SALAMANDRA	45	1	25-38	Rheinbach, 20 February 2009	ISSN 0036-3375

A Bornean amphibian hotspot: the lowland mixed dipterocarp rainforest at Ulu Temburong National Park, Brunei Darussalam

T. Ulmar Grafe & Alexander Keller

Abstract. We investigated the amphibian species richness within the Ulu Temburong National Park, Brunei Darussalam. Standardized visual and acoustic transect sampling and encounter surveys were conducted from April 2005 – October 2006. We identified a total of 54 amphibian species, 53 frogs and 1 caecilian. 15 species were new records for the park while 12 were new records for Brunei Darussalam. This brings the total number of amphibian species in Ulu Temburong to 66 species. Robust abundance measures are provided for 42 of the 66 species. Two-thirds of the regional, lowland and hilly forest frog diversity of Borneo was found within 25 km² of the Ulu Temburong National Park. This is a remarkable percentage, suggesting that this site deserves high conservation priority. High species richness is likely to result from the high diversity of breeding habitats and the confluence of the regional faunas of two biogeographical units in Borneo: East Sarawak and the hilly heart of Borneo.

Key words. Brunei Darussalam, Borneo, rainforest, amphibians, species richness, abundance.

Introduction

Extensive sampling of the amphibian fauna of northern Borneo has largely been restricted to the Malaysian states of Sarawak and Sabah (Inger & Tan 1996, Malkmus et al. 2002, Inger & Stuebing 2005). In contrast, less work has been conducted in the small sultanate of Brunei despite its success in preserving large tracts of its forest in pristine condition. As part of an ongoing study of the community ecology of stream breeding frogs, we carried out extensive visual and acoustic transect sampling and encounter surveys in both riparian and non-riparian habitats within the Ulu Temburong National Park (UTNP), in the Temburong district of Brunei Darussalam (Figure 1). The UTNP lies in the transitional zone of two biogeographical units of Borneo: Eastern Sarawak/Brunei and the central mountain ranges of Borneo (Auliya 2006). Therefore, this area is likely to harbour faunal elements typical of both regions and thus show an exceptionally high richness of amphibian species.

Das (1995) conducted detailed amphibian and reptile surveys within the UTNP (previously known as the Batu Apoi Forest Reserve) reporting 50 species of amphibians. In this study, we update and substantially expand the amphibian species list for the UTNP. In addition, we provide estimates of the relative species abundance of the anuran stream communities. The aim of this species inventory and abundance estimates is to further fill the gaps in distribution patterns of Bornean frogs that are essential for evaluating a species' range and conservation status. We also discuss the importance of the UTNP in conserving Bornean frogs.

Materials and methods

Ulu Temburong is the largest national park in Brunei Darussalam with a protected area of 50,000 hectares of lowland mixed dipterocarp rainforest. We studied the amphibian fauna within 25 km² near the Kuala Belalong Field Studies Centre (KBFSC) at 115°09'E,

Fig. 1. Lowland mixed dipterocarp rainforest of the Ulu Temburong National Park, Brunei Darussalam.

4°33'N and about 50-200 m above sea level. Annual rainfall at the site ranges between 2500-4000 mm (Das 1995).

Standardized visual and acoustic transect sampling and encounter surveys were conducted from April 2005 - October 2006 covering most of the months in this period. Intensive sampling was performed from June - October 2006 in both riparian and non-riparian habitats. Ten independent stream transects were surveyed and species richness and relative abundance recorded. Small to medium sized streams were selected and five plots of 5x10 m set-up within each stream (Figure 2; Keller & Grafe in press). We

Fig. 2. Representative examples of a small (a) and a medium (b) sized stream at which surveys of anuran communities were carried out.

conducted systematic visual and acoustic encounter surveys of these plots by carefully searching the ground and vegetation up to

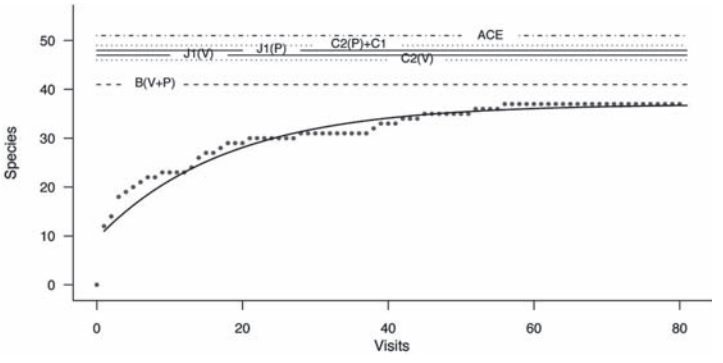


Fig. 3. Species accumulation curve fitted on the cumulative number of species found during visits of riparian plots. Diversity estimators are drawn as lines. Incidence based diversity estimators are C2 = Chao 2, J1 = Jacknife 1, and B = Bootstrap. Abundance based estimators are C1 = Chao 1 and ACE = abundance-based coverage estimator. V = by visits and P = by plots.

