

On the cutting edge – The anuran fauna of the Mabura Hill Forest Reserve, Central Guyana

RAFFAEL ERNST, MARK-OLIVER RÖDEL & DEOKIE ARJOON

Abstract. Data on herpetofaunal communities in Guyana are very limited. However, it is of utmost importance that existing information is made available for policy makers at an early stage in the process of developing and planning protected areas. The study presented here provides first time information and essential data on anuran diversity, composition and endemism of the Mabura Hill Forest Reserve. So far, 41 anuran species, belonging to eight families, were recorded between November 2002 and September 2004, including a number of rare, secretive or unusual species rarely recorded in field surveys and thus hardly represented in collections, as well as several taxa new to science or species of uncertain taxonomic status. Two species represent interesting range extensions and are new records for the country. The status of the anuran fauna is discussed with regard to faunas of comparable sites in the Guianan region of northern South America and with respect to general conservation issues. The exceptional taxonomic composition of the Mabura Hill assemblage emphasizes the high conservation relevance of the site.

Key Words. Amphibia; Anura; communities; conservation; diversity; Central Guyana; South America.

Introduction

The forests of the Guiana Shield, particularly those of the Co-operative Republic of Guyana, have had among the lowest deforestation rates of the world, with very little change over the past decades (LANLY 1982, LUNING 1987, BURGESS 1993, BRYANT et al. 1997). The study site at Mabura Hill is part of the Guianan Shield Frontier Forest (sensu BRYANT et al. 1997), one of the four remaining extensive pristine forested areas left in the world (Amazon, Congo, Papua New Guinea and Guiana Shield). Historically, pressures on natural resources in these forests have been relatively low (HADEN 1999, OJASTI 1996) and therefore, the Guianan Shield Frontier Forests represent one of the highest per capita forested areas in the world (CARTER & ROSAS 1997). However, rapid economic and social changes increase pressures on these relatively well-conserved forest ecosystems. Guyana is at a crossroads concerning decisions and trade-offs among utilization, conservation and preservation of its forests and thus substantial parts of the country's biodiversity.

Whereas the local phytodiversity has been covered extensively (e.g. Ek 1997), knowledge of the faunal diversity in general and the herpetofaunal diversity in particular is still very limited. Even basic biological and ecological data inevitable for sound conservation projects and urgently needed by policy makers at an early stage in the process of developing and planning protected areas are most often lacking. The amphibian fauna of the Guiana Shield region is moderately diverse but comprises a high number of endemic species. The Guyana Highlands have recently even been identified as a previously overlooked biodiversity hotspot on grounds of species richness and endemism (ORME et al. 2005, POSSINGHAM & WILSON 2005). The taxonomy of most groups is relatively well known (but compare note added in proof) and the different species are often tightly connected to certain species-specific types of habitats. Yet, reasonably good species inventories for Guyana are still scarce. So far surveys and collection expeditions either have focused on highland faunas (e.g. MACCULLOCH & LATHROP 2002, NOONAN &

BONETT 2003) or sites already regarded as high priority conservation areas, such as Iwokrama Forest (DONNELLY et al. 2005). Despite their potential importance, a number of smaller lowland forest sites, particularly in Central Guyana, have been largely neglected. In this study we provide first time information and essential data on amphibian diversity, community composition and endemism of the Mabura Hill Forest Reserve (MHFR), Central Guyana. In addition we comment on the status of species that are considered particularly rare or secretive or represent new country records and undescribed taxa. We also address their conservation status in the light of current threats imposed by selective logging. Detailed life-history and ecological data will be presented in a separate publication.

Study site

The Mabura Hill Forest Reserve is situated approximately 20 km south-east of the township of Mabura Hill, Central Guyana (5°13' N, 58°48' W, Fig. 1). It comprises an area of approximately 2000 ha of primary rain forest (see TER STEEGE et al. 1996) and is part of the Wappu compartment located within a 503,415 ha Timber Sales Agreement concession granted to Demerara Timbers Limited (DTL). The MHFR was established in late 1987 through a mutual agreement between Demerara Woods Limited (a predecessor of DTL) and the Forest Project Mabura Hill (a joint research project of the Universities of Guyana and Utrecht). It has been managed by the Research Unit, now Planning and Research Development Division, of the Guyana Forestry Commission, since January 2002. This area within the country's main forestry belt is part of a geological formation known as White Sands Plateau. It is gently undulating but occasionally penetrated by Laterite-covered dolerite dykes from the Pre-Cambrian Plateau, forming ridges and hills (TER STEEGE et al. 1996, VAN KEKEM et al. 1997). Soil types belong to one of two major groups, clayey Plinthosols on one hand and a group

