



Seasonal activity of terrestrial amphibians in the monsoon lowland forest of southern Vietnam

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The all-year round pit-fall trap monitoring and natural history observations in Cat Tien National Park (southern Vietnam) describe patterns of migratory and vocal activities of terrestrial anurans. Vocalisation activity was low during the driest period of the year and rose explosively after the first strong rains in April (up to 19 species registered), and was high during the rainy season (May–September), however, decreased abruptly towards its end (October–November). Amphibian migratory activity changed from the dry to rainy season, generally increasing when average monthly rainfall was higher. Some species started aestivation in the dry season. However, some species were active during the dry season or even increased migratory activity at this period of the year. We suggest the existence of two ecological types of forest anurans: aestivating and non-aestivating species. The average monthly activity of aestivating amphibians coincided with rising rainfall from April to August and reduced abruptly two months before the dry season started. Juveniles of aestivating species appeared mostly in August and September; juveniles of non-aestivating anurans were abundant throughout the year.

Key words: amphibians, breeding, Cat Tien National Park, migratory activity, monsoon, Vietnam

INTRODUCTION

The timing of the movement and reproductive activity in terrestrial amphibians is strongly influenced by temperature, humidity and rainfall (Wiest, 1982). Low temperatures are the main factor forcing amphibians to hibernate in high latitudes (Savage, 1961) and reduce activity at high altitudes of low latitudes (Kam & Chen, 2000; Chen et al., 2001; Maltchik et al., 2008). In a warm non-seasonal climate typical for lowland tropics, amphibian activity might be expected to be continuous throughout the year, as observed in Singapore and Malaysia (Goh, 1962; Berry, 1964). However, amphibian activity in some tropical regions is also known to be cyclic. Since the rapid dehydration of the ground surface is a real threat for terrestrial anurans (Thorson & Svihla, 1943), the presence of a dry and a rainy season greatly influences frog activity in tropical monsoon climates (Heyer, 1973). Aestivation and sheltering are the main strategies used by terrestrial amphibians to avoid desiccation during the dry season (Zug & Zug, 1979; Seebacher & Alford, 2002). Reproduction and other types of activity are also restricted during the dry season due to a decrease of the number of water bodies (Heyer & Belin, 1973; Duellman

& Trueb, 1986; Aichinger, 1987; Bertolucci, 1998; Bertolucci & Rodriguez, 2002; Kanamadi et al., 2002). Thus, the reproductive activity of amphibians in a tropical region is often timed to coincide with the rainy season. At this period, several different reproductive strategies can be observed. Particular strategies of surviving dry periods and preferences for the timing of reproduction might differ even within the same species among regions and years (Berry, 1964; Heyer, 1973). Certain parts of the population start vocalisation and oviposition just after the first heavy rains; others wait until the months with the heaviest precipitation; the rest delay breeding activity until the end of the rainy season (Berry, 1964; Kanamadi et al., 2002; Gottsberger & Gruber, 2004; Shahriza et al., 2010).

Here we conducted a one year pit-fall trap monitoring and natural history observations in Cat Tien National Park (southern Vietnam) to describe migratory and vocal activities of terrestrial anurans. The study area is located in the zone of a typical monsoon climate, characterised by relatively mild annual temperature fluctuations and strong differences in precipitation between the dry and rainy season. Southern Indochina displays relatively high amphibian diversity. The total number of anuran species

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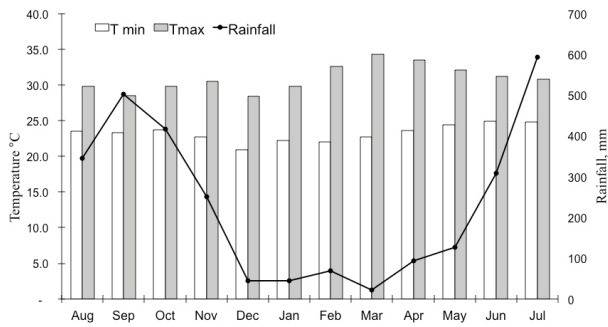


Fig. 1. The mean monthly temperature (minimum and maximum) and rainfall totals recorded near the headquarters of Cat Tien National Park during the period August 2011–July 2012.

recorded for Cat Tien National Park is about 40 (Vassilieva et al., 2016), including several recently described species (Poyarkov et al., 2014, 2015; Vassilieva et al., 2014). However, remarkably little is known about the biology, ecology and life histories of amphibians in this region. In the present study, we aimed to determine how the activity of anurans varies during the year in the monsoon forests of southern Vietnam. Terrestrial movement of adult amphibians is usually caused by migrations to or from breeding sites and by the postmetamorphic dispersion of juveniles (Fellers & Kleeman, 2007; Sinsch, 2014). We hypothesised that amphibian migratory and breeding activity should change between the dry and rainy seasons, and raise with increased rainfall. We also describe the annual activity pattern of several common terrestrial amphibian species.