Tab. 1. Amphibian species recorded from the Ulu Temburong National Park.
Species names follow Frost (2004) with changes in classification after Frost et al. (2006) in parenthesis: S = changes in genus and species names and F = changes in family memberships. [1] Populations on Borneo formerly referred to as *S. natator* (Iskandar & Colijn 2000). Data source (P = encountered in plots, N = encountered outside of plots in the UTNP and L = literature). Country codes of known species distribution: 1 = First records for Brunei Darussalam (UBD Catalog Number), BD = Bangladesh, BN = Brunei Darussalam, CN = China, ID = Indonesia, IN = India, KH = Cambodia, LA = Lao People's Democratic Republic, MM = Myanmar, MY = Malaysia, NP = Nepal, PH = Philippines, SG = Singapore, TH = Thailand and VN = Vietnam. Species listed as not identified and with first records for Brunei were new species for science. Species listed as not identified, but not marked as first records were not identifiable. Conservation status follows the Global Amphibian Assessment (2007) listings of IUCN red list categories (LC = Least Concern, NT = Near Threatened, VU = Vulnerable, EN = Endangered, DD = data deficient). Further information was based on plot visits: Total abundance (sum of individuals) encountered at stream transects only. Rank abundance (highest = 1) of species encountered at stream transects only.

Species	Data source	Country code	Conservation status	Total abundance at streams	Rank abundance at streams
Ichthyophiidae					
Caudacaecilia nigroflava	P	BN, MY	DD	2	28
Bufonidae					
Ansonia sp.	P	1 (GK06-068)	–	1	33
Ansonia albomaculata	P	BN, ID, MY	NT	56	6
Ansonia leptopus	P	BN, ID, MY	NT	18	17
Ansonia longidigita	P	BN, ID, MY	NT	44	9
Ansonia platysoma	P	1 (GK06-066), MY	EN	5	26
Bufo asper (S: *Phrynoidis aspera*)	P	BN, ID, MM, MY, TH	LC	1	33
Bufo divergens (S: *Ingerophrynus divergens*)	P	BN, ID, MY	LC	1	33
Bufo juxtasper (S: *Phrynoidis juxtaspera*)	P	BN, ID, MY	LC	25	13
Pedostibes hosii	P	BN, ID, MY, TH	LC	2	28
Pedostibes rugosus	N	BN, ID, MY	NT	0	–
Pelophryne signata	N	BN, MY	NT	0	–
Megophryidae					
Leptobrachella mjobergi	P	BN, ID, MY	LC	287	3
Leptobrachella parva	P	1 (GK06-027, 060), ID, MY	NT	231	4
Leptobrachium abbotti	N	BN, ID, MY	LC	0	–
Leptobrachium montanum	P	BN, ID, MY	LC	22	15.5
Leptolalax dringi	P	1 (GK06-038-042), ID, MY	NT	41	9
Leptolalax gracilis	P	BN, ID, MY	NT	12	22
Leptolalax pictus	N	1 (GK06-035), ID, MY	VU	0	–
Megophrys edwardinae	L	BN, MY	VU	0	–
Megophrys nasuta	P	BN, ID, MY, SG, TH	LC	26	12

