

Reproduction and diet of *Hyla euphorbiacea* (Anura: Hylidae) in a pine-oak forest of southeastern Puebla, Mexico

RICARDO LURÍA-MANZANO & GUADALUPE GUTIÉRREZ-MAYÉN

Laboratorio de Herpetología, Escuela de Biología, Benemérita Universidad Autónoma de Puebla, C.P. 72570, Puebla, México.
Corresponding author: Ricardo Luría-Manzano; [doumbek\(at\)hotmail.com](mailto:doumbek(at)hotmail.com)

Accepted 25.v.2014.

Published online at www.senckenberg.de/vertebrate-zoology on 15.vii.2014.

Abstract

We studied some reproductive characteristics and diet of the hylid frog *Hyla euphorbiacea* in a pine-oak forest from Sierra Negra, south-eastern Puebla, Mexico. The breeding season lasted from June to September; during this period males exhibited monthly variation in gonadal activity, whereas females did not. Sexual size dimorphism was observed, with females being larger than males, and female size was positively correlated with number and diameter of ovarian follicles. Diet during the rainy season was composed of invertebrates, classified into 16 prey categories. The most important was Lepidoptera (larvae), followed by Coleoptera (adults), and Araneae. Diet diversity and trophic niche overlap between sexes were relatively high. We discuss some recent findings and biological characteristics of *H. euphorbiacea*, which potentially make this species more susceptible to population declines than other members of the genus.

Key words

Hyla euphorbiacea, reproduction, diet, pine-oak forest.

Introduction

In terms of the length of their reproductive season, anurans usually are classified as either prolonged or explosive breeders (WELLS, 1977), while according to their feeding habits they can be categorized as generalist or specialist predators (VITT & CALDWELL, 2014). Although some species fit into one of these categories (WELLS, 1979; DONELLY, 1999; BERAZATEGUI *et al.*, 2007) most anurans do not, and therefore these categories actually represent the extremes along a continuum. This has been demonstrated in several studies for both length of the reproductive activity (e.g., AICHINGER, 1987; SALVADOR & CARRASCAL, 1990), and the degree of specialization in diet (e.g., TOFT, 1980).

In a recent systematic review, the genus *Hyla* was rearranged, and is currently represented by 32 species

(FAIVOVICH *et al.*, 2005). Studies of reproduction have shown that members in this genus are prolonged breeders, with reproductive season varying in length among and within species (GARTON & BRANDON, 1975; RITKE *et al.*, 1990; SALVADOR & CARRASCAL, 1990). Considering feeding habits, it is recognized that their diet is principally composed of several orders of insects, as well as other arthropods, and they are therefore considered to be generalist predators (HIRAI & MATSUI, 2000; MAHAN & JOHNSON, 2007; KOVÁCS *et al.*, 2007).

The above cited studies have focused on species inhabiting the United States, Europe, and Asia, while ecological studies of the Central American species are scarce. *Hyla euphorbiacea* (Fig. 1) is a species endemic to Mexico, distributed in the southern portion of the Sierra



Fig. 1. Adult female *Hyla euphorbiacea* from Cuitzala, Puebla, Mexico.

Madre Oriental, and in the Central Valley of Oaxaca (DUELLMAN, 2001). Available information about its natural history is fragmentary and restricted to populations in the states of Veracruz and Oaxaca (DUELLMAN, 2001). This study therefore aims to gain a better understanding of the ecology of *H. euphorbiacea*, by analyzing its reproductive season, size at sexual maturity, sexual size dimorphism, fecundity, diet composition, and sexual variation in feeding habits.

Materials and Methods

The study was carried out in two sites, Cuitzala (18° 17' N, 97° 04' W; 2565 m a.s.l.) and Tecoltepec (18° 19' N, 97° 04' W; 2328 m a.s.l.), which both belong to the region known as Sierra Negra, in southeastern Puebla, Mexico. At both sites, *H. euphorbiacea* breeds in temporary ponds which are formed during the rainy season in grassy fields of pine-oak forest habitat. Mean annual temperature in the study area is 16° C, and the annual precipitation is 1762 mm (GARCÍA, 1998).