METHODS

Data was collected in the Nam Cat Tien sector (39.627 ha; in Dong Nai Province) of Cat Tien National Park (CTNP). The forested areas of the park occupy a transitional position between the Truong Son Mountains in the north

and the plains of the Mekong in the south (Blanc et al., 2000; Kuznetsov & Kuznetsova, 2011). This is reflected in the diversity of landscapes, including hills up to a moderate elevation of 600 m a.s.l., lowland forests with an average elevation of approximately 100 m, swamps and wetlands in the basin of Dac Lua stream and on the banks of the Dong Nai River. The dominant trees in the NP are *Lagerstroemia calyculata* (Lythraceae), *Dipterocarpus alatus* (Dipterocarpaceae), *Azelia xylocarpa* (Fabaceae) and *Tetrameles nudiflora* (Datisceae) (Kuznetsov & Kuznetsova, 2011). These landscapes, together with the mainly volcanic geology, including basalt and tuff stones, and shallow soils explain the mosaic of forest types in CTNP (Blanc et al., 2000).

The climate of CTNP is characterised by alternating between a hot and dry season (October–March), and a rainy season (May–September). This type of climate is classified as tropical monsoon (McKnight & Hess, 2000). The average annual temperature and precipitation fluctuate among years from 24 to 27°C and from 2400 to 3000 mm respectively (Deshcherevskaya et al., 2013). December is the driest and the coldest month (average temperature 23°C), April is the warmest month (average temperature 29°C) and the rainiest period is July–September, when up to 400–450 mm of precipitation falls and some parts of the forest become flooded. Monthly daylight hours vary annually from 1127 in December to 1247 in June (Deshcherevskaya et al., 2013). Our own meteorological data registered in 2010–2011 (Fig. 1) are within the range of the many climate observations in the study area (Nguyen et al., 2000; Deshcherevskaya et al., 2013).

The survey sites were located within the representative landscapes of CTNP (Fig. 2). Seven study areas were chosen in the basic forest types of CTNP, and pit-fall traps were installed on several model plots where many studies in plant and soil invertebrates have been conducted (Anichkin, 2011; Anichkin & Tiunov, 2011). The first survey site (Site 1), in the area of the CTNP headquarters, was located in a private garden 100 m from the Dong Nai River (11°25'22N; 107°25'41E, here and below datum WGS 84). Sites 2 and 3 were situated



Fig. 2. The placement of survey sites in Nam Cat Tien National Park.

Table 1. List of species registered in the survey sites in Cat Tien National Park and methods used for the study of their annual activity.

	Species	Studying methods			
		Visual observations	Captures by pit-fall traps	Acoustic monitoring	Finds in shelter
Bufonidae	<i>Duttaphrynus melanostictus</i> (Schneider, 1799)	+	–	–	+
	<i>Ingerophrynus galeatus</i> (Günther, 1864)	+	–	–	–
Rhacophoriidae	<i>Chiromantis nongkhorensis</i> (Cochran, 1927)	+	–	+	–
	<i>Chiromantis vittatus</i> (Boulenger, 1887)	+	–	+	–
	<i>Polypedates megacephalus</i> Hallowell, 1861	+	+	+	–
	<i>Rhacophorus annamensis</i> Smith, 1924	+	+	+	–
	<i>Theلودerma vietnamense</i> Poyarkov, Orlov, Moiseeva, Pawangkhanant, Ruangsuan, Vassilieva, Galoyan, Nguyen, Gogoleva 2015	+	–	+	–
Dicroglossidae	<i>Hoplobatrachus rugulosus</i> (Wiegmann, 1834)	+	+	+	+
	<i>Fejervarya limnocharis</i> (Gravenhorst, 1829)	+	+	+	–
	<i>Limnonectes dabanus</i> (Smith, 1922)	+	+	+	–
	<i>Occidozyga lima</i> (Gravenhorst, 1829)	+	–	+	–
	<i>Occidozyga martensii</i> (Peters, 1867)	+	+	+	+
Microhylidae	<i>Calluella guttulata</i> (Blyth, 1855)	+	+	+	+
	<i>Kalophrynus interlineatus</i> (Blyth, 1855)	+	+	+	–
	<i>Kaloula indochinensis</i> Chan, Blackburn, Murphy, Stuart, Emmett, Ho & Brown, 2013	+	–	–	–
	<i>Kaloula pulchra</i> Gray, 1831	+	+	+	+
	<i>Microhyla berdmorei</i> (Blyth, 1856)	+	+	+	–
	<i>Microhyla butleri</i> Boulenger, 1900	+	+	+	–
	<i>Microhyla fissipes</i> (Boulenger, 1884)	+	+	+	–
	<i>Microhyla heymonsi</i> Vogt, 1911	+	+	+	–
	<i>Microhyla minuta</i> Poyarkov, Vassilieva, Orlov, Galoyan, Tran, Le, Kretova & Geissler, 2014	+	–	+	–
	<i>M. pulchra</i> (Hallowell, 1861)	+	+	+	–
<i>Micryletta erythropoda</i> (Tarkhnishvili, 1994)	+	+	+	+	
Ranidae	<i>Hylarana milleti</i> (Smith, 1921)	+	–	+	–