of sandy and loamy soils of various types on the other hand (JETTEN 1994, VAN KEKEM et al. 1997). The climate in the area can be described as hot and humid with an annual mean daily average temperature of 27 °C and an average annual precipitation of 2,700 mm, respectively. Rainfall follows a bimodal pattern with maxima in May-July and in December (JETTEN 1994, TER STEEGE et al. 1996). The vegetation is classified as Evergreen Rain Forest (Mixed Forest, see Fig. 2) and Dry Evergreen Forest (TER STEEGE 1993, TER STEEGE et al. 1996). Major forest types present in the concession are represented within the reserve and forest types vary across soil types and drainage types (TER STEEGE 1993, JETTEN 1994, EK 1997). The acidic soils of the Mabura Hill region are poor in nutrients and thus typical of deeply weathered soils in the humid tropics (VAN KEKEM et al. 1997). A second site (Pibiri Reserve) located in the same general area (5°02' N, 58°38' W) has only briefly been investigated during several short visits. Detailed descriptions of particular sites surveyed at the MHFR are presented in Appendix 1.

Methods

Field data were acquired between November 2002 and September 2004 following the research routine established by RÖDEL & ERNST (2004). Quantitative faunistic data collection was carried out employing standardized visual transect sampling (SVTS) and standardized acoustic transect sampling (SATS). Sampling was performed both day and night and independent of prevailing weather conditions. A total of twelve rectangular transects was established (seven in primary forest, five in exploited forest, Fig. 1). The complete transect length of 600 m was subdivided in 25 m subunits (SUs; 24 SUs / transect). For brief site descriptions and GPS-coordinates see Appendix 1. A complete list of recorded species and their habitat associations is provided in Tab. 3 and Appendix 2. Forest types present within the study area

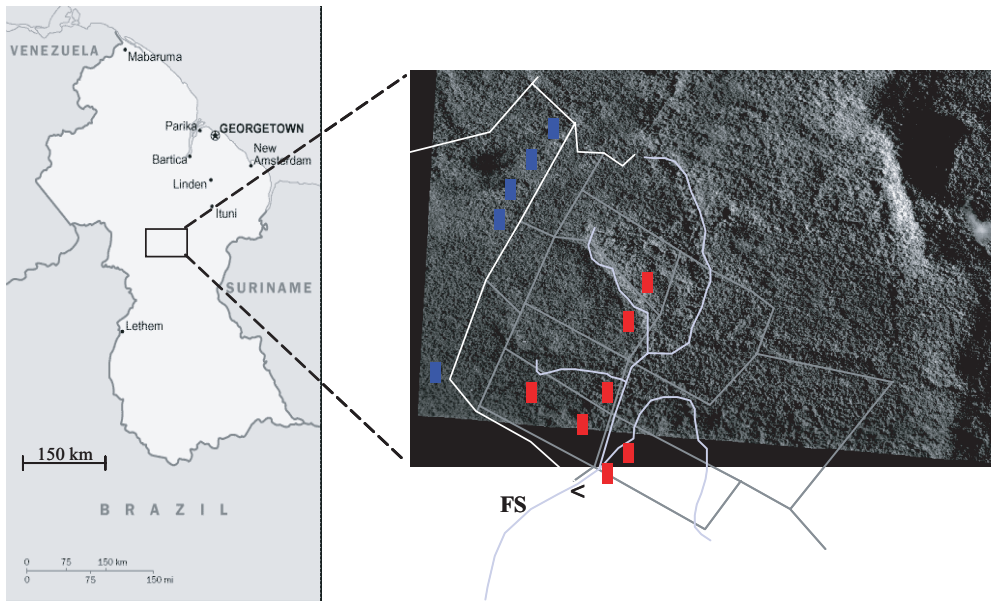


Fig. 1. Map of Guyana (left) with Mabura Hill area (box) and aerial photography of MHFR (right, not to scale) with location of transects (red rectangles = primary sites, blue rectangles = exploited sites), access road (white), trail system (dark grey), and creek drainage (light grey). FS = Field Station.

varied across soil types and drainage types (TER STEEGE et al. 1996, JETTEN 1994, EK 1997). Therefore, logging intensity differed between sites with regard to the presence of commercially valuable species. To circumvent this bias, transects covered all existing major forest types.

