SPRING-BREEDING AND REPRODUCTIVE MODE IN *Leptolalax khasiorum* (ANURA, MEGOPHRYIDAE) IN NORTH-EASTERN INDIA

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We examined the breeding habitat, oviposition site and timing of breeding in *Leptolalax khasiorum* at its type locality at Mawphlang, Meghalaya State, north-eastern India. Surveys were conducted along a stream within a fragmented patch of forest for adults, tadpoles, eggs and nesting sites, with data collected monthly between January 2009 and December 2011. The species starts emerging from wintering microhabitats with the onset of the premonsoonal showers in February. Breeding activity (specifically, deposited eggs) was observed for a few weeks after emergence and lasted a few weeks between early March and April. Adults were found under rocks along the stream banks. Eggs are deposited on the underside of rocks that are flatly embedded on the gravel and over leafy bottom of the dry stream bed. The eggs of *Leptolalax khasiorum* are cream-colored, lacking an animal pole, and covered with a transparent jelly, showing adaptations for terrestrial development in sheltered microhabitats via avoidance of moisture loss and damage of eggs from solar radiation. In producing eggs out of water, showing free-swimming tadpoles, the reproductive mode can be classified as Mode 18, a first for a member of the genus *Leptolalax*. It is arguably the first report of terrestrial reproduction and parental care for a member of the family Megophryidae. Placement of eggs outside of water may coincide with low water levels of early spring, advantages of choice of timing being reduced competition for egg-laying sites and food for the larval and postlarval stages.

Keywords: *Leptolalax khasiorum*; North-eastern India; Mawphlang; oviposition; reproductive mode.

Sympatric anuran amphibian species may differ in habitat use for breeding, calling site, annual reproductive period, daily period of calling activity and acoustic features of advertisement call, which are interpreted as important isolating mechanisms (Wells, 1977; Haddad et al., 1990). Anuran amphibians are vulnerable to desiccation, at least in one phase of three- egg, tadpole, or postmetamorphic stages and are therefore dependent on water and/or atmospheric humidity for their activities especially for reproduction. The selection of oviposition sites by frogs can directly influence larval development (Resetarits and Wilbur, 1989), largely influences the distribution of tadpoles (Alford, 1999; Evans et al., 1996), and can be of critical importance for the reproductive success of organisms lacking parental care (Murphy, 2003). Selection of breeding sites in response to abiotic factors, such as pond depth, water temperature, water transparency, pH, density and surrounding vegetation cover, permanency and vegetation cover and biotic factors, such as the presence of predators and competitors, has been frequently documented (Crump, 1991; Evans et al., 1996; Blaustein, 1999; Skelly, 2001; Hazell et al., 2003; Goldberg et al., 2006). Many workers have identified rainfall as the primary extrinsic factor affecting the time of the breeding activity for most tropical and subtropical anuran species (Haddad and Sazima, 1992; Duellman and Trueb, 1994). Many hylid species have been documented to depend on rain to reproduce (Wiest, 1982; Aichinger, 1987). Most Neotropical species show association between the wet season and prolonged reproduction during the year (Pombal, 1997) while many can reproduce more than once during the breeding season (Wells, 1977; Telford and Dyson, 1990). Species exhibiting breeding seasonality have been described to display two basic patterns: (1) tropical species capable of breeding throughout the year; where rainfall is the major extrinsic factor controlling reproduction; and (2) temperate species with seasonal breeding activity that is dependent on a combination of temperature and rainfall (Duellman and Trueb, 1986; Bertoluci and Rodrigues, 2002).

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Our earlier publication briefly describes the site of collection and habitat of *Leptolalax khasiorum* (Das et al., 2010). Recent studies on *Leptolalax* concentrate on species descriptions (Rowley and Trung, 2009, Sengupta et al., 2010, Ohler et al., 2011, Rowley et al., 2010, Dehling, 2012), and there appears to be a scarcity of publications on the reproductive biology of frogs of this genus (an exception being Inger 1985, whose larval inventory included *L. gracilis* from Sarawak, Borneo, and Malkmus and Kosuch, 1999, which describes larval habits, but not egg-laying sites, of *L. arayai* in Sabah, Borneo). However, no investigation on the oviposition sites of any species appears to have been published, the aforementioned studies referring to larval descriptions and their associated microhabitats; eggs or egg clutches of the genus has, to the best of our knowledge, have never been described, apart from brief mention of clutch size (Das, 2007) or lack of pigmentation (Das et al., 2010). Our study involves the documenting of the breeding habitats and oviposition site of *Leptolalax khasiorum*. The objective was to investigate the characteristics of the breeding habitat and other factors that can help us understand their breeding behavior.