Species	Data source	Country code	Conservation status	Total abundance at streams	Rank abundance at streams
Microhylidae					
Chaperina fusca	P	ID, MY, PH, TH	LC	7	24.5
Kalophrynus intermedius	N	BN, ID, MY	VU	0	–
Kalophrynus pleurostigma	N	BN, ID, MY, PH, SG, TH	LC	0	–
Kalophrynus subterrestris	N	1 (GK06-034), ID, MY	NT	0	–
Metaphrynella sundana	N	BN, ID, MY	LC	0	–
Microhyla borneensis	N	BN, ID, MY, SG, TH	LC	0	–
Microhyla petrigena	N	BN, ID, MY, PH	NT	0	–
Ranidae					
Ingerana baluensis (F: Ceratobatrachidae)	P	BN, ID, MY	LC	38	11
Ingerana sp. (F: Ceratobatrachidae)	P	1 (GK06-047, 048, 051-053)	–	23	14
Limnonectes ibanorum (F: Dicroglossidae)	L	BN, ID, MY	NT	0	–
Limnonectes ingeri (F: Dicroglossidae)	P	BN, ID, MY	NT	1	33
Limnonectes kuhlii (F: Dicroglossidae)	P	BN, CN, ID, IN, LA, MM, MY, TH, VN	LC	463	1
Limnonectes laticeps (F: Dicroglossidae)	L	BN, ID, IN, MM, MY, TH	LC	0	–
Limnonectes leporinus (F: Dicroglossidae)	P	BN, ID, MY	LC	11	23
Limnonectes palavanensis (F: Dicroglossidae)	P	BN, ID, MY, PH	LC	2	28
Limnonectes paramacrodon (F: Dicroglossidae)	P	BN, ID, MY, SG, TH	NT	1	33
Meristogenys jerboa	P	1, MY	VU	7	24.5
Meristogenys orphnocnemis	L	BN, ID, MY	LC	0	–
Meristogenys poecilus	P	BN, ID, MY	NT	16	18.5
Occidozyga baluensis (F: Dicroglossidae)	N	BN, ID, MY	NT	0	–
Occidozyga laevis (F: Dicroglossidae)	N	BN, ID, MY, PH, SG, TH	LC	0	–
Rana erythraea (S: *Hylarana erythraea*)	L	BN, ID, KH, LA, MM, MY, SG, TH, VN	LC	0	–
Rana hosii	N	BN, ID, MY, TH	LC	0	–
Rana picturata (S: *Pulchrana picturata*)	P	BN, ID, MY	LC	22	15.5
Rana raniceps (S: *Hydrophylax raniceps*)	P	BN, ID, IN, MY, SG, TH	LC	14	21
Rana signata (S: *Pulchrana signata*)	P	BN, ID, MY, TH	LC	49	7
Staurois latopalmatus	P	BN, ID, MY	LC	16	18.5

Species	Data source	Country code	Conservation status	Total abundance at streams	Rank abundance at streams
Staurois guttatus[1]	P	BN, ID, MY, PH	LC	143	5
Staurois tuberilinguis	P	BN, ID, MY	NT	301	2
Rhacophoridae					
Nyctixalus pictus	L	BN, ID, MY, PH, SG, TH	NT	0	–
Philautus hosii	P	1 (GK06-055, 056, 059), ID, MY	NT	1	33
Philautus tectus	P	BN, MY	VU	15	20
Philautus sp.	P	1 (GK06-071-074)	–	1	33
Polypedates leucomystax	N	BD, BN, CN, ID, IN, KH, LA, MM, MY, NP, PH, SG, TH, VN	LC	0	–
Polypedates macrotis	N	BN, ID, MY, PH, TH	LC	0	–
Polypedates otilophus	N	BN, ID, MY	LC	0	–
Rhacophorus belalongensis	P	1 (ZMB 70377-70379)	–	45	8
Rhacophorus cyanopunctatus	N	1 (GK06-013), ID, MY, SG, TH, VN	LC	0	–
Rhacophorus dulitensis	L	BN, ID, MY	NT	0	–
Rhacophorus fasciatus	L	BN, ID, MY	VU	0	–
Rhacophorus harrissoni	L	BN, ID, MY	NT	0	–
Rhacophorus kajau	L	BN, ID, MY	NT	0	–
Rhacophorus nigropalmatus	L	BN, ID, MY, TH	LC	0	–
Rhacophorus pardalis	N	BN, ID, MY, PH	LC	0	–
Rhacophorus rufipes	N	1 (GK06-008), ID, MY	NT	0	–
Theloderma sp.	L	-	–	0	–

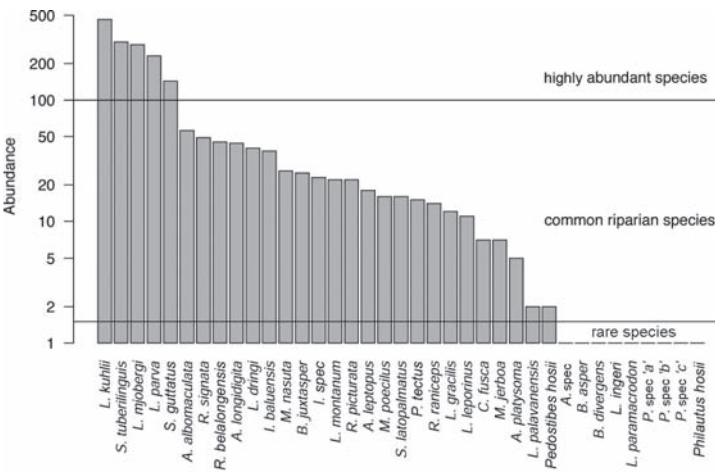


Fig. 4. Rank abundance of species found within all riparian plots (log-scaled).