For a detailed description and discussion of the transect design, definition of habitat variables and data acquisition routine see RÖDEL & ERNST (2004). A total of 7,799 individuals of anurans belonging to 30 species were registered during 393.5 hours of transect sampling, equaling a total of 787 transect walks. In analyses, covering amphibian monitoring programs on transects in East Africa, West Africa, Madagascar and Borneo, VEITH et al. (2004) have recently shown that ≥ 20 independent transect walks seem to be necessary to achieve a species saturation. Every MHFR transect has been walked independently at least 65 times. It thus is justified to assume that the local species assemblages have been sufficiently sampled.



Fig. 2. Typical aspect of an evergreen rain forest (mixed forest), central Guyana.

Standardized transect sampling methods were supplemented by qualitative techniques, such as visual and acoustic encounter surveys (VES and AES), opportunistic sampling of major habitat types, as well as the installation of pitfall traps and drift fences (HEYER et al. 1994). These supplementary methods yielded additional records. Only qualitative methods have been employed

during investigations at Pibiri Reserve. Museum acronyms referred to in the text are as follows: AMNH = American Museum of Natural History, New York; USNM = National Museum of Natural History, Washington, D.C.

Results and Discussion

Sampling results

AES proved to be an important tool, especially for most arboreal species that vocalize frequently but are rarely encountered otherwise [e.g. *Osteocephalus oophagus* JUNGFER & SCHIESARI, 1995, *Phrynohyas resinifictrix* (GOELDI, 1907), *Hyalinobatrachium* spp.]. Yet, 39 amphibian species belonging to eight families were recorded employing VES, whereas AES only yielded 35 species, belonging to seven families. Among those, however, were two species not recorded during VES. SVTS and SATS together (transects) yielded 30 species belonging to six families. Seven species belonging to four families were recorded using pitfall traps and drift fences. One species, *Ctenophryne geayi* MOCQUARD, 1904, was exclusively recorded using this method (Fig. 3). SVTS and SATS are indispensable whenever quantitative data are needed. VES and AES are especially

useful for simple short term surveys. However, they do not yield adequate quantitative data. Due to their high level maintenance required, pitfall traps and drift fences can only be recommended if studies are not time constrained. They do not provide quantitative data for most anurans but may be useful for recording secretive and/or fossorial species not sampled otherwise. These results corroborate the findings and methodological recommendations of our previous study on amphibian communities in West Africa (RÖDEL & ERNST 2004).

Sampling efficiency

Species accumulation curves show how many new species were added each month of investigation (Fig. 4). The curve reaches saturation, indicating that sampling time was sufficient to record most of the occurring species. Hence, even if sampling time would be increased, the chance of adding new species would be relatively low. Calculations of the approximate total numbers of amphibians occurring at the site corroborated these results (Fig. 4). We used the presence/absence data based Jack-knife 1 and Chao2 estimators (program: BiodivPro from the Natural History Museum, London) to allow di-

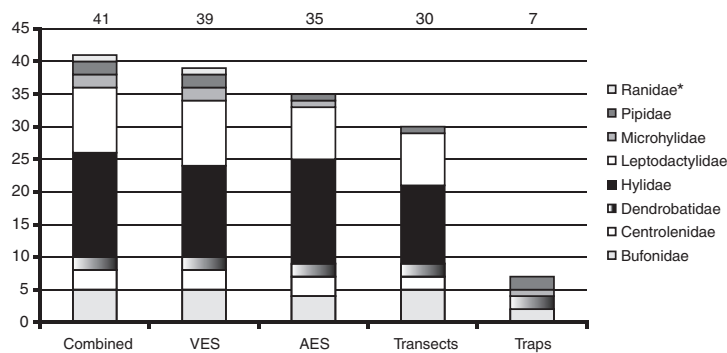


Fig. 3. Number of frog species recorded using a particular sampling method. VES = visual encounter surveys; AES = acoustic encounter surveys; Transects = acoustic and visual transect sampling; Traps = pitfall traps with drift fences; Combined = VES, AES, Transects + Traps. Figures above bars represent total number of species recorded with the respective method. * = recorded at Pibiri only.

rect comparisons with other faunal studies that most often do not provide relative abundance data. Estimated species numbers were very close to the actual number of species observed.