Samples were taken monthly, from January to December 2006. Each month, a maximum of five specimens for each sex and site were collected for analyses of feeding habits and reproductive characteristics. Snout-vent length (SVL) and mouth width (MW) were measured

with a caliper (to the nearest 0.1 mm), and sex was determined based on the yellow colouration of the throat and presence of nuptial excrescences in males, which was later confirmed by direct observation of gonads. Frogs were euthanized within four hours of capture. Individuals found beyond this established limit were only analyzed for sexual size dimorphism, for which SVL was measured, sex was recorded, and toes were clipped for individual identification. These individuals were released immediately after sampling.

Collected specimens were dissected, and the liver, fat bodies, gonads, and digestive tract were removed. In order to analyze monthly gonadal activity and other reproductive characteristics, liver, fat bodies, and ovaries were weighed with an electronic balance (to the nearest 0.0001 g). Ovarian follicles were taken from 10% of the ovarian mass, and counted in order to extrapolate the total number for each female specimen (TSIORA & KYRIAKOPOULOU-SKLAVOUNOU, 2002). Length and width of testes, and the diameter of 10 randomly selected ovarian follicles from each ovary were measured with a digital caliper (to the nearest 0.01 mm) under a stereoscopic microscope. Testicular volume was estimated by using the formula for an ellipsoid:

$$V = 4/3 \pi (\text{length}/2) (\text{width}/2)^2$$

In males, the SVL of the smallest specimen with nuptial excrescences and yellow throat colouration was used to estimate the minimum size at sexual maturity. In females, the presence of ovarian follicles and convoluted

oviduct were considered for this purpose (KHONSUE *et al.*, 2000).

For dietary analyses, prey items found in each digestive tract were identified to the level of order, with the exception of hymenopterans, which were further classified as formicids and non-formicids. In the case of holometabolous insects, we considered larvae and adults as different prey categories (HIRAI & MATSUI, 2000). For each prey category, we obtained the numeric abundance, volume (by using the formula for an ellipsoid), and frequency of occurrence for the entire sample. Using these three variables, we calculated the importance index of each prey category by using the following formula (BIAVATI *et al.*, 2004):

$$I = (F\% + N\% + V\%)/3$$

where F% = frequency of occurrence percentage, N% = numeric percentage, and V% = volumetric percentage. Diet diversity was estimated with the Shannon index (SHANNON & WEAVER, 1949):

$$H' = -\sum_{i=1}^S p_i \ln p_i$$

where p_i = proportion of the resource i (prey category) in the diet, \ln = natural logarithm and S = total number of prey categories. The obtained values were transformed to effective number of species (prey categories) with the following formula: $^1D = \exp(H')$ (true diversity, *sensu* JOST, 2006). Trophic niche overlap between sexes was calculated with the O_{jk} Pianka's index (PIANKA, 1973):

$$O_{jk} = \sum_{i=1}^n P_{ij} P_{ik} / \sqrt{\sum_{i=1}^n P_{ij}^2 \sum_{i=1}^n P_{ik}^2}$$

where P_{ij} and P_{ik} are the proportions of utilization of the i resource, by the j and k species, respectively. Diet diversity and overlap values were calculated with the numeric proportions of prey categories.

Because we found a significant relationship between SVL and testicular volume in males, and between SVL and number of ovarian follicles in females, we calculated residuals from regressions of these gonad variables with SVL of the frogs to produce size-adjusted variables. These residuals were used to determine whether significant monthly variation in gonadal activity existed, using one-way ANOVAs, followed by Tukey post hoc tests. Sexual dimorphism in SVL was analyzed with a Student t -test, and the number of prey items per stomach and volume of stomach contents between sexes were compared with Mann-Whitney U -tests. Pearson's correlation coefficient was used to test the relationships between the following variables: gonadal activity-fat bodies and liver mass, female SVL-number and size of follicles, and frog SVL-number and size of prey eaten.