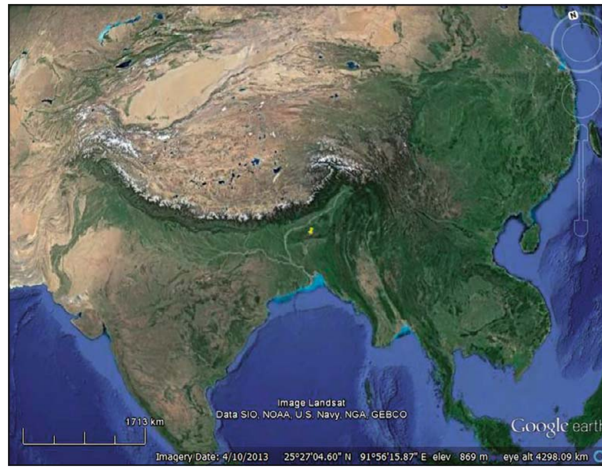

Fig. 1. Map of north-eastern India (inset) and of Meghalaya State, showing the location of Mawphlang.

MATERIAL AND METHODS

We conducted weekly surveys for amphibians along a submontane forest stream in Mawphlang (25°26′80.8″ N 91°44′99.8″ E, alt. 1813 m a.s.l.; datum wgs-84), East Khasi Hills District, Meghalaya State,

Fig. 2. The sacred forest of Mawphlang, seen from the edge of Mawphlang village, East Khasi Hills, Meghalaya State, north-eastern India.

Fig. 3. Adult *Leptolalax khasiorum*, an endemic of the Mawphlang sacred forest, Meghalaya State, north-eastern India.

north-east India (Figs. 1 and 2), between the years 2009 – 2012. Geographical coordinates were taken with a Garmin™ 12XL GPS. Field sampling was carried out during afternoon to early evening hours (13:00 – 17:00), along ~100 – 150 m length of stream. Water bodies were deep-netted for tadpoles; searches were conducted on banks and dried-up stream bed for presence of egg masses, metamorphs and adults. After confirming identification and retaining voucher specimens for other studies (RNLk01), frogs were released back at the point of capture. Since larval sampling effort differed between months, abundance values are not presented here. However, data presented here document larval phenology, as well as local weather conditions. These data have been coded as present/absent during a particular period of sampling. We used visual and acoustic encounter surveys to evaluate the presence or absence of *Leptolalax khasiorum* (Fig. 3), a mid-sized megophryid frog, adult males of which show an SVL range of 24.5 – 27.3 (mean 25.6 ± 0.6 SE) mm, while adult females are 31.2 – 33.4 (mean 32.5 ± 0.7 SE) mm (Das et al., 2010). The stream (Fig. 4) examined originated near the forest edges, and consequently, fieldwork was carried out following it downstream. During the day, we searched for newly-laid egg clutches and for adults by lifting rocks along the

Fig. 4. Breeding habitat of *Leptolalax khasiorum* along an unnamed stream flowing through the Mawphlang forest, Meghalaya, north-eastern India.

stream bed and close to stream banks. Eggs and tadpoles were brought back to the lab and matched to parent species through rearing to metamorphosis. Measurements of eggs were taken using a Mitutoyo™ dial caliper under a Leica™ ES2 binocular microscope at 10× magnification. Habitat variables, including air temperature, water temperature and humidity, were recorded (Table 1). The air temperature and percent relative humidity in the field was measured by using a thermo-hygrometer and water temperature was recorded with a mercury bulb thermometer. pH was measured using a waterproof digital pH tester (pH Tester 10, Oakton, Eutech Instruments). Ecological parameters like air temperature, humidity and rainfall were also compared to figures measured at the Department of Public Health Engineering (PHE), Mawphlang.

TABLE 1. Environmental Data Recorded at the Breeding Site of *Leptolalax khasiorum* at Mawphlang, Meghalaya State, North-Eastern India, for 2009 – 2011