Taxonomic remarks and range extensions

At least two taxa that were recorded have not yet been formally described scientifically, *Physalaemus* sp. and *Colostethus* sp.; the latter has previously been referred to as *Colostethus beebei* (NOBLE, 1923) (e.g. LESCURE & MARTY 2000). *C. beebei*, however, is a species restricted to the Guiana Highlands (Pakaraimas and perhaps Venezuela). It differs from *Colostethus* sp. in morphological and ecological aspects (compare BOURNE et al. 2001). Its local name, the “golden frog”, refers to the distinct bright yellow color of reproductive males, not exhibited in *Colostethus* sp. The holotype of *C. beebei* (AMNH 18683, type locality: “near Kaieteur Falls, British Guiana”) fits the description of frogs from populations found at Kaieteur National Park (R. REYNOLDS pers. comm.). These frogs are clearly distinct from populations of *Colostethus* sp. found at the MHFR (R. ERNST unpubl. data).

Physalaemus sp. (Fig. 5) is the first known member of the genus occurring in Guyana. Only one other species, *P. petersi* (JIMENEZ DE LA ESPADA, 1872), has been recorded from French Guiana (BORN & GAUCHER 2001, LESCURE & MARTY 2000).

The taxonomy of an additional group of frogs, namely the three members of the genus

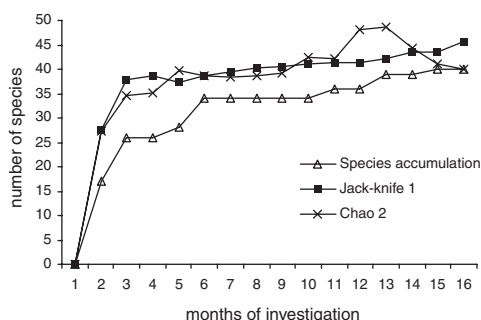


Fig. 4. Species accumulation, Jack-knife1, and Chao 2 estimator curves for the anurans of the MHFR. Estimated species richness for anurans Jack-knife 1: 46, recorded: 40 (87.0 %); Chao 2: 40, recorded: 40 (100.0 %).

Hyalinobatrachium, are currently subject of phylogenetic analyses conducted in cooperation with S. CASTROVIEJO and co-workers from the Department of Evolutionary Biology at Uppsala University. First results indicate that the species herein referred to as *Hyalinobatrachium* sp. 1 is new to science and will be described elsewhere. It resembles *H. taylori* (GOIN, 1968) but differs from the later in a number of morphological and advertisement call characteristics as well as on the basis of molecular genetics (R. ERNST et al. unpubl.). The status of *Hyalinobatrachium* sp. 2 (Fig. 6) could not be clarified as yet. It resembles *H. ignioculus* NOONAN & BONETT, 2003 recently described from the Highlands of Guyana (NOONAN & BONETT 2003). This species, however, may prove to be a junior synonym of *H. crurifasciatum* MYERS & DONNELLY, 1997 (S. CASTROVIEJO & J. AYARZAGÜENA

	primary							exploited				
year of logging	no logging							1992 1988				
transect	P 1	P 2	P 3	P 4	P 5	P 6	P 7	S 1	S 2	S 3	S 4	S 5
S_{obs}	26	22	13	15	8	23	29	9	9	11	10	9
complete	30							14				

Tab. 1. Total number of species observed (S_{obs}) in transects (P = primary forest; S = exploited forest) and in habitat complexes combined = complete (entire study period).



Fig. 5. Amplectant pair of *Physalaemus* sp. constructing foam nest.



Fig. 7. Male *Synapturanus mirandaribeiroi*.



Fig. 6. Male *Hyalinobatrachium* sp. 2, guarding clutch.