in a long-boled (with dominant trees up to 35–40 m tall and 60–120 cm in diameter), seasonally flooded forest with a co-dominance of *Lagerstroemia calyculata* and *Tetrameles nudiflora* (11.25'43N; 107.25'38E). Site 4 (11°26'13N; 107°26'23E) was located farther from the Dong Nai River in a non-flooded *Lagerstroemia–Tetrameles* forest. The placement of Site 5 was chosen in the non-flooded forest with co-dominance of *Lagerstroemia* spp. and *Dipterocarpus* spp., 8 km from the Dong Nai River (11°27'02N; 107°21'52E). Study Sites 6 (11°26'48N; 107°26'23E), 7 (11°26'49N; 107°26'24E) and 8 (11°26'48N; 107°26'25E) were placed in a long-boled (35–40 m tall with 80–110 cm diameter trees) riverine forest dominated by *Dipterocarpus* spp.

The study was carried out during the period from August 2011 to July 2012. Nocturnal minimum and diurnal maximum temperatures in shadow at the headquarters area were recorded every day of the study period (from 1 August 2011 to 22 July 2012), and precipitation was measured using a rain-measure cylinder.

Pit-fall trap monitoring, visual observations on excursions, acoustic monitoring and searches for sheltering animals were the main study methods of amphibian registration (Table 1). Eight standard pit-fall traps with drift-fences (Karns, 1986; Willson & Gibbons, 2009) were placed within the survey sites. Each trap consisted of four plastic buckets (capacity 15 L each) dug into the ground in a Y-shape, with all buckets placed 3 meters apart from each other and connected with plastic fences, 40 cm in height. Such traps are considered adequate for the effective capture of small terrestrial amphibians, however, they are not suitable for catching arboreal species (Vogt & Hine, 1982). Each bucket was buried to the edge of the substrate. An inner plastic collar prevented the escape of the frogs from the trap, and a 1–2 cm layer of water on the bottom prevented the desiccation of captured animals. The traps were monitored once per 24 h during 10–14 days every month (usually one week at the beginning and one week at the end of each month). Animals taken out of the buckets were released at a distance of 4–5 kilometres from the trap to avoid the recapture of the same individuals. According to Sinsch (2014), such a distance exceeds the average individual amphibian dispersal distance and homing abilities of 1–4 km. The traps were closed between working periods to avoid the accidental mortality of animals. This capture technique is commonly applied to estimate the species composition in the study area and to reveal the movement activity of anurans (Willson & Gibbons, 2009).

Qualitative analysis of the species composition in the areas of the study sites was revealed both by catches in the traps and by visual observations during trap attendance. This was important because some species were not captured in the pit-fall traps (Table 1).

Vocal activity was registered during regular nocturnal excursions on the same days with monitoring of pit-fall traps. The length of excursion routes was around 27 km per day (Fig. 2). Forest ponds and pools in the area of the park headquarters where amphibians could breed were visited during these excursions. The number of vocalising

species and the relative abundance of vocalising individuals were also evaluated as “single” (when less than 10 vocalising individuals were registered) or “chorus” (when tens or hundreds of vocalising animals produced a loud noise and it was impossible to distinguish particular vocalisations).

The search for aestivating animals was carried out during the dry season by cutting and rolling of rotten logs, inspection of the tree holes and caves and looking under stones.

Snout-vent length (SVL, from snout tip to cloacal opening) was measured in all captured animals with callipers to the nearest 0.5 mm. Animals with SVL similar to animals of the same species bearing signs of breeding (nuptial pads or a vocal sack in males, mature ovaries in females) during the breeding period were classified as adults. Frogs with a lesser SVL and without signs of breeding were identified as juveniles.

The number of captures in pit-fall traps was standardised by calculating individuals per trap day (IPTD) using the formula: $IPTD = N / (T * D)$ where N = number of frogs, T = number of traps, D = number of trapping days.

A distribution model was made to test whether frog capture rate was proportional to rainfall, using the relative number of frogs caught in traps during a month period (n/N) compared to the relative amount of monthly rainfall (p/P). The standard error (\pm SE) was calculated for the IPTD values of empirical distribution. We did not take temperature into account (mean monthly nocturnal temperature fluctuation in 2010/2011 was less than four degrees; Fig. 1). Juveniles were excluded from these analyses because their annual proportional fluctuations differed from those of adults and could affect the result. A Spearman's rank correlation (r_s) was used for comparing the number of individuals within pit-fall traps among months.