Month	Average air temperature, °C		Average water temperature, °C		Average monthly rainfall, mm	Relative humidity, %	
	max	min	max	min		morning	evening
				2009			
January	15.1	0.1	12.0	8.2	0	62	60
February	18.4	2.5	15.2	10.1	0	51	48
March	21.0	5.6	18.3	14.0	172	48	48
April	23.0	10.8	20.5	15.5	433	68	59
May	22.7	12.7	19.4	15.0	660	74	68
June	23.6	14.6	21.0	19.0	721	79	78
July	23.3	16.4	20.5	17.0	463	85	85
August	22.9	15.8	20.1	16.5	1126	85	88
September	23.4	14.2	20.3	16.0	431	82	82
October	22.1	9.7	19.3	14.5	506	70	67
November	19.2	4.5	15.7	9.0	0	62	57
December	14.3	0.3	10.9	7.5	0	65	70
				2010			
January	16.4	–2.2	13.2	7.0	0	47	46
February	16.3	1.7	13.3	9.5	22	52	49
March	22.2	7.7	19.4	16.5	184	56	51
April	22.9	12.6	19.7	17.0	303	70	62
May	23.0	13.8	20.0	18.0	595	75	71
June	22.6	15.6	19.5	17.0	1171	85	82
July	23.3	16.1	20.2	19.0	862	86	85
August	23.3	15.7	20.4	18.5	1232	85	83
September	22.9	14.5	19.8	15.5	386	83	82
October	21.3	10.8	18.4	12.5	342	75	73
November	18.3	4.5	15.5	9.5	98	63	61
December	16.0	–0.4	11.9	8.1	11	53	52
				2011			
January	14.2	–2.3	10.8	7.5	11	50	46
February	17.2	1.4	14.3	9.0	4	70	48
March	20.1	7.3	16.8	10.2	502	57	53
April	20.8	9.8	17.6	10.0	372	64	66
May	22.1	12.5	18.8	13.0	567	77	80
June	22.7	15.4	19.8	15.5	834	95	85
July	23.3	15.6	20.1	18.5	527	90	89
August	22.8	15.1	19.5	16.0	871	89	87
September	23.5	14.3	20.0	14.3	707	83	80
October	21.8	9.1	18.4	10.5	212	71	67
November	18.4	2.7	15.1	10.0	58	58	48
December	15.2	0.4	11.9	8.2	0	58	52

TABLE 2. Ecological Parameters of Study Site and Presence/Absence of Adults, Eggs, and Tadpoles of *Leptolalax khasiorum*

Date	Time of visit	Observations								
		Sky condition/rainfall	Ecological parameters					Adults sighted	Eggs	Tadpole
			Temperature		Water pH	Humidity, %	DO			
			air	water						
12 March 2009	15:00	Light clouds/no rain	–	–	–	–	–	+	–	+
28 March 2009	14:00	Cloudy with light rain	18.0	11.0	–	70	–	+	–	+
4 April 2009	14:00	Clear sky/no rain	20.0	16.0	–	75	–	+	+	+
18 April 2009	15:00	Light clouds/no rain	22.6	19.1	–	85	–	+	–	+
6 May 2009	15:00	Clear sky/no rain	23.0	18.0	–	80	–	–	–	+
23 May 2009	14:00	Cloudy/no rain	24.0	19.2	–	75	–	–	–	+
21 February 2010	14:00	Clear sky/no rain	15.2	12.2	7.8	65	–	+	–	–
4 March 2010	13:00	Light clouds/no rain	19.3	14.5	6.4	75	–	+	+	–
12March 2010	14:00	Light clouds/no rain	23.5	18.3	6.5	65	–	+	–	–
24 March 2010	15:30	Clear sky/no rain	24.1	19.0	6.8	80	–	+	–	+
3 April 2010	13:00	Light clouds/no rain	23.0	19.3	7.3	70	–	+	–	+
14 April 2010	14:00	Cloudy/light rain	24.7	19.2	6.8	90	–	+	–	+
24 April 2010	15:00	Cloudy/no rain	23.5	21.0	6.8	70	–	+	–	+
3 May 2010	14:00	Clear sky/no rain	21.6	20.0	6.7	75	–	+	–	+
8 May 2010	16:00	Light clouds/no rain	22.6	20.1	6.6	75	–	–	–	+
19 May 2010	14:00	Light clouds/light rain	24.2	21.0	6.5	90	–	–	–	+
29 May 2010	15:00	Cloudy/light rain	22.4	19.2	6.7	85	–	–	–	+
9 June 2010	14:00	Clear sky/no rain	25.0	21.2	–	75	–	–	–	+
2 March 2011	14:00	Light clouds/no rain	18.8	16.8	6.6	75	–	+	–	–
9 March 2011	14:00	Light clouds/no rain	21.0	18.5	6.5	80	6.2	+	–	–
12 March 2011	13:00	Cloudy/no rain	21.6	19.1	6.8	75	–	+	–	+
26 March 2011	15:00	Cloudy/moderate rain	22.0	19.6	6.8	85	6.6	+	+	+
5 April 2011	15:00	Clear/no rain	21.9	18.4	6.6	70		+	–	+
10 April 2011	14:00	Cloudy/no rain	23.1	19.3	6.6	65	6.9	+	–	+
15 April 2011	14:00	Clear sky/no rain	21.4	18.4	6.2	65	–	+	–	+
23 April 2011	15:00	Cloudy/heavy rain	23.2	19.2	6.5	75	7.4	+	–	+
14 May 2011	15:00	Cloudy/moderate rain	21.0	18.6	6.5	80	–	–	–	+
28 May 2011	14:00	Cloudy/light rain	23.3	18.2	6.3	75	6.6	–	–	+
22 February 2012	14:00	Clear sky/no rain	15.6	12.6	7.1	65	4.5	+	–	–
8 March 2012	15:00	Clear sky/No rain	20.0	18.2	6.7	75	6.6	+	–	–
17 March 2012	14:00	Cloudy/no rain	18.8	16.1	7.4	75	6.7	+	–	–
7 April 2012	15:00	Light clouds/no rain	18.6	17.0	6.5	80	7.2	+	–	–
18 April 2012	15:00	Light clouds/light rain	23.1	18.8	7.1	85	9.5	+	+	+
28 April 2012	14:00	Heavy clouds/No rain	23.7	19.0	6.3	70	7.6	+	–	+
2 May 2012	14:00	Light clouds/no rain	22.9	18.0	6.7	80	6.7	+	–	+
19 May 2012	15:00	Light clouds/light rain	23.9	17.6	6.2	95	6.6	–	–	+