Fig. 8. Male *Pipa aspera*.

pers. comm.). The record from the lowland rainforest site at MHFR would thus be the easternmost record of the species that has so far been reported from montane environments of Venezuela and western Guyana. The third species recorded, *H. nouraguensis* LESCURE & MARTY, 2000 was previously only known from the type locality in French Guiana. It thus represents a first country record for Guyana. The status of *H. nouraguensis*, however, is uncertain and it may prove to be a junior synonym of *H. iaspidiensis* AYARZAGÜENA, 1992 (S. CASTROVIEJO & J. AYARZAGÜENA pers. comm.), a species recorded from Estado Bolívar and Estado Delta Amacuro, Venezuela (AYARZAGÜENA 1992, SEÑARIS & AYARZAGÜENA in press). The Guyana record would thus represent a distributional gap link between known populations.

Another first country record is represented by *Hyla brevifrons* DUELLMAN & CRUMP, 1974, a small hylid of the *Hyla parviceps*-group. This species has previously also been reported from French Guiana (LESCURE & MARTY 2000). These records are especially interesting since species of the *H. parviceps*-group are known to have their distributional centers in the Upper Amazon Basin of Colombia, Ecuador, and Peru. Widely scattered populations of *H. brevifrons* are also known from the Madeira and Amazon River regions in Amazonas State, Brazil. The Guyana and French Guiana records are thus the most northern records of the species.

The remaining 34 anurans comprise some remarkable, rare, secretive or unusual species rarely recorded in field surveys and thus hardly represented in collections. Among

Anurans of the Mabura Hill Forest Reserve, Guyana

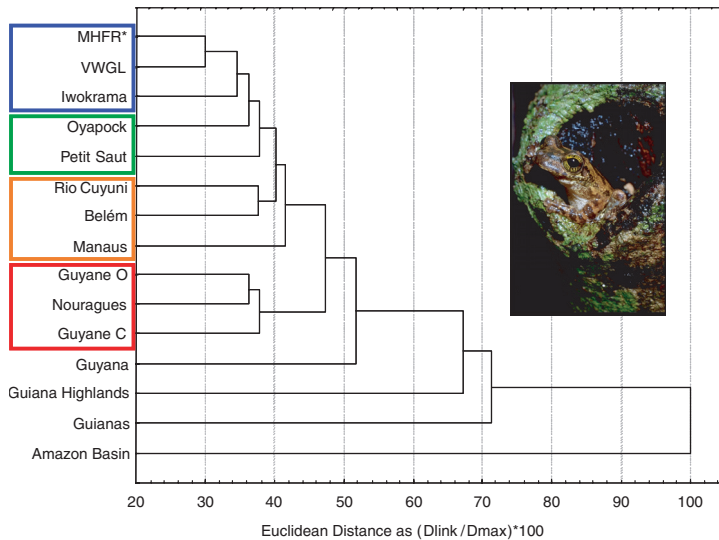


Fig. 9. Community composition and relatedness of anurans in northern South America and central Amazonia. Dendrogram based on presence-absence data (unweighted pair group average, Euclidean Distance). Calculations performed using the freely available software R (<http://www.r-project.org>). Blue = Guyana locations; green = eastern French Guianan locations; orange = Central Amazonian and Venezuelan forest locations; red = Guiana, biogeographic regions sensu LESCURE & MARTY 2000; cluster at bottom of dendrogram = large biogeographic realms or sites with high endemism (Guyana Highlands). Inset picture, male *Osteocephalus oophagus*, a phytotelmata breeding species frequently encountered in disturbed forest sites. Own data: Mabura Hill Forest Reserve (MHFR* = including Pibiri record of *R. palmipes*; R. ERNST unpubl. data), Variety Woods and Greenheart Ltd.-Concession (VWGL; R. ERNST unpubl. data); literature data: Guianas (HOOGMOED 1979, IUCN et al. 2004); Guyana Highlands (DUELLMAN 1999, McCULLOCH & LATHROP 2002); Guyana (IUCN et al. 2004, JUNGFER & BÖHME 2004); Amazon Basin (DUELLMAN 1999); Belém (CRUMP 1971); Rio Cuyuni (DUELLMAN 1997); Manaus (ZIMMERMAN & RODRIGUES 1990); Oyapock (DUELLMAN 1997); Petit Saut (DUELLMAN 1997); Nouragues (BORN & GAUCHER 2001); Guyane (O)riental and Guyane (C)entral (sensu LESCURE & MARTY 2000); Iwokrama Forest (D. ARJOON & G. WATKINS pers. comm. of unpubl. data, DONNELLY et al. 2005 and unpubl. data).