Means are shown \pm SE, unless otherwise indicated. Standard parametric analyses were used when possible. Otherwise, analogous nonparametric tests were applied. Statistical analyses were performed with the program Statistica 7.0 (Statsoft), with the significance level set at

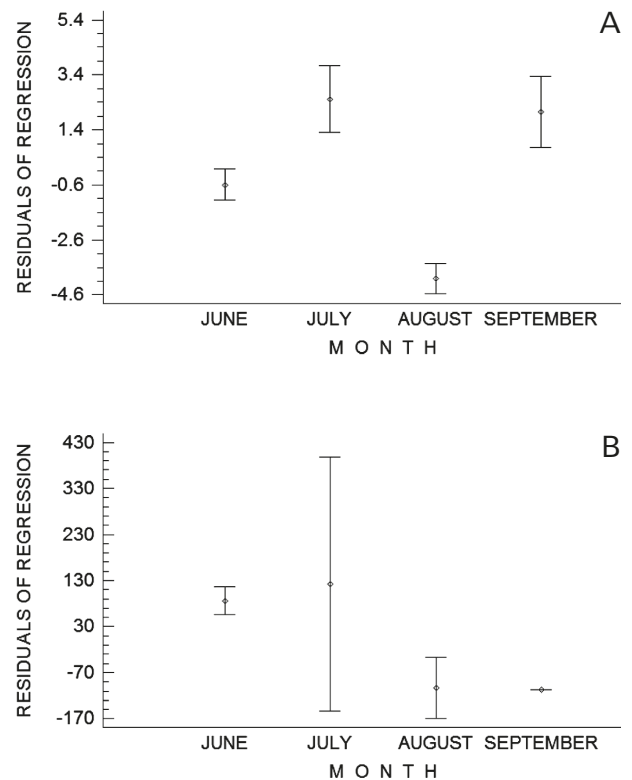


Fig. 2. Monthly variation in (A) testicular volume in males and (B) number of ovarian follicles in females of *Hyla euphorbiacea* (mean \pm SE). Values are depicted as residuals from variables of gonads versus SVL (see methods).

0.05. Euthanized specimens are kept in the herpetological collection of Escuela de Biología, Benemérita Universidad Autónoma de Puebla, in Puebla City.

Results

In the study area, the rainy season lasts from June to September, and these were the only months in which adult individuals of *H. euphorbiacea* were found. Males were found emitting advertisement calls and females were observed with ovarian follicles for the duration of this period. This implies that the reproductive period of *H. euphorbiacea* in the region lasts approximately three months, with precipitation as a factor affecting the initiation and duration of reproductive behavior. Gonadal activity in males showed significant variation among months ($F_{3,22} = 7.92$, $p < 0.005$, Fig. 2A). This increased slightly from June to July, decreased in August, and again increased in September. Significant differences were observed between the following months: July-August ($Q = 5.8$, $p < 0.005$) and August-September ($Q = 5.39$, $p = 0.005$). In females, gonadal activity was constant in June and July and decreased slightly in August and

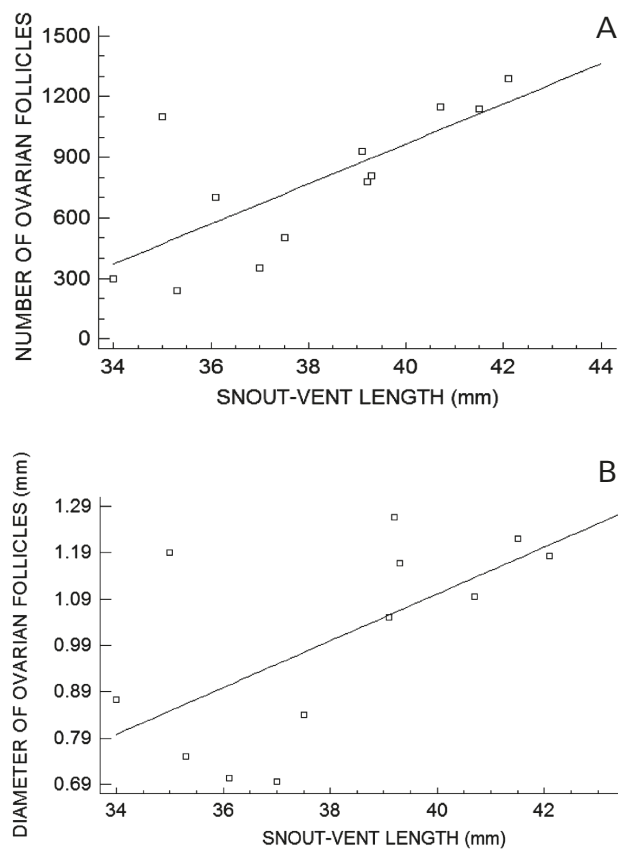


Fig. 3. Relationship between size (SVL) of females and (A) number and (B) mean diameter of ovarian follicles in *Hyla euphorbiacea*.