Note. +, Present; –, absent

OBSERVATIONS

Adults of *Leptolalax khasiorum* started emerging from early February onwards, before the first (premonsoonal) showers (Table 2). Adults were seen throughout the months of March and April. The emergence pattern of this species has been recorded to be synchronous with the onset of the first shower of rainfall for the year. *L. khasiorum* appears to respond more to weather cues for their emergence and breeding, rather than to seasonal cues. They are encountered underneath flat stones embedded on the stream bed. The adults were rarely seen on the surface of rocks or calling on the outside by day.

Amplexus in this species was not observed. Adult males were found near egg mass for a day or two after egg-deposition, which is here taken as evidence of nest attendance by the male parent. Clutches of eggs were laid

TABLE 3. Clutch Size and Diameter of Eggs of *Leptolalax khasiorum*

Clutch number	Clutch size		Eg diameter, mm	Egg weight, mg
1	432	1	2.1	4.3
		2	2.2	7.1
		3	2.2	6.0
		4	2.2	5.4
		5	2.4	7.6
		6	2.1	4.2
		7	2.2	9.0
		8	2.1	6.3
		9	2.2	5.6
		10	2.2	6.8
2	392	1	2.3	6.7
		2	2.1	5.6
		3	2.2	7.0
		4	2.1	4.6
		5	2.2	6.8
		6	2.2	6.9
		7	2.1	6.4
		8	2.2	6.6
		9	2.2	7.2
		10	2.1	6.5
3	401	1	2.1	6.0
		2	2.7	11.6
		3	2.7	6.1
		4	2.0	3.5
		5	2.1	5.9
		6	2.2	6.0
		7	2.1	6.4
		8	2.5	9.6
		9	2.2	8.9
		10	2.2	8.0

Note. Average egg diameter ($n = 10$) was 2.2 ± 0.3 mm and average egg weight was 6.6 ± 0.5 mg.

on the side of, or underside rocks (Fig. 5*a*). The substratum can be characterized as rock covered, with mud and sand deposit, topped with leaf litter. At the time of emergence, the area remains dry, except for isolated shallow pools, with moisture-saturated muddy, sandy soil or wet leaf matter trapped within rocks. The water level in the streams remains low in the winter months, almost drying up except at certain deeper pools formed in depressions in the rocky stream bottom.

Along portions of the stream, such places can be found where a small puddle of water remains hidden beneath layers of rocks and fallen leaves. The depth of the water at a puddle buried underneath the rocks and leaves varies from 2 to 15 cm. The eggs are cream colored, lacking animal poles and adhere by means of a transparent gelatinous layer ("jelly" or "jelly layers" of Altig and McDiarmid, 2007; Fig. 5*b*). Three clutches (data in Table 3) included 392 – 432 eggs, mean egg diameter ($n = 30$) was 2.2 ± 0.3 mm and mean egg weight 6.6 ± 0.5 mg. Tadpoles emerge 7 – 10 days after deposition in the laboratory. When water levels are low, the tadpoles (Fig. 5*c*) are found in small puddles of water formed in cavities after lifting rocks. As the rain sets in, water level

Fig. 5. *a*, Egg mass of *Leptolalax khasiorum* under an upturned rock at Mawphlang, Meghalaya, north-eastern India; *b*, part of a clutch of eggs, showing lack of animal pole; *c*, a late stage larva.

rises and the tadpoles are washed with the current and reach downstream of the breeding site within a few weeks.