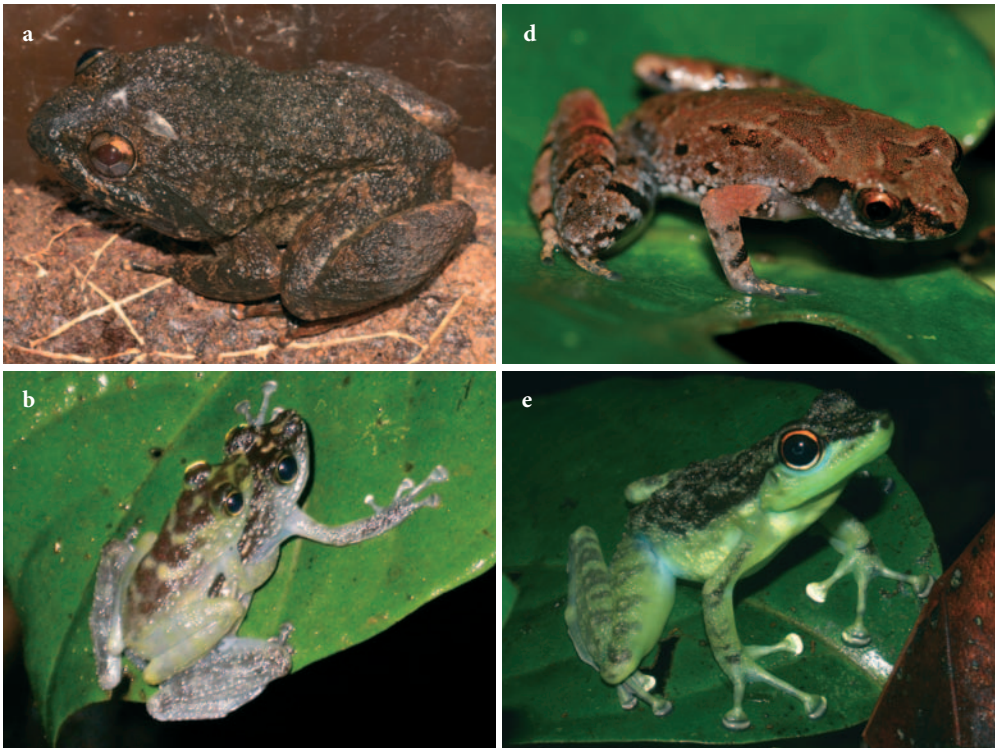


Fig. 5. The five most abundant species encountered within riparian plots. (a) *Limnonectes kuhlii*, (b) *Staurois tuberilinguis*, (c) *Leptobrachella mjobergi*, (d) *Leptobrachella parva*, and (e) *Staurois guttatus*.

right page: Fig. 6. Common riparian species sorted by relative abundance within riparian plots. (a) *Ansonia albomaculata*, (b) *Rana signata*, (c) *Rhacophorus belalongensis*, (d) *Ansonia longidigita*, (e) *Leptolalax dringi*, (f) *Ingerana baluensis*, (g) *Megophrys nasuta*, (h) *Bufo juxtasper*, (i)-(t) see pp. 34-35.

3 m for amphibians on eight occasions. The mean time spent within each plot searching for frogs was 20 minutes (± 3 min).

In addition, two independent non-riparian leaf-litter transects were sampled on 14 occasions using the same methods as for the riparian sites. To attract leaf-litter frogs and arboreal frogs, 20 plastic containers filled with river water were placed along each of two 50 m transects. Finally, one artificial permanent water body at KBFSC was monitored on a regular basis and provided several repeated records of arboreal species that came here to breed. These methods were complemented by chance sampling of both riparian and non-riparian, leaf litter habitats. In general, sampling was restricted to within 3 m from the ground and took place at night between 18.30-01.00.

Robust abundance estimates were obtained during surveys of riparian transects by marking frogs individually by toe clip-


a
b
c
d
e
f
g
h

ping. For all habitats surveyed, the relative abundance of species was estimated from the number of sites at which each species was encountered. For riparian sites, we categorized species as highly abundant, abundant, or rare depending on if they were encountered in all 10 transects, in 2-9 transects or in only one transect, respectively. Species from non-riparian sites were categorized similarly. The abundances of eight species encountered independently from these transects were not estimated and were classified as data deficient (*Caudacaecilia nigroflava, Pelophryne signata, Microhyla borneensis, Leptobrachium abbotti, Kalophrynus subterrestris, K. intermedius, Occidozyga balunesis, O. laevis* and *Rhacophorus cyanopunctatus*).

We used the open access statistical software R (R Development Core Team 2006) to analyse our data.