The database, calculations and plots were made in Microsoft Excel v. 14.00 and R v. 3.2.2.

RESULTS

Species composition

The total number of amphibian species registered in the survey area by visual observations and trap captures was 25 (Table 1). Species composition broadly overlapped among study sites and five of them (*L. dabanus*, *O. martensii*, *C. guttulata*, *M. heymonsi* and *Mi. erythropoda*) were found on all sites (Table 2). In total, 2670 amphibians (1850 adults and 810 juveniles) of 16 species were captured in pit-fall-traps during 144 trapping days in CTNP (Table 1). Three species were arboreal (*R. annamensis*, *P. megacephalus* and *T. vietnamense*), and 13 species were terrestrial.

Vocal activity

After almost no vocalisation during the dry season, the number of vocalising species increased rapidly to 19 species with the first strong rains in April (Fig. 3). After explosive vocalisations in April, vocalising activity decreased until July to 14 species, despite rainfall increasing markedly from April (93 mm) to July (593

Table 2. Distribution of the amphibians in the pit-fall traps during the year-round monitoring from August 2011 to July 2012 (N=2670).

Landscape	Species	Headquarters		Seasonally flooded <i>Lagerstroemia- Tetrameles</i> forest		Not flooded <i>Lagerstroemia- Dipterocarpus</i> forest		Riverine <i>Dipterocarpus</i> forest		Sum
		No 1	No 2	No 3	No 4	No 5	No 6	No 7	No 8	
Rhacophoridae	1. * <i>Polypedates megacephalus</i>	1	2					1	1	5
	2. * <i>Rhacophorus annamensis</i>					2			2	4
	3. * <i>Theلودerma vietnamense</i>		2							2
Dicroglossidae	4. <i>Hoplobatrachus rugulosus</i>		5	2						7
	5. <i>Fejervarya limnocharis</i>							2		2
	6. · <i>Limnonectes dabanus</i>	4	42	1	8	4	27	19	23	127
	7. · <i>Occidozyga martensii</i>	67	215	43	168	9	423	414	309	1648
Microhylidae	8. · <i>Calluella guttulata</i>	6	24	37	13	17	6	8	6	117
	9. <i>Kalophrynus interlineatus</i>	25	7	1	11			2	7	53
	10. <i>Kaloula pulchra</i>	1	25	3	4		4	2	1	40
	11. <i>Microhyla berdmorei</i>					1				1
	12. <i>Microhyla butleri</i>					3		3	1	7
Microhylidae	13. <i>Microhyla fissipes</i>	1	9	9	3		1	3		26
	14. · <i>Microhyla heymonsi</i>	1	4	3	2	1	1	9	4	25
	15. · <i>Micryletta erythropoda</i>	36	123	370	13	4	4	32	22	604
Ranidae	16. <i>Hylarana milleti</i>							2		2
* arboreal species		142	458	469	222	41	467	499	466	2670
· species, found in all biotopes										

mm). High vocalising activity was observed in August (16 species) and September (13 species).

The number of species vocalising in choruses declined to nine and seven in October and November and to three and one in December and January. This decrease generally coincided with precipitation diminution to 346 and 502 mm in August and September respectively and to 44 mm in December and January. Some species, such as *M. berdmorei*, formed loud choruses near small water bodies and spawned even in November–December. The lowest number of vocalising animals was recorded in January–March, the driest and warmest period, when only single vocalisations of *T. vietnamense*, *L. dabanus* and *M. fissipes* could be heard.

Movement activity

Two species (*O. martensii* and *L. dabanus*) were active throughout the year with an increase of movement activity to its maximum from November to January and a decrease of movement activity to its minimum in July

and August (Table 3; Fig. 4). The captures of *C. guttulata*, *Mi. erythropoda*, *M. fissipes*, *M. heymonsi*, *K. pulchra* and *Ka. interlineatus* were more common during the rainy season, with a maximum of captures in June and July (Table 3; Fig. 4). Almost no animals of these species, except *Ka. interlineatus* and *M. fissipes*, were captured during the dry season (Fig. 4). Maximum activity and number of captures of most species active during the rainy season were observed after precipitation of 40–60 mm. Such heavy rains occurred mainly in the mid-rainy period. Five species, namely *M. butleri*, *M. berdmorei*, *H. rugulosus*, *F. limnocharis* and *Hy. milleti*, were rare in traps (less than 10 captures per study period) (Table 2). Our data did not allow us to determine their terrestrial activity pattern, although according to our visual observations, they appeared to be more active during the rainy season.

