E. Soule (ed.), *Conservation Biology, the Science of Scarcity and Diversity*, pp. 286–303. Sinauer Associates, Sunderland, Massachusetts, USA.

Lee, J.C. 1996. *The Amphibians and Reptiles of the Yucatán Peninsula*. Comstock Publishing, Ithaca, New York, USA.

Morin, P.J. 1983. Predation, competition, and the composition of larval anuran guilds. Ecological Monographs 53:119–138.

Ramirez-Bautista, A. 1994. *Manual y Claves Ilustradas de los Anfibios y Reptiles de la Region de Chamela, Jalisco, México*. Universidad Nacional Autónoma de México, Cuadernos del Instituto de Biología, México, D.F.

Rowe, C.L. and W.A. Dunson. 1994. The value of simulated pond communities in mesocosms for studies of amphibian ecology and ecotoxicology. Journal of Herpetology 28:346–356.

SAS Institute, Inc. 1989. *SAS/STAT Users Guide, Version 6, Fourth Edition,Volume II*. SAS Institute, Inc., Cary, North Carolina, USA.

Sokal, R.R. and F.J. Rohlf. 1981. *Biometry, Second Edition*. Freeman, New York, USA.

Toft, C.A. 1985. Resource partitioning in amphibians and reptiles. Copeia 1985:1–21.

Travis, J., W.H. Keen, and J. Juilianna. 1985. The role of relative body size in a predator-prey relationship between dragonfly naiads and larval anurans. Oikos 45:59–65.

Wilbur, H.M. 1987. Regulation of structure in complex systems: experimental temporary pond communities. Ecology 68:1437–1452.