Results

In total, we recorded 54 species of amphibians within 25 km² of the UTNP (Table 1). A further 12 species were recorded by previous surveys of that area (Das 1995) and revisions thereof (Das 2007, I. Das pers. communication) bringing the total number of amphibians in the Ulu Temburong National Park to 66 (Table 1). Of the 54 species we found, 12 were new records for Brunei, with one new rhacophorid frog recently described as *Rhacophorus belalongensis* (Dehling & Grafe 2008). In addition, we regularly encountered individuals of a second *Ingerana* species for Borneo that needs to be described. Finally, we found five individuals that we could not assign to known species and therefore are not listed as new records (one *Ansonia* and four *Philautus* individuals).

We found 37 frog species within the plots of the stream sites and 12 species within the non-riparian leaf-litter or ponds. Pooling data from all ten streams visited, the species accumulation curve leveled off and reached a plateau after 80 surveys (Figure 3), suggesting that most species of the riparian anuran community within the UTNP have now been detected. Figure 4 shows the rank abundance for each species. Five species were found in high abundance (*Limnonectes kuhlii*, *Staurois tuberilinguis, S. guttatus, Leptobrachella mjobergi*, and *L. parva;* Figure 5a-e). 23 species had intermediate abundances (Figure 6a-t). Nine species were found only once within the plots and were considered rare. In contrast to riparian sites, the species accumulation curve for leaf-litter anurans did not level off after 12 surveys, suggesting that additional species are likely to be found in this habitat. Five anuran species were attracted to the artificial ponds (*Chaperina fusca*, *Kalophrynus pleurostigma*, *Microhyla petrigena*, *Polypedates macrotis*, and *Rhacophorus rufipes*).

The relative abundance of species across all habitats surveyed (both riparian and leaf litter) could be estimated for 42 out of the 66 species, based on the frequency of occurrences along our transects (Figure 7). Seven species were highly abundant occurring on all transects in high abundance. Rare species, those encountered only once, made up 44 % of all species for which sufficient data was available. The majority of all species (65 %) were either rare or their abundances hard to determine, because they were encountered only outside of our transects or not encountered at all by us (Table 1).

Discussion

We identified a total of 54 amphibian species, 53 frogs and 1 caecilian in a restricted area of the UTNP. 15 species were new records for the park while 12 species were new for Brunei Darussalam. Das (1995, 2007) lists 12 additional frog species for the park. This brings the total number of identified amphibian species in Ulu Temburong to 66 species.

Out of the 148 frog species listed by Inger & Stuebing (2005) as occurring in Borneo, 33 are montane species found only above 900 m. Others such as *Fejervarya cancrivora*, *Rana*

baramica, or *Kaloula pulchra* are specialized mangrove denizens, inhabit peat swamps or are synanthropic species. We conservatively estimate 10 species in these latter categories. Out of the remaining 105 species, 66 frogs are found in Ulu Temburong or 62 % of the frog fauna of Bornean lowland and hilly forests. In other words, nearly two-thirds of the regional, lowland and hilly forest frog diversity is found within 25 km² of the UTNP.

The rich elevational profile of our study site is likely to explain, in part, the high species richness when compared to other lowland rainforest sites in Borneo with less steep terrain. In addition to species found in leaf litter and those known to breed in streams with slow currents and silty substrates, Ulu Temburong harbors species that breed in torrential streams. Comparable sites with similar topography, such as Nanga Tekalit and Segaham in Sarawak, however, have lower species richness than Ulu Temburong (60 and 47 species, respectively; Inger 2004). The species richness of Ulu Temburong is exceptionally high given the lack of distinct elevational zonation as found in Gunung Mulu (90 species; Malkmus 2002, I. Das personal communication, J.M. Dehling personal communication), Mt. Kinabalu (77 species; Malkmus et al. 2002), or Crocker Range National Park (59 species; Das 2006) and the limited spatial scope of surveys conducted within the UTNP.

We suggest that the high species richness found in the UTNP is likely to be the result of both the rich topography and the fact that it constitutes a transitional zone of two biogeographical units in Borneo: East Sarawak and the hilly heart of Borneo (Auliya 2006). Under this scenario, the UTNP may be regarded as a connecting link between these areas that favours faunal exchange between lowland adapted forms and those that need swift, torrential streams and rivers to breed but occur below 900 m.

High anuran diversities within transitional zones have also been found in the Neotropics and Madagascar (Duellman 1988; Fauth et al. 1989; Ramanamanjato et al. 2002). Investigations of other taxa such as plants (Gottfried et al. 1998; Hamann et al. 1999), reptiles (Ramanamanjato et al. 2002) and mammals (Gelderblom & Bronner 1995; Ramanamanjato et al. 2002) show similar results. Transition zones of large geographic areas, which strongly differ in their physical characteristics, often host communities that include species from both neighboring areas (Ramanamanjato et al. 2002). This may result in higher species diversity than within the adjacent regions.