DISCUSSIONS

Selection of egg deposition site in *Leptolalax khasiorum* appears dependent on multiple factors. In previous studies on breeding habitat selection (Beebee, 1985; Ancona and Capietti, 1995; Augert and Guyetant, 1995; Ensabella et al., 2003), a large number of environmental variables were used to characterize the monitored water bodies as fully as possible, due to the difficulty of foreseeing factors that may influence the selection of a certain water body as breeding habitat. Earlier studies also reported that amphibians use water depth or the water-holding capacity of pools as a criteria for oviposition site selection (Crump, 1991, Spieler and Linsenmair, 1997, Rudolf and Rödel, 2005). The presence of amphibian species in an aquatic habitat depends not only on suitability of the aquatic habitat, but also on the suitability of the surrounding terrestrial environment (Kats et al., 1988). In species with complex life cycles, it is also important that the permanency of the breeding habitat exceeds the total length of the larval period (Edgerly et al., 1998; Murphy, 2003b; Rudolf and Rödel, 2005). In more ephemeral habitats, desiccation is often a major source of larval mortality (Newman, 1988; Smith, 1983). Some studies have shown that adults can discern future habitat permanence and make oviposition decisions that minimize the risk to their offspring (Crump, 1991; Rudolf and Rödel, 2005; Spieler and Linsenmair, 1997). Since breeding habitats may deteriorate in quality over time or dry up entirely, cues that indicate the likely permanence of a habitat can also be important to breeding site choice. Clutches of *L. khasiorum* are deposited under rocks, and are pale, unpigmented. Eggs of a number of unrelated amphibian lineages that are produced at secluded sites tend to be pale to unpigmented (Altig and McDiarmid, 2007). The same review, however, generalized that early breeding species of North American ranids produces darker eggs, to enhance heat absorption, and thereby hasten development. In terms of ovipositional sites, clutches in the study species are semiterrestrial, produced near free water while not submerged, and the site itself ephemeral in that it is part of the drainage during the wet season.

The clutch size in the species (392 – 432) is relatively small for a frog of this size (mean female SVL 32.5 mm), and at 2.2 mm, relative egg size is large. Comparable data for congeners are unavailable, except for the Bornean *L. gracilis*, that has been reported to have clutches of 185 – 194 (Das, 2007). Low clutch size has been associated with terrestrial reproduction in a recent review (Van Gomez-Mestre et al., 2012). The proximity of adult males to egg clutch for a few days is suggestive of parental care, previously unreported within the family. In a review of social and environmental influences on anuran amphibian egg size evolution, Summers et al. (2007), found a relationship between male parental care, stream breeding and montane habitats on one hand, and large egg size on the other.

Salthe (1969), and subsequently, Salthe and Duellman (1973) and Duellman and Trueb (1994) used a combination of egg-laying sites and development factors, to classify amphibian reproduction types into distinct categories, referred to as reproductive modes. A total of 40 modes are recognized at present (Haddad and Prado, 2005; Gururaja, 2010), although plasticity in reproductive modes have also been reported (Touchon and Warkentin, 2008). In producing terrestrial eggs out of water, that are placed under rocks, exophagous and free-swimming tadpoles, the reproductive mode of *Leptolalax khasiorum* may be appropriately classified as Mode 18, a first record for the genus and family. Confamilial genera of the family Megophryidae who reproductive habits are known (including *Leptobrachella*, *Megophrys*, and *Xenophrys*), produce eggs in loticwater bodies, and are consequently allocated to Mode 2. Further, these species do not show male attendance of clutches.

Leptolalax khasiorum is one of the earliest breeders of amphibians in the forest stream of Mawphlang. The forest streams are the only water body found inside the forest, and all local amphibian species that depend on water for breeding utilize the forest streams (the sole exception is *Philautus*, known to be a direct-developer; see Hertwig et al., 2011). Different species utilize sections of the stream for breeding, and hence a diversity of tadpole morphotypes may breed at the same time. Breeding activities in the species may be initiated by increase in ambient atmospheric and water temperatures, as noted in previous studies (Reading, 1998; Richter-Boix et al., 2006). Early breeding may be advantageous for anurans. By completing oviposition early, frogs maximize the probability that tadpoles will metamorphose before the pond dries; and because many potential predators are not active in early spring, larvae of early breeders may grow large enough to attain a size refuge from predation (e.g., Calef, 1973; Heyer et al., 1975). Yet, early breeding is a risky strategy, as eggs and larvae may be adversely affected by harsh environmental conditions (Wright, 1914; Wright and Wright, 1949; Licht, 1971).