Individuals of several species were recorded aestivating during the dry season in moist leaf litter or near streams and water bodies. Large species (*C. guttulata*, *K. pulchra*,

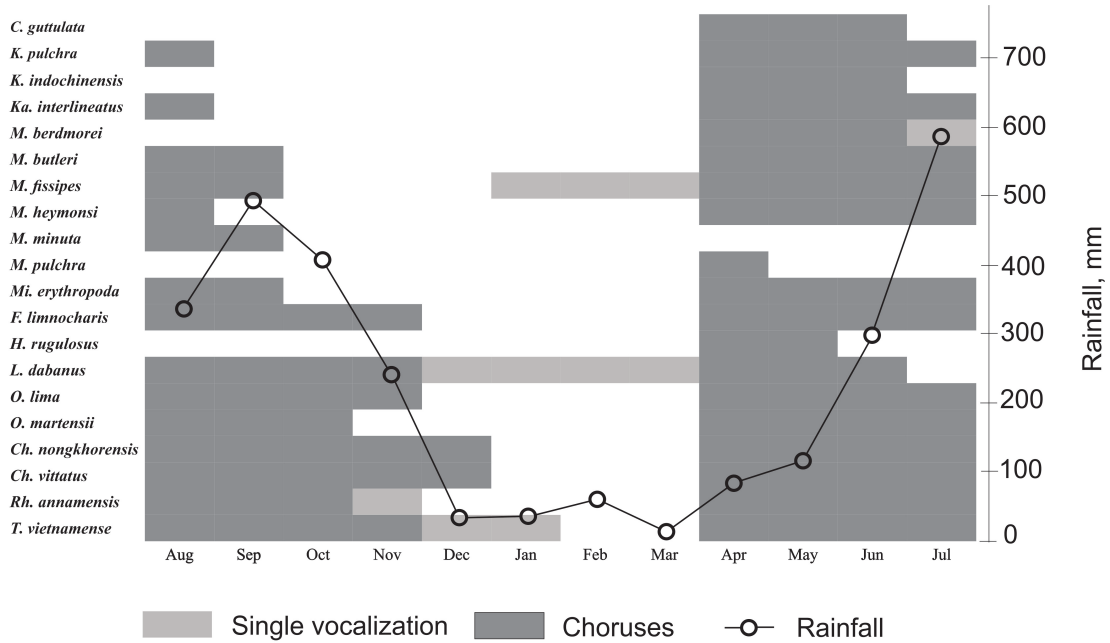


Fig. 3. Vocal activity of the frog species during annual cycle in Cat Tien National Park. The number of vocalising species and the relative abundance of vocalising individuals (single if less than 10 vocalising individuals were registered and chorus if tens or hundreds of vocalising animals produced loud noise with undistinguishable particular vocalisations) were evaluated.

H. rugulosus and *D. melanostictus*) were observed in underground burrows and cave hollows. Small aestivating frogs (*Microhyla* spp. and *Mi. erythropoda*) were found hidden in or under rotten logs, as well as in caverns and

under stones large enough to keep moisture under them during the dry season.

Predicted movement activity for two active all-year-round species (*O. martensii* and *L. dabanus*) coincided

Table 3. Activity peaks and depressions for the eight anuran species most common in the study sites in Cat Tien National Park. Activity is noted in individuals per trap-day (IPTD). Species, which were rare in traps (less than 10 catches), are excluded.

Species	Activity Peaks (IPTD)	Min. of activity (IPTD)	Activity type	N (ind.)
<i>O. martensii</i>	December – January (2.99–3.38)	April – August (0.10–0.90)	Throughout the year	1658
<i>L. dabanus</i>	December – January (0.28–0.29)	July – October (0.03–0.06 IPTD)	Throughout the year	121
<i>Ka. interlineatus</i>	June (0.14)	November – January (0.01)	Throughout the year	52
<i>Mi. erythropoda</i>	July (up to 4.15)	October – April (0.01)	Aestivating	603
<i>C. guttulata</i>	June (0.35); November – December (0.23–0.19)	December – April (0.00)	Aestivating	101
<i>K. pulchra</i>	June (0.14); August – September (0.08–0.12)	December – April (0.00)	Aestivating	40
<i>M. fissipes</i>	October – December (0.04–0.06); June – July (0.05–0.04 IPTD).	December – April (<0.01)	Throughout the year	26
<i>M. heymonsii</i>	August – September & November (0.09, 0.04, 0.03)	April – June (<0.01)	Aestivating	23