September (Fig. 2B); however, no significant differences were found among three months (excluding September from the analysis, because of a small sample size; $F_{2,8} = 0.86$, $p = 0.46$).

Snout-vent length ranged from 30–36 mm, and 34–42.1 mm in males and females, respectively. We found sexual size dimorphism in adults ($t = -8$, $p < 0.001$), with females SVL (mean = 38.3 ± 0.64 mm, $n = 16$) larger than males (mean = 33.8 ± 0.24 mm, $n = 38$). Fat bodies ($r = 0.05$, $p = 0.79$) and liver mass ($r = 0.25$, $p = 0.22$) were not correlated with male gonadal activity. There were no significant correlations in the case of females, however, we observed a negative tendency between fat body mass and gonadal activity ($r = -0.38$, $p = 0.22$), and a positive tendency between gonadal activity and liver mass ($r = 0.56$, $p = 0.06$). Adult females had between 240–1290 ovarian follicles (mean = 774.17 ± 104.58 , $n = 12$); there was a positive relationship between the number of ovarian follicles and frog's size ($r = 0.73$, $p = 0.007$, Fig. 3A). Similarly, SVL and number of ovarian follicles were significantly correlated with the diameter of ovarian follicles ($r = 0.62$, $p = 0.03$, for SVL, Fig. 3B; $r = 0.79$, $p < 0.005$, for number of follicles).

Of the 38 specimens (25 males and 13 females) analyzed for feeding habits, 35 were adults. The remaining three (two males and one female) were considered subadult individuals, and were included in the analyses. Thirty-six frogs (94.7%) had gastrointestinal contents,

in which a total of 128 prey items (mean = 3.76 ± 0.42 per individual), representing 16 categories was found (Table 1). All categories belonged to the arthropod group, and were represented by three classes: Insecta, Arachnida, and Malacostraca. The most abundant and frequent prey categories were spiders, coleopterans (adults), and lepidopterans (larvae). In terms of volume, the predominant categories were lepidopterans (larvae), followed by orthopterans, dermapterans, and coleopteran (adults). Considering these variables, the most important prey category was Lepidoptera (larvae, $I = 26.05$), followed by Coleoptera (adults, $I = 19.4$), and Araneae ($I = 19.13$; Table 1). Plant remains (stems, seeds, and flowers) and debris (small minerals), were found in 13 (36.11%) and three (8.33%) of the 36 specimens with contents, respectively.

Dietary diversity was 11.94. Diet composition was similar between sexes, as indicated by a high trophic niche overlap ($O_{jk} = 0.78$). However, a difference in consumption of ants is evident, since in males these ranked eleventh in terms of numeric proportion (2.5%), whereas in females they were the top prey (16.67%) along with spiders (Table 1). Both sexes fed on similar quantities of prey (males mean = 3.64 ± 0.48 , females mean = 4 ± 0.82 ; $U_{22,12} = 7.5$, $p = 0.8$), and also had similar mean volumes of gastrointestinal contents (males mean = 79.27 ± 26.94 mm³, females mean = 75.53 ± 22.92 mm³; $U_{22,11} = 3$, $p = 0.92$). The size of frogs was not significantly correlated with the number of prey they consumed ($r = 0.26$, $p = 0.14$), and mouth width was not correlated with the size of the largest prey per stomach ($r = 0.01$, $p = 0.95$). In fact, the largest prey recorded was a lepidopteran larva of 28.3 mm length, ingested by a small adult male of 30 mm SVL.

Discussion

Hyla euphorbiacea exhibits a seasonal reproductive pattern which lasts approximately three months in the studied region. According to WELLS (1977), this species is a prolonged breeder, similar to many other species within the same genus (GARTON & BRANDON, 1975; PERRILL & DANIEL, 1983; RITKE *et al.*, 1990). Despite these similarities, the timing of reproductive activities seems to occur earlier in North American than Mexican and Central American species. For example, *Hyla chrysoscelis* breeds from mid-April to mid-August in Tennessee (RITKE *et al.*, 1990), *Hyla gratiosa* from March to August in Georgia, and *Hyla cinerea* from mid-April to mid-August in Georgia (PERRILL & DANIEL, 1983), and from May to August in Illinois (GARTON & BRANDON, 1975). On the other hand, *Hyla eximia* in the Mexican Plateau breeds from June to August (DUELLMAN, 2001), and *H. euphorbiacea* in Sierra Negra from June to September.