those is a rare microhylid, *Synapturanus mirandaribeiroi* NELSON & LESCURE, 1975 (Fig. 7), which was only recorded during a period of three weeks in November 2002. However, throughout this short period, calling males were very abundant locally. The species has never been recorded at other occasions, even when climatic conditions, i.e. temperatures and rainfall, were comparable. A single specimen of a second microhylid, *Ctenophryne geayi*, was recorded during the peak rainy season of 2004. We have no hints for successful reproductive events during that period. A country record of the rare pipid *Pipa aspera*

MÜLLER, 1924 (Fig. 8) that was based on a single juvenile specimen from the Takutu Mountains, Mazaruni-Potaro (USNM-284392) was confirmed at the MHFR, where it represented the most abundant pipid species.

Species composition and biogeographical patterns

A total of 40 anuran species belonging to seven different families was recorded during the 16 month study period. One additional

Index	P 1	P 2	P 3	P 4	P 5	P 6	P 7	S 1	S 2	S 3	S 4	S 5	primary	exploited
Shannon H' Log Base 10	1.13	0.89	0.83	0.71	0.63	1.04	1.18	0.36	0.47	0.70	0.71	0.58	1.17	0.70
Shannon Hmax Log Base 10	1.42	1.34	1.11	1.18	0.90	1.36	1.46	0.95	0.95	1.04	1.00	0.95	1.48	1.15
Shannon J' (evenness)	0.80	0.66	0.75	0.60	0.70	0.76	0.81	0.38	0.50	0.67	0.71	0.61	0.79	0.61
Fisher's Alpha	4.77	4.21	2.28	2.84	1.92	4.96	5.82	1.87	1.68	1.97	1.78	1.26	4.31	1.89
Berger-Parker (1/d)	5.29	3.80	3.32	1.96	2.07	3.52	6.02	1.28	1.59	2.44	2.84	2.54	6.13	3.20
Simpsons Diversity (1/D)	10.10	5.34	5.41	3.29	3.25	7.08	11.22	1.59	2.18	3.74	4.14	3.08	11.04	4.10
Hill's Number H1	62.44	27.67	23.02	15.10	11.64	45.09	72.74	4.79	6.92	14.80	15.25	9.91	69.38	14.62

Tab. 2. Diversity indices for each transect (P = primary forest; S = exploited forest) and for *primary* and *exploited* transects combined (entire study period). Highest index-values within particular habitat complex in bold letters.

species [*Rana palmipes* (SPIX, 1824)] was recorded at the Pibiri site, only 30 km south of the MHFR. It is thus highly likely that the species also occurs at the MHFR, raising the total species number to 41. Species differed greatly in their abundance and hence were recorded in varying frequencies. The anuran species most commonly encountered were (in order of number of individual records, excluding tadpole records): *Osteocephalus oophagus* (1,750), *Eleutherodactylus marmoratus* BOULENGER, 1900 (1,228), *Dendrophryniscus minutus* (MELIN, 1941) (1,182), *Colostethus* sp. (1,025), *Allobates femoralis* (BOULENGER, 1884 "1883") (457). In terms of species richness, the MHFR is as species rich as, e.g. the well known site of the Iwokrama Forest (compare DONNELLY et al. 2005), when looking at the number of species at a given site. The same probably holds true with regard to alpha diversity, i.e. the diversity (species richness and abundance distributions) within a single site. Yet, this has not been tested as no comparable quantitative data were available for Iwokrama. Fifty-one species of amphibians have been recorded at Iwokrama, compared to 40 (+1) at the MHFR. However, the area of Iwokrama Forest comprises various clearly distinct habitat types, such as lowland rainforests, highland forests, savannas, Muri Scrub, seasonally flooded marsh forests, etc., which in turn are likely to harbor clearly distinct herpetofaunas. When excluding all non-forest species, the number of species recorded drops to 38 (35 when regarding anurans exclusively, i.e. excluding caecilians) at Iwokrama Forest and to 37 at the MHFR, respectively. In addition, the