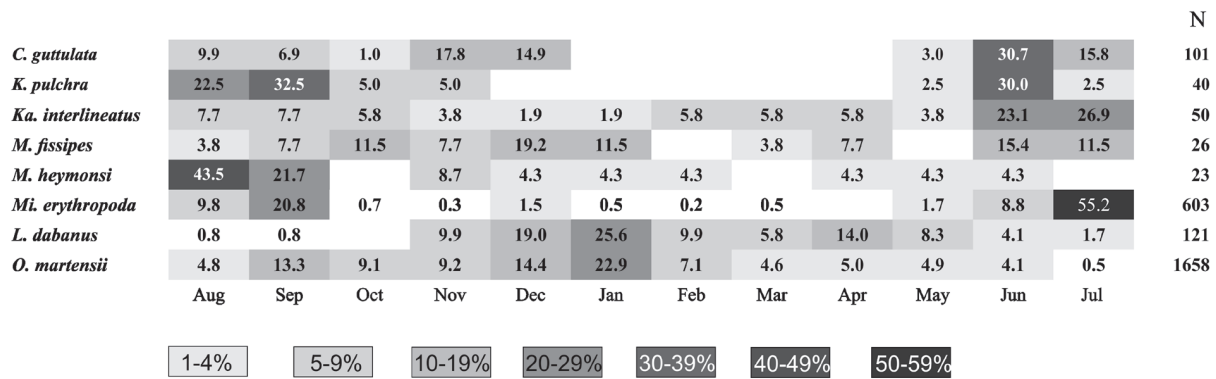


Fig. 4. Annual percentage (%) of captures in pit-fall traps for eight terrestrial species. *N* – number of captured individuals. The percentage is calculated within each species.

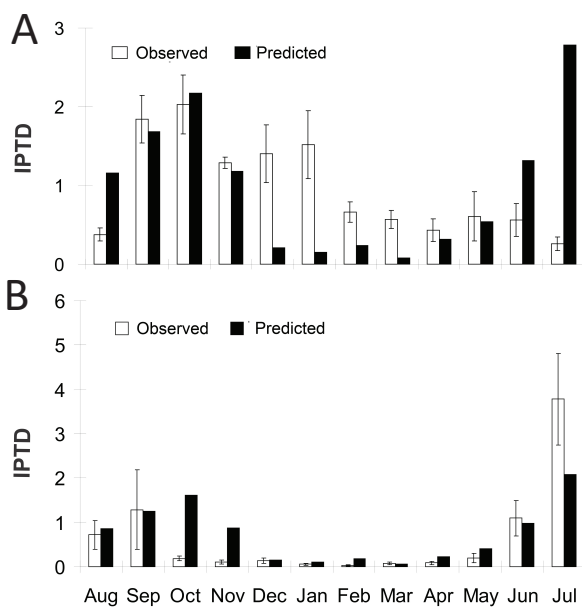


Fig. 5. Observed (mean \pm SE) and predicted (based on precipitation) distribution of the number of adult individuals captured (IPTD): (A) *O. martensii* and *L. dabanus*; (B) 11 other terrestrial species found in traps (*C. guttulata*, *K. pulchra*, *Ka. Interlineatus*, *M. berdmorei*, *M. butleri*, *M. fissipes*, *M. heymonsi*, *Mi. erythropoda*, *F. limnocharis*, *H. rugulosus*).

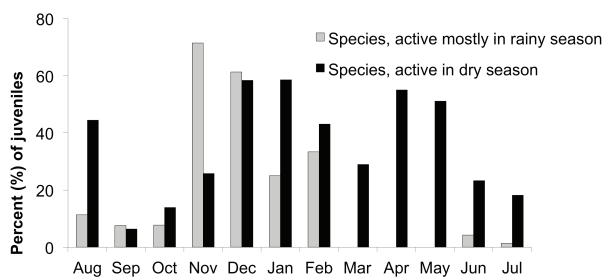


Fig. 6. Annual distribution of the ratio of juvenile individuals of species, active mostly during the dry season (*O. martensii* and *L. dabanus*; ad=789, juv=77) and the rainy season (*C. guttulata*, *K. pulchra*, *Ka. Interlineatus*, *M. berdmorei*, *M. butleri*, *M. fissipes*, *M. heymonsi*, *Mi. erythropoda*, *F. limnocharis*, *H. rugulosus*; ad=1058, juv=721).

with their observed occurrence in traps from April to May and from September to November (Fig. 5A). In June–August, rains were regular and abundant; however, the number of captures of these species was below the theoretical prediction. The number of captures of other species corresponded well with the predicted values for most of the year, namely from December to June and from August to September (Fig 5B). July was the month with the highest precipitation, and the number of catches was even higher than expected. The empirical number of catches decreased sharply in October–November, though rainfall was abundant during that period and frogs were expected to be active and common in the traps. A positive correlation was found between monthly precipitation and the number of adult individuals per trap over 12 months for species more common in traps during the rainy season ($r_s=0.786$; $p=0.024$). No such correlation was found for two species, which were more abundant in traps during the dry season (*O. martensii* and *Limnonectes dabanus*; $r_s=0.307$; $p=0.925$).

Annual age dynamics

The proportion of adult and juvenile frogs varied in traps between seasons. Juveniles of two species with high migratory activity during the dry season (*L. dabanus* and *O. martensii*) were observed throughout the year. The percentage of young frogs of these amphibians in traps fluctuated from 5% in September to 58% in January. Their ratio in traps fluctuated from 5% in September to 58% in January decreasing from January to March and increasing again from April to July (Fig. 6). The proportion of captured juveniles of other species, mostly active during the rainy season, increased explosively in November and December and reduced to almost zero in the late dry period (February and March). No juveniles of these species were found in traps until June (Fig. 6); however, juveniles of *Microhyla* spp., *C. guttulata*, *Ka. interlineatus*, *Hy. nigrovittata*, *L. dabanus* and *O. martensii* were observed active in the moist areas in January–March.