Three of the species we encountered are usually reported from elevations above 900 m a.s.l. and are therefore classified as montane species (Malkmus et al. 2002). These were *Ingerana baluensis*, *Leptobrachium montanum*, and *Leptolalax pictus*. Our study suggests that these species are not restricted to montane regions. Typical characteristics of montane regions such as mist-generated humidity (Giaretta et al. 1999) were generally lacking. Thus, habitats and microclimates found exclusively at higher elevations are not necessary determinants of these species distributions.

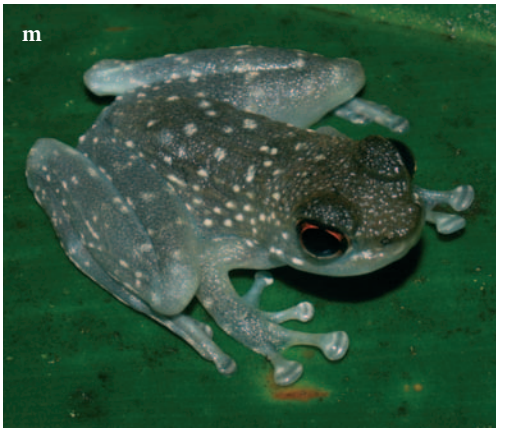
An additional factor that is likely to explain the high anuran species richness in the UTNP is the high diversity of breeding sites available. Duellman (1988) argues that the lowland rainforests near the base of the Andes and near the Brazilian Highlands are more diverse in anurans than other Central American and South American regions. He concludes that for amphibians this pattern is not only a reflection of the historical biogeography of the taxa, but also of reproductive modes. Transition zones show a high diversity of breeding habitats: hilly submontane rainforests are adequate for breeders of lentic (ponds), terrestrial (high moisture content in the air), aerial aquatic (phytotelmata) and torrential stream habitats (steep terrain). The UTNP shows a high abundance of these breeding habitats and thus satisfies the reproductive requirements of a large section of the Bornean anuran fauna.


i


j


k


l


m


n

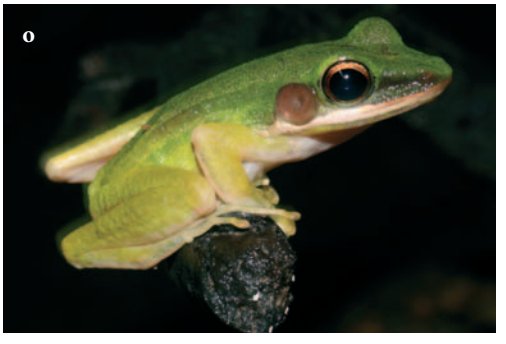

o

Fig. 6. Common riparian species sorted by relative abundance within riparian plots. (a)-(h) see p. 31, (i) *Leptobrachium montanum*, (j) *Rana picturata*, (k) *Ansonia leptopus*, (l) *Meristogenys poecilus*, (m) *Staurois latopalmatus*, (n) *Philautus tectus*, (o) *Rana raniceps*, (p) *Limnonectes leporinus* (large male and small female in nest), (q) *Chaperina fusca*, (r) *Meristogenys jerboa*, (s) *Limnonectes palavanensis*, and (t) *Pedostibes hosii* (female).

The species accumulation curve for the riparian transects suggests that the inventory of anurans found at such sites is largely complete within the northern parts of the UTNP and we suggest that the data can be used as a basis for comparisons between tropical lowland rain forests and can serve as a base-line for evaluating to what degree logging and silvicultural practices alter species diversity.

Our measure of abundance for riparian anurans suggests that there are a few highly abundant species and many more rare species. The same seems to be the case for non-riparian anuran communities within the UTNP. This follows the general trend found among many tropical taxa (May 1975). There was a high number of species for which not enough data was available to make an assessment, especially among fossorial and arboreal frogs. In fact, given this data set, none of

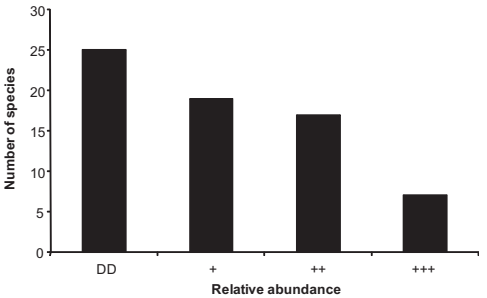


Fig. 7. Relative abundance of anurans found in the Ulu Temburong National Park as estimated from pooled surveys of both stream and leaf-litter transects. DD = data deficient. For riparian transects: + indicates species found only on a single transect, ++ indicates species found in 2 - 9 transects, and +++ indicates species found on all 10 transects in high abundance. For leaf litter transects with artificial ponds: + indicates species found on one transect only, i.e. encountered only once, ++ indicates species found on both transects, and +++ indicates species found on both transects in high numbers.

the arboreal frogs can be regarded as highly abundant. The lack of quantitative abundance data for arboreal frogs suggests that there is a great need to develop methods to access the vegetation above three meters from the ground.