Amphibian species occurring in sympatry at Mawphlang include: *Xenophrys oropedion*, *Hyla danieli*, *H. leptoglossa*, *Philautus* sp., *Polypedates himalayensis*, *Rhacophorus bipunctatus*, *Hyla arborea*, *Euphlyctis cyanophlyctis*, *Duttaphrynus melanostictus*, *Amolops* cf.

gerbillus, *Amolops formosus*, and *Fejervarya senguptai* (Mahony, 2008; Das et al., 2010; Purkayastha and Matsui, 2010; Mahony et al., 2013). A majority of these breed during the monsoon months, that extend between June and September (Tron, personal observation), and apart from *L. khasiorum*, only *H. danieli* breeds during the spring months (eggs undetected but metamorph emergence period coincides with that of *L. khasiorum*). Early breeding thus confers the advantage of reduced competition for deposition sites of eggs and larval microhabitats, but may be constrained by lower food availability and other unfavorable environmental conditions.

The emergence of *Leptolalax khasiorum* has been observed to correspond with the onset of the spring rain in the area (see Table 1). Precipitation has been shown to be a primary extrinsic factor affecting the time of the breeding activity for most tropical and subtropical anuran species (Haddad and Sazima, 1992; Duellman and Trueb, 1994). The synchronization of rainy season and reproductive activity of amphibians (Gallardo, 1974; Cei, 1980) has been interpreted as an adaptive response to fluctuations in environmental conditions, reducing the risk of reproductive failure due to desiccation (Goldberg et al., 2006) and greater abundance of arthropod prey (Watling and Donnelly, 2002).

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REFERENCES

Aichinger M. (1987), "Annual activity patterns of anurans in a seasonal neotropical environment," *Oecologia*, **71**, 583 – 592.

Alford R. A. (1999), "Ecology. Resource use, competition, and predation," in: R. W. McDiarmid and R. Altig (eds.), *Tadpoles. The Biology of Anuran Larvae*, Univ. of Chicago Press, Chicago – London, pp. 240 – 278.

Altig R. and McDiarmid R. W. (2007), "Morphological diversity and evolution of egg and clutch structure in amphibians," *Herpetol. Monogr.*, **21**, 1 – 32.

Ancona N. and Capietti A. (1995), "Analysis of the breeding site characteristics of amphibians in a prealpine area (Triangolo Lariano)," in: G. A. Llorente, A. Montori, X. Santos, and M. A. Carretero (eds.), *Scientia Herpetologica*, Asociacion Herpetol. Esp., Barcelona, pp. 160 – 164.

Augert D. and Guyetant R. (1995), "Space occupation for egg deposition in amphibians living in plain woodland and pasture land (east of France)," in: G. A. Llorente, A. Montori, X. Santos, and M. A. Carretero (eds.), *Scientia Herpetologica*, Asociacion Herpetol. Esp., Barcelona, pp. 165 – 169.

Beebeee T. J. C. (1985), "Discriminant analysis of amphibian habitat determinants in southeast England," *Amphibia–Reptilia*, **6**, 35 – 43.

Bertoluci J. and Rodrigues M. T. (2002), "Seasonal patterns of breeding activity of Atlantic rainforest anurans at Boracéia, southeastern Brazil," *Amphibia–Reptilia*, **23**, 161 – 167.

Blaustein L. (1999), "Oviposition habitat selection in response to risk of predation: consequences for population dynamics and community structure," in: S. P. Wasser (ed.), *Evolutionary Theory and Processes*: *Modern Perspectives*, Kluwer Academic Publishers, Dordrecht, pp. 444 — 456.

Calef G. W. (1973), "Natural mortality of tadpoles in a population of *Rana aurora*," *Ecology*, **54**, 741 – 758.

Cei J. M. (1980), "Amphibians of Argentina," *Italian J. Zool. Monogr.*, **2**, 1 – 609.

Crump M. L. (1991), "Choice of oviposition site and egg load assessment by a treefrog," *Herpetologica*, **47**, 308 – 315.

Das I. (2007), *Amphibians and reptiles of Brunei. A Pocket Guide*, Natural History Publications (Borneo) Sdn Bhd, Kota Kinabalu.

Das I., Tron R. K. L., Rangad D., and Hooroo R. N. K. (2010), "A new species of *Leptolalax* (Anura: Megophryidae) from the sacred groves of Mawphlang, Meghalaya, north-eastern India," *Zootaxa*, **2339**, 44 – 56.