DISCUSSION

The influence of rainfall pattern on amphibian activity has been demonstrated for the forested regions of the Amazon basin (Aichinger, 1987), Peninsular Malaysia

(Shahriza et al., 2010), India (Kanamadi et al., 2002) and other tropical regions. Our data extend this observation to the lowland monsoon forests of southern Vietnam. However, great interspecies variation in activity patterns was observed. Based on the distribution of the pit-fall trap captures, four species, *O. martensii*, *L. dabanus* and, to a lesser degree, *M. fissipes* and *Ka. interlineatus*, were active more or less all year round. The movement activity of the first two species was poorly correlated with rainfall and even increased during the dry season. *M. fissipes* and *Ka. interlineatus* were more active during rainy months (Table 3; Fig. 4). In contrast, the catches of *C. guttulata*, *K. pulchra*, *M. erythropoda*, *M. butleri*, *M. berdmorei* and *M. heymonsii* were strictly seasonal and positively affected by rainfall (Table 3; Fig. 4). These frogs, along with *F. limnocharis*, *H. rugulosus* and *Hy. milleti*, according to observations on excursions, became common on the forest floor after the first rains in April–May, and their movement activity reached its maximum in July–August. In September–October, these species decreased their activity and moved on to aestivation in soil hollows and under logs and stones. Subterranean aestivation for *K. pulchra* and small microhylids was also noted by Berry (1964). Skeletochronological data from several Southeast Asian amphibians also suggest that some frogs are not active during the dry season (Khonsue et al., 2000; Lai et al., 2005; Andia et al., 2010). Thus, we suggest two ecological groups to exist in the monsoon forests of southern Vietnam: aestivating, such as *C. guttulata*, *Ka. pulchra*, *M. heymonsii* and *Mi. erythropoda*, and non-aestivating, such as *M. fissipes*, *K. interlineatus*, *O. martensii* and *L. dabanus*. However, it may also be possible to find some aestivators in moistened microhabitats (near swamps and streams) during the dry season. We observed such examples, though it seems that their terrestrial activity in this period reduces significantly. Aestivation is not an absolute tactic; the degree of aestivation depends on the precipitation pattern in a particular year and on microclimatic features of the habitat.

It has previously been shown that amphibians found in some Southeast Asian regions (Singapore and Thailand), which are also common in Vietnam (*D. melanostictus*, *P. leucomystax*, *M. heymonsii* and *F. limnocharis*), profit from favourable climate conditions suitable for year round breeding (Church, 1960; Berry, 1964; Heyer, 1973). According to Crump (1974), such species are considered continuous breeders. However, in other regions with a monsoon climate, the same species do not breed, and they decrease their vocal activity during the dry period (Zeller, 1960). We recorded single vocalisations of *L. dabanus* and *M. fissipes* and of the phytotelm-breeder *T. vietnamense* from January to March, though the peak of their vocalising activity fell in the rainy season. Juveniles of *L. dabanus* and *O. martensii* were found in traps throughout the year (Fig. 6); thus, we may expect these species to be continuous breeders in the studied area.

The terrestrial frogs *Mi. erythropoda*, *M. heymonsii*, *M. fissipes* and *F. limnocharis* were abundant and vocalised near temporary breeding ponds when the

precipitation level exceeded 40 mm per day. According to Crump (1974), these species are opportunistic breeders, reproducing in temporary ponds only after heavy rains. Mass movements of *C. guttulata*, *Ka. interlineatus* and *K. pulchra* were unpredictable even when strong rains (30–40 mm per day) occurred. Such species, which reproduce after heavy rains but not regularly, are considered sporadic breeders (Crump, 1974). The species *M. berdmorei* had two evident peaks of vocalising and reproductive activity: April–June and December–January.

The juvenile stage is one of the most mobile periods in the life of an amphibian due to dispersal necessity (Sinsch, 2014). Juveniles become vulnerable to excessive dehydration because of breeding pond desiccation; thus, they must leave ephemeral wetlands before the dry season arrives. Young frogs migrate from the natal patch in all directions (Sinsch, 2014), and therefore their dispersal activity in the forest can be revealed through trap captures and direct observations. According to our data, juveniles of sporadic breeders with a tendency to aestivation started to appear only in June and became more abundant in the late rainy season (November–December, Fig. 7), indicating the absence of reproduction during the dry period.