Of the 66 amphibians recorded for the UTNP, 62% are endemic for Borneo. According to the Global Amphibian Assessment (GAA 2007) one species (*Ansonia platysoma)* is listed as critically endangered and seven species are listed as vulnerable (*Leptobrachella parva, Leptolalax pictus, Megophrys edwardinae, Kalophrynus intermedius, Meristogenys jerboa, Philautus tectus and Rhacophorus fasciatus*). Thus, in addition to the high species richness, the occurrence of endangered and vulnerable species emphasizes the importance of the UTNP for the conservation of Borneo's amphibian fauna.

We document 12 additional species for Brunei Darussalam. Six of these (*A. platysoma, L. parva, K. subterrestris, P. hosii, R. cyanopunctatus and R. rufipes*) fill in gaps of disjunct distribution patterns. Three species have extended ranges, minor westward range extensions into Brunei for two species (*Leptolalax dringi and L. pictus*) and a substantial northeastern range extension for *M. jerboa* that previously has been found only in western Sarawak (www.globalamphibians.org). The latter may be surprising at first, however, other species in the region, such as *Rhacophorus rufipes*, show similar disjunct distribution patterns. Of the remaining three species, one remains to be identified (*Philautus* sp.) while two are new species (*Ingerana* sp. nov. and *Rhacophorus belalongensis*).

In addition to documenting the range extensions of anurans in northern Borneo, the results of this study suggest that even in well studied sites such as the UTNP the species richness can be underestimated. Some species may go unrecorded because of their small size, insect-like voices and secretive habits. For example, the tiny *Leptobrachella parva*, not recorded at UTNP previously, is in fact the fourth most abundant frog in riparian habitat. Thus, substantial inventory work is still needed to further reduce the large gaps in distribution data of the amphibian fauna of Borneo, despite extensive sampling (Inger & Voris 2001). Furthermore, we also see the need for evaluating the functional roles of each species within the habitats sampled. Measures of functional diversity will be crucial for estimating the degree and impact of community disassembly after fragmentation (Ernst et al. 2006; Keller 2007).

Acknowledgements

This study would have been impossible without the logistic support by the staff of the Kuala Belalong Field Studies Centre (KBFSC), its director Kamariah Abu Salim, the station supervisors Md. Salleh Abd. Bat and Rodzay Abd. Wahab and the cook Sucipto Wasid Alm. We also thank the boatmen Razit Anak Sapoh, Ramlah Anak Sapoh, and Samsida Hj. Momin who skillfully maneuvered through treacherous currents to take us to designated streams: Terima kasih. We also thank Jan Beck, Thiemo Braasch, J. Maximilian Dehling, Rosli Kasah, Sebastian Proksch

and Matthias Siegle for their assistance in the field. We much appreciate the help provided by Indraneil Das in verifying several species that were new records. J. Maximilian Dehling and Alexander Haas made valuable comments on the manuscript. TUG received financial support from a University Brunei Darussalam Research Grant (UBD/PNC2/2/RG/1(58)). AK acknowledges the support of the German Academic Exchange Service (DAAD).

References

Auliya, M. A. (2006): Taxonomy, life history and conservation of giant reptiles in West Kalimantan. – Natur und Tier Verlag, Münster. 432 pp.

Das, I. (1995): Amphibians and reptiles recorded at Batu Apoi, a lowland dipterocarp forest in Brunei Darussalam. – Raffles Bulletin of Zoology, **43**: 157-180.

Das, I. (2006): Crocker range national Park, Sabah, as a refuge for Borneo's montane herpetofauna. – Amphibian and Reptile Conservation, **4**: 3-11.

Das, I. (2007): Amphibians and reptiles of Brunei. – Natural History Publications, Kota Kinabalu. pp. 200.

Dehling, J. M. & T. U. Grafe (2008): A new treefrog of the genus *Rhacophorus* (Anura: Rhacophoridae) from Brunei Darussalam (Borneo) – Salamandra, 44**(2):** 101-112.

Duellman, W. E. (1988): Patterns of species diversity in anuran amphibians in the American tropics. – Annals of the Missouri Botanical Garden, **75**: 79-104.

Ernst, R., K. E. Linsenmair & M.-O. Rödel (2006): Diversity erosion beyond the species level: Dramatic loss of functional diversity after selective logging in two tropical amphibian communities. – Biological Conservation, **133**: 143-155.