Dehling J. M. (2012), "Redescription of *Leptolalax gracilis* (Günther, 1872) from Borneo and taxonomic status of two populations of *Leptolalax* (Anura: Megophryidae) from peninsular Malaysia," *Zootaxa*, **3328**, 20 – 34.

Duellman W. E. and Trueb L. (1994), *Biology of Amphibians*, McGraw-Hill, New York.

Edgerly J. S., McFarland M., Morgan P., and Livdahl T. (1998), "A seasonal shift in egg-laying behaviour in response to cues of future competition in a treehole mosquito," *J. Animal Ecol.*, **67**, 805 – 818.

Ensabella F., Loriga S., Formichetti P., Isotti R., and Sorace A. (2003), "Breeding site selection of *Bufo viridis* in the city of Rome (Italy)," *Amphibia–Reptilia*, **24**, 396 – 400.

Evans M., Yáber C., and Hero J. M. (1996), "Factors influencing choice of breeding site by *Bufo marinus* in its natural habitat," *Copeia*, **1996**, 904 – 912.

Gallardo J. M. (1974), *Anfibios de los alrededores de Buenos Aires*, Editorial Universitaria de Buenos Aires, Buenos Aires.

Goldberg F. J., Quinzio S., and Vaira M. (2006), "Oviposition site selection of the toad, *Melanophryniscus rubriventris* in an unpredictable environment," *Can. J. Zool.*, **84**, 699 – 705.

Gururaja K. V. (2010), "Novel reproductive mode in a torrent frog *Micrixalus saxicola* (Jerdon) from the Western Ghats, India," *Zootaxa*, **2642**, 45 – 52.

Haddad C. F. B., Cardoso A. J., and Castanho L. M. (1990), "Hibridação natural entre *Bufo ictericus* e *Bufo crucifer* (Amphibia: Anura)," *Rev. Brasil Biol.*, **50**, 739 – 744.

Haddad C. F. B. and Prado C. P. A. (2005), "Reproductive modes in frogs and their unexpected diversity in the Atlantic forest of Brazil," *BioScience*, **55**, 207 – 217.

Haddad C. F. B. and Sazima I. (1992), "Anfíbios anuros da Serra do Japi," in: L. P. C. Morellato (ed.), *História natural da Serra do Japi: ecologia e preservação de uma área florestal no sudeste do Brasil*, Unicamp, Campinas, pp. 188 – 211.

Hazell D., Hero J.-M., Lindenmayer D., and Cunningham R. (2003), "A comparison of constructed and natural habitat for frog conservation in an Australian agricultural landscape," *Biol. Conserv.*, **119**, 61 – 71.

Hertwig S., Das I., Schweizer M., Brown R. M., and Haas A. (2011), "Phylogenetic relationships of the *Rhacophorus everetti*-group and implications for the evolution of reproductive modes in *Philautus* (Amphibia: Anura: Rhacophoridae)," *Zool. Scripta*, **41**, 29 – 46.

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

Inger R. F. (1985), "Tadpoles of the forested regions of Borneo," *Fieldiana Zool. N. Ser.*, **26**, 1 – 89.

Kats L. B., Petranka J. W., and Sih A. (1988), "Antipredator defenses and the persistence of amphibian larvae with fishes," *Ecology*, **69**, 1865 – 1870.

Licht L. E. (1971), "Breeding habits and embryonic thermal requirements of the frogs, *Rana aurora aurora* and *Rana pretiosa pretiosa*, in the Pacific Northwest," *Ecology*, **52**, 116 – 124.

Mahony S. (2008), "Redescription and generic reallocation of *Rana mawphlangensis* Pillai and Chanda, 1977 (Amphibia: Ranidae)," *Hamadryad*, **33**, 1 – 12.

Mahony S., Teeling E. C., and Biju S. D. (2013), "Three new species of horned frogs, *Megophrys* (Amphibia: Megophryidae), from northeast India, with a resolution to the identity of *Megophrys boettgeri* populations reported from the region," *Zootaxa*, **3722**, 143 – 169.

Malkmus R. and Kosuch J. (1999), "Beschrijving van het kikkervisje van *Leptolalax arayai* Matsui, 1997, eenkikkeruit de familie Megophryidae," *Lacerta*, **57**(5), 161 – 165.

Murphy P. J. (2003), "Does reproductive site choice in a Neotropical frog mirror variable risks facing offspring?" *Ecol. Monogr.*, **73**, 45 – 67.

Newman R. A. (1988), "Adaptive plasticity in development of Scaphiopus couchii tadpoles in desert ponds," *Evolution*, **42**, 774 – 783.