In general, the number of vocalising species in Asian tropical forests increases early in the rainy season (Hsu et al., 2006). In Taiwan, frogs living in conditions with a similar annual rainfall regime in CTNP (Fig. 3) demonstrate similar vocalisation patterns. Choral vocalisation of 14 species was mostly recorded after the first rains in March when precipitation reached 100 mm per month. The number of vocalising species decreased to 13 in April–August when precipitation increased to 650 mm (July) and then to seven species in September when rainfall suddenly decreased to <500 mm (Hsu et al., 2006). It was hypothesised that the aestivation period synchronises gonadal ripening in tropical anurans (Church, 1960) and drives them to start reproduction more or less simultaneously in the early rainy season (Inger & Greenberg, 1963; Inger & Stuebing, 1989) when a “larval bloom” is commonly observed (Blair, 1961). Thus, some portions of the population of each species start vocalisation and spawning just after the early strong rains in April. Early reproduction provides several benefits for anuran larvae, allowing them to avoid aquatic predators, such as dragonflies, beetle larvae and snakehead fish (*Channa* spp.), and to reduce interspecific competition among tadpoles (Heyer et al., 1975) and growth inhibition of the younger larvae by older tadpoles of other species (Licht, 1967; Griffiths & Denton, 1991). However, an early reproduction strategy is risky because of the high probability of temporary pond drying. The increase of vocalising activity in April and May (Fig. 3) and the observed clutches in the first temporary ponds indicated that some part of the population of each studied species preferred early but risky reproduction. However, the mass appearance of juvenile frogs on the limits of the rainy and dry seasons (Fig. 6) suggests that most individuals reproduce in the mid-rainy period when precipitation reached 300 mm per month and the number of stable pools suitable for breeding increased.

Although the maximum number of vocalising species occurred in the early rainy season, movement activity reached its maximum in the mid-rainy season when the number of temporary ponds increased. Searching for pools suitable for spawning could explain the increase in amphibian movement activity in June and July rather than in May.

Desiccation can be a problem for anurans even in a tropical forest (Thorson & Svihla, 1943). Frogs use leaf litter and small hollows in and under the logs and stones when they move through the forest. Leaf-fall in CTNP occurs mostly during the dry season when leaves of *Lagerstroemia* spp., *A. xylocarpa*, *T. nudiflora* and *Dipterocarpus* spp. accumulate on the forest floor (Anichkin & Tiunov, 2011). Leaf litter and soil become permanently moist after regular rains in late May–June (Anichkin & Tiunov, 2011). Hiding under moist leaves allows small anurans to move without suffering from desiccation (Wells, 2007). Moreover, the number and biomass of potential prey, such as relatively large invertebrates (Oligochaeta, Isopoda, Cryptopidae, Geophilidae, Lithobiidae, Diplopoda, Diptera and Staphylinidae) increases rapidly during the same period (Anichkin, 2011). A positive correlation between the number of invertebrate leaf litter decomposers and leaf litter biomass was also demonstrated for neotropical lowland tropical forests (Scott, 1976; McGlynn et al., 2009). Thus, we suggest that moist leaf litter, a large number of temporal water bodies and the increasing diversity and biomass of invertebrates together provide the most favourable conditions for terrestrial amphibians in the mid-rainy season.

We found that the movement activity of aestivating species throughout the year was mostly correlated with annual precipitation. However, this correlation did not hold in the late rainy season (September and October) when rainfall was still strong. The terrestrial activity of these species fell dramatically (Fig. 5B), suggesting some changes in the environment indicating the approach of the dry season. However, daylight duration, temperature and precipitation did not differ significantly between September and October. According to our observations, the abrupt reduction in the amphibian activity happened in October, before the actual rainy period finished; this activity changes coincide with a decrease of leaf-litter mass and decomposer biomass described for the study area in the previous years (Anichkin & Tiunov, 2011). The link between leaf litter invertebrate biomass and amphibian population density is well documented (Whitefield et al., 2014). Species diversity is also greater in thick leaf litter (Lieberman, 1986). In our case, it is likely that leaf litter depth and/or invertebrate biomass influenced frog activity.

The frog species *O. martensii* and *L. dabanus* were commonly observed breeding in water bodies during the rainy season. However, their movement activity was much lower than expected (Fig. 5A) and was not correlated with precipitation. The movement activity of these two species increased in the late rainy period and became even higher than was predicted. The large number of captures during the dry period may be explained by desiccation avoidance behaviour, when

these particular species are searching for water bodies or moist areas.

In conclusion, the annual variation of amphibian activity described here corroborates with other studies in regions with similar monsoon climates. An increase in terrestrial movement and reproductive activity during the rainy period in a lowland forest in southern Vietnam was observed. However, it was noticed that some amphibian species reduce their activity long before the onset of the dry season. Factors that drive such behaviour are poorly studied, although amphibian activity patterns within a year were highly correlated with annual patterns of other forest system components, such as invertebrate biomass. Future ecological studies of anuran species are required to understand the interactions between seasonal activity of amphibians and the different components of the tropical forest ecosystem.

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