Table 1. Diet composition of males (n = 23) and females (n = 13) of *Hyla euphorbiacea* during the reproductive season. N% = numeric percentage, V% = volumetric percentage, F% = frequency of occurrence percentage, and I = importance index.

Prey category	Males				Females				Total			
	N%	V%	F%	I	N%	V%	F%	I	N%	V%	F%	I
Insecta												
Hymenoptera (no ants)	3.75	3.17	13.04	6.65	6.25	3.19	15.38	8.27	4.69	3.18	13.89	7.25
Hymenoptera (ants)	2.5	0.23	8.69	3.81	16.67	1.07	30.77	16.17	7.81	0.5	16.67	8.33
Coleoptera (adults)	18.75	11.44	39.13	23.11	8.33	7.08	23.08	12.83	14.84	10.03	33.33	19.4
Coleoptera (larvae)	1.25	6.3	4.35	3.96	2.08	3.96	7.69	4.58	1.56	5.54	5.55	4.22
Diptera	10	0.72	30.43	13.72	4.17	—	15.38	6.52	7.81	0.49	25	11.1
Orthoptera	6.25	18.95	17.39	14.19	6.25	26.23	23.08	18.52	6.25	21.3	19.44	15.66
Dermaptera	7.5	10.93	21.74	13.39	6.25	11.03	15.38	10.89	7.03	10.97	19.44	12.48
Lepidoptera (adults)	—	—	—	—	2.08	—	7.69	3.26	0.78	—	2.78	1.19
Lepidoptera (larvae)	12.5	33.28	43.48	29.75	6.25	28.99	23.08	19.44	10.16	31.89	36.11	26.05
Homoptera	3.75	2.76	13.04	6.52	8.33	7.42	23.08	12.94	5.47	4.27	16.67	8.8
Hemiptera	1.25	—	4.35	1.86	—	—	—	—	0.78	—	2.78	1.19
Arachnida												
Araneae	17.5	5.09	34.78	19.12	16.67	2	38.46	19.04	17.19	4.09	36.11	19.13
Acari	6.25	0.01	17.39	7.88	2.08	< 0.01	7.69	3.26	4.69	0.01	13.89	6.19
Opilionida	6.25	5.25	8.69	6.73	12.5	9	23.08	14.86	8.59	6.46	13.89	9.65
Pseudoscorpiones	1.25	0.24	4.35	1.94	2.08	0.01	7.69	3.26	1.56	0.16	5.55	2.43
Malacostraca												
Isopoda	1.25	1.63	4.35	2.41	—	—	—	—	0.78	1.1	2.78	1.55

Because Mexican species are generally more closely-related to each other than North American species (FAIVOVICH *et al.*, 2005), some of the variation in the timing of the reproductive period may possibly be explained by the phylogenetic relationships within the members of the genus. However, the variation in the reproductive season of a widely-distributed species (*H. chrysoscelis*; RITKE *et al.*, 1990), suggests that local environmental conditions may be more important in determining the timing and duration of reproduction. Future research is needed to further examine the relative importance of phylogeny and local conditions over breeding behavior and other life history characteristics. These studies are especially important for species with limited distribution that live in different environments (e.g., *H. euphorbiacea*).

Throughout the reproductive season, males showed a monthly variation in gonadal activity, whereas females did not. Females did however exhibit a decrease in reproductive activity during the final months of the breeding period, similar to results reported previously in *H. cinerea* (GARTON & BRANDON, 1975). This phenomenon may occur as a life-history strategy that would ensure that most recently metamorphosed individuals would have enough time for activities such as feeding before the hibernation period. This strategy was suggested by RITKE *et al.* (1992), as an explanation for the early cessation of reproduction in *H. chrysoscelis* under favorable temperature and rainfall conditions.