Pombal J. P., Jr. (1997), "Distribuição espacial e temporal de anuros (Amphibia) em uma poça permanente na Serra de Paranapiacaba, sudeste do Brasil," *Rev. Brasil Biol.*, **57**, 583 – 594.

Purakayastha J. and Matsui M. (2010), "A new species of *Fejervarya* (Anura: Dicroglossidae) from Mawphlang, northeastern India," *Asian Herpetol. Res.*, **3**, 31 – 37.

Reading C. J. (1998), "The effect of winter temperatures on the timing of breeding activity in the common toad *Bufo bufo*," *Oecologia*, **117**, 469 – 475.

Resitarits W. J., Jr. and Wilbur H. M. (1989), "Choice of oviposition site by *Hyla chrysoscelis*: role of predators and competitors," *Ecology*, **70**, 220 – 228.

Richter-Boix A., Llorente G. A., and Montori A. (2006), "Breeding phenology of an amphibian community in a Mediterranean area," *Amphibia–Reptilia*, **27**, 549 – 559.

Rowley J. and Trung C. T. (2009), "A new species of *Leptolalax* (Anura: Megophryidae) from central Vietnam," *Zootaxa*, **2198**, 51 – 60.

Rowley J., Stuart B. L., Richards S. J., Phimmachak S., and Sivongxay N. (2010), "A new species of *Leptolalax* (Anura: Megophryidae) from Laos," *Zootaxa*, **2681**, 35 – 46.

Rudolf V. H. W. and Rödel M. O. (2005), "Oviposition site selection in a complex and variable environment: the role of habitat quality and conspecific cues," *Oecologia*, **142**, 316 – 325.

Salthe S. N. (1969), "Reproductive modes and the number and sizes of ova in the urodela," *Am. Midl. Nat.*, **81**, 467 – 490.

Salthe S. N. and Duellman W. E. (1973), "Quantitative constraints with reproductive mode in anurans," in: J. L. Vial (Ed.), *Evolutionary Biology of the Anurans*, Univ. of Missouri Press, Columbia, pp. 229 – 249.

Sengupta S., Sailo S., Lalremsanga H. T., Das A., and Das I. (2010), "A new species of *Leptolalax* (Anura: Megophryidae) from Mizoram, north-eastern India," *Zootaxa*, **2406**, 57 – 68.

Skelly D. K. (2001), "Distributions of pond-breeding anurans: an overview of mechanisms," *Israel J. Zool.*, **47**, 313 – 332.

Smith D. C. (1983), "Factors controlling tadpole populations of chorus frog (*Pseudacris triseriata*) on Isle Royale, Michigan," *Ecology*, **64**, 501 – 510.

Spieler M. and Linsenmeir K. E. (1997), "Choice of optimal oviposition sites by *Hoplobatrachus occipitalis* (Anura: Ranidae) in an unpredictable and patchy environment," *Oecologia*, **109**, 184 – 199.

Summers K., McKeon C. S., Heying H., Hall J., and Patrick W. (2007), "Social and environmental influences on egg size evolution in frogs," *J. Zool. London*, **271**, 225 – 232.

Telford S. R. and Dyson M. L. (1990), "The effect of rainfall on interclutch interval in Painted Reed Frog (*Hyperolius marmoratus*)," *Copeia*, **1990**, 644 – 648.

Touchon J. C. and Warkentin K. M. (2008), "Reproductive mode plasticity: aquatic and terrestrial oviposition in a treefrog," *Proc. Natl. Acad. Sci. USA*, **105**, 7495 – 7499.

Van Gomez-Mestre I., Pyron R. A., and Wiens J. J. (2012), "Phylogenetic analyses reveal unexpected patterns in the evolution of reproductive modes in frogs," *Evolution*, **66**, 3687 – 3700.

Watling J. I. and Donnelly M. A. (2002), "Seasonal patterns of reproduction and abundance of leaf litter frogs in a Central American rainforest," *J. Zool. London*, **258**, 269 – 276.

Wells K. D. (1977), "The social behaviour of anuran amphibians," *Anim. Behav.*, **25**, 666 – 693.

Wiest J. A. (1982), "Anuran succession at temporary ponds in a pot oak-savanna region of Texas," *Herpetological Communities*, **13**, 39 – 47.

Wright A. H. (1914), *North American Anura. Life-Histories of the Anura of Ithaca*, Carnegie Institution of Washington, New York – Washington.

Wright A. H. and Wright A. A. (1949), *Handbook of Frogs and Toads*, Comstock, Ithaca, NY.