Fauth, J. E., B. I. Crother & J. B. Slowinski (1989): Elevational patterns of species richness, evenness, and abundance of the Costa Rican leaf-litter herpetofauna. – Biotropica, **21**: 178-185.

Frost, D. R. (2004): Amphibian species of the world: an online reference. Version 5.0 (1 February, 2007). http://research.amnh.org/herpetology/amphibia/index.php.

Frost, D. R., T. Grant, J. Faivovich, R. Bain, A. Haas, C. F. B. Haddad, R. O. de Sa, S. C. Donnellan, C. J. Raxworthy, M. Wilkinson, A. Channing, J. A. Campbell, B. L. Blotto, P. Moler, R. C. Drewes, R. A. Nussbaum, J. D. Lynch, D. Green & W. C. Wheeler (2006): The amphibian tree of life. – Bulletin of the American Museum of Natural History, **297**: 1-219.

GAA (2007): Global Amphibian Assessment, http://www.globalamphibians.org.

Gelderblom, C. & G. Bronner (1995): Patterns of distribution and protection status of the endemic mammals in South Africa. – South African Journal of Zoology, **30**: 127-135.

Giaretta, A. A., K. G. Facure, R. J. Sawaya, J. K. De. M. Meyer & N. Chemin (1999): Diversity and abundance of litter frogs in a montane forest of southeastern Brazil: Seasonal and altitudinal changes. – Biotropica, **31**: 669-674.

Gottfried, M., H. Pauli & G. Grabherr (1998): Predictions of vegetation patterns at the limits of plant life: a new view of the alpine-nival ecotone. – Arctic and Alpine Research, **30**: 207-221.

Hamann, A., E. B. Barbon, E. Curio & D. A. Madulid (1999): A botanical inventory of a submontane tropical rainforest on Negros Island, Philippines. – Biodiversity and Conservation, **8**: 1017-1031.

Inger, R. F. (2004): Sampling biodiversity in Bornean frogs. – The Natural History Journal of Chulalongkorn University, **3**: 9-15.

Inger, R. F. & F. L. Tan (1996): Checklist of the frogs of Borneo. – Raffles Bulletin of Zoology, **44**: 551-574.

Inger, R. F. & R. B. Stuebing (2005): A field guide to the frogs of Borneo. – Natural History Publications, Kota Kinabalu. 201 pp.

Inger, R. F. & H. K. Voris (2001): The biogeographical relations of the frogs and snakes of Sundaland. – Journal of Biogeography, **28**: 863-891.

Iskandar, D. T. & E. Colijn (2000): Preliminary Checklist of Southeast Asian and New Guinean amphibians. – Treubia, **31** (suppl.), 1-134.

IUCN, Conservation International, and NatureServe. (2006): Global Amphibian Assessment. – http://www.globalamphibians.org. Accessed on 11 December 2006.

Keller, A. (2007): Bornean frogs: What influences riparian communities in a lowland dipterocarp forest? – MSc Thesis. University of Würzburg, Germany.

Keller, A., M.-O. Rödel, M.-O., K. E. Linsenmair & T. U. Grafe (in press): The importance of environmental heterogeneity for species diversity and assemblage structure in Bornean stream frogs. – Journal of Animal Ecology.

Malkmus, R. (2002): Die Amphibien des Mulu-Nationalparkes in Sarawak/Malaysia. – Natur und Museum, **132**: 93-105.

Malkmus, R., Manthey, U., Vogel, G., Hoffmann, P. & J. Kosuch (2002): Amphibians and reptiles of Mount Kinabalu (North Borneo). – Gantner Verlag, Ruggell. 424 pp.

May, R. M. (1975): Patterns of species abundance and diversity. – pp. 81-119 in Cody, M. L. & J. M. Diamond (eds.): Ecology and evolution of communities. – Harvard University Press, Cambridge.

Ramanamanjato, J.-B., P. B. Mcintyre & R. A. Nussbaum (2002): Reptile, amphibian and lemur diversity of the Maléalo Forest, a biogeographical transition zone in southeastern Madagascar. – Biodiversity and Conservation, **11**: 1791-1807.

R Development Core Team (2006): R: A language and environment for statistical computing. – R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org.

Manuscript received: 12 August 2007

Authors' addresses: T. Ulmar Grafe, Department of Biology, University Brunei Darussalam, Tungku Link, Gadong BE 1410, Brunei Darussalam. E-Mail: grafe@biozentrum.uni-wuerzburg.de; Alexander Keller, Department of Animal Ecology and Tropical Biology, University of Würzburg, Biozentrum, Am Hubland, D-97074 Würzburg, Germany.