Hyla euphorbiacea exhibits sexual dimorphism in body size, in which females are larger than males, a common pattern in other species of this genus (RITKE *et al.*, 1990; HIRAI & MATSUI, 2000) and in anurans in

general (SHINE, 1979). There are several hypotheses that explain this phenomenon, such as a limited growth in reproductive males caused by costs associated with reproduction, lower food intake in males, and fecundity selection on females (SHINE, 1979; WOOLBRIGHT, 1983). In our study, both sexes ingested the same amount of food during the reproductive season, and in females SVL was positively correlated with both the number and the diameter of ovarian follicles. These results suggest that in *H. euphorbiacea*, fecundity selection on females is a major factor in determining sexual size dimorphism.

The diet of *H. euphorbiacea* during the rainy season is composed of a variety of insects and arachnids, and one group of crustaceans (isopods). The latter is the only aquatic prey category, and was only found in one individual. This suggests that foraging by *H. euphorbiacea* within water bodies is minimal, and is primarily carried out in grassy fields that surround the ponds used for reproduction. MAHAN & JOHNSON (2007) found similar results in *Hyla versicolor*, whereas KOVÁCS *et al.* (2007) reported a high consumption of isopods by *Hyla arborea* during the reproductive period, followed by a much lower consumption in the post-reproductive season.

Among studies that analyze sexual variation in diet composition, DONNELLY (1991) found in the dendrobatid frog *Oophaga pumilio*, that females feed on higher amounts of ants than males. He suggested that the difference in ant consumption between sexes is related to behavioural differences during the reproductive season, since only females of this species exhibit the parental care behaviour of carrying and feeding their

larvae. In *H. euphorbiacea*, behaviour also may play a role in explaining the different consumption rates of ants between sexes, but through another mechanism: because this hylid frog is a prolonged breeder, males acquire mates by means of advertisement calls, which are emitted from relatively stationary sites. Presumably, males move relatively short distances. On the other hand, females actively search for potential mates, and presumably move both larger distances and more frequently. This difference in reproductive behaviour could put males and females in different points on the continuum of foraging modes (active in females, and sit-and-wait in males). Accordingly, females would have more access to prey types that tend to be aggregated (like ants). A similar relationship between consumption of aggregated prey types and an active foraging behavior has been documented in dendrobatids (TOFT, 1980).

Numerous studies did not find a relationship between mouth size of the frog and size of ingested prey (OVASKA, 1991; DURÉ & KEHR, 2004; this study). OVASKA (1991) suggested that the combination of data from different nights may account for the lack of such a relationship, whereas PARMELEE (1999) mentioned that this result may be a consequence of a narrow range in SVL of analyzed frogs. Furthermore, in the study species, the high consumption of ants (a relatively small prey) by females (which are larger than males) may be related to the lack of a predator size-prey size relationship.

Among members of the genus, *H. euphorbiacea* shows some characteristics that could potentially make it more susceptible to population declines than other species. The range of *H. euphorbiacea* is relatively small, likely no greater than 20000 km² (SANTOS-BARRERA & CANSECO-MÁRQUEZ, 2004), and breeds exclusively in temporary lentic waters, potentially exposing it to the effects of global warming more than species that breed in permanent water bodies (e.g., *H. cinerea*; GARTON & BRANDON, 1975). Additionally, the chytrid fungus *Batrachochytrium dendrobatidis*, which is responsible for population declines of numerous anuran species (BERGER *et al.*, 1998; BOSCH *et al.*, 2001), has been recently found in a population of *H. euphorbiacea* from Oaxaca State (FRÍAS-ALVAREZ *et al.*, 2008), and in a population of *Plectrohyla arborescens* from Sierra Negra that lives in sympatry with *H. euphorbiacea* (LURÍA-MANZANO *et al.*, 2011). These findings reveal the importance of analyzing the population dynamics of this species in response to global warming and emerging infectious diseases, in order to determine the effects of these factors on populations of this anuran endemic to Mexico.

Acknowledgments

We thank E. Melgarejo, L. Canseco, E. Jiménez, R. Flores, A. Tobón, A. Rendón, T. Saldaña, J. Tonacatl, S. Sánchez, D. Hernández, J. Juárez, R. Luría, and J. Herrera, for their assistance in the field; and A. Ramírez-Bautista for helpful comments on the manuscript. We also thank SEMARNAT for approving this research (permit # DGVS/04528/06). People from Mexcalcorral, Cuitzala, provided us with a place to stay during our visits to Sierra Negra.

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