composition of the MHFR is very unique and clearly distinct from that of the Iwokrama Forest. Eleven species recorded at the MHFR are not known to occur at Iwokrama Forest. This indicates that the Essequibo River may be an effective biogeographical barrier at least for less mobile taxa, such as most amphibians. In a general comparison of amphibian communities of other northern South-American and Central Amazonian sites that have been studied previously (literature data), the assemblage of the MHFR groups along with assemblages of two other Central Guyanan sites, namely those of the Variety Woods and Greenheart Ltd-Concession at Upper Berbice and of the Iwokrama Forest, with closer links to the first. Interestingly, the Central Guyana cluster has close affinities to two locations (Petit Saut and Oyapock) that are part of the biogeographical region of Guyane Oriental sensu LESCURE & MARTY (2000). However, both of the larger biogeographical regions, Guyane Oriental and Central sensu LESCURE & MARTY (2000), as well as the French Guianan location of the Réserve des Nouragues form a clearly separated cluster (Fig. 9). These patterns indicate that the biogeographical classification of LESCURE & MARTY (2000) may not hold, especially as more sites within the region are being studied extensively and new species records are added. The Amazonian species *H. brevifrons* and *R. palmipes* have previously not been recorded east of a suggested biogeographical demarcation line that runs north-south connecting the locations of Iracoubo and Saül, French Guiana. This was interpreted in favor of the validity of the suggested classifica-

Anurans of the Mabura Hill Forest Reserve, Guyana

taxa	primary	secondary	BT	FS	Access-Rd	W-Fall	MHFR	restricted to			habitat			CITES & Red List status	
								SA	AM	GU	F	S	D		
Amphibia – Anura															
Bufonidae															
<i>Atelopus spumarius</i>	1						1			1	1			vulnerable A3ce	
<i>Bufo guttatus</i>	1	1		1	1	1	1		1		1	1			
<i>Bufo margaritifera</i>	1	1		1	1		1	1			1	1			
<i>Bufo marinus</i>	1	1		1	1		1	1 ^a			1	1	1		
<i>Dendrophryniscus minutus</i>	1	1					1		1			1	1		
Centrolenidae															
<i>Hyalinobatrachium nouraguensis</i>	1						1			1	1				
<i>Hyalinobatrachium</i> sp. 1	1						1			1?	1				
<i>Hyalinobatrachium</i> sp. 2	1					1	1			1?	1				
Dendrobatidae															
<i>Colostethus</i> sp.	1	1	1	1	1		1			1	1		1	CITES App.II	
<i>Allobates femoralis</i>	1	1	1	1	1		1		1		1		1		
Hylidae															
<i>Hyla boans</i>	1						1	1			1				
<i>Hyla brevifrons</i>	1						1		1		1				
<i>Hyla calcarata</i>	1						1		1		1				
<i>Hyla crepitans</i>					1			1				1	1		
<i>Hyla geographica</i>	1						1		1		1				
<i>Hyla granosa</i>		1					1		1		1		1		
<i>Hyla minuscula</i>	1						1			1	1				
<i>Hyla minuta</i>					1		1	1			1		1		
<i>Osteocephalus lepieurii</i>	1						1		1		1				
<i>Osteocephalus oophagus</i>	1	1		1			1		1		1		1		
<i>Osteocephalus taurinus</i>	1	1					1		1		1		1		
<i>Phrynohyas resinifictrix</i>	1	1		1			1		1		1		1		
<i>Phyllomedusa bicolor</i>	1						1		1		1				
<i>Phyllomedusa tomopterna</i>					1		1		1		1		1		
<i>Phyllomedusa vaillantii</i>	1						1		1		1				
<i>Scinax ruber</i>				1			1	1			1		1		
Leptodactylidae															
<i>Adenomera andreae</i>	1	1		1			1		1		1		1		
<i>Eleutherodactylus marmoratus</i>	1	1		1	1		1			1	1		1		
<i>Eleutherodactylus zeuctotylus</i>	1						1			1	1				
<i>Leptodactylus bolivianus</i>	1						1	1			1				
<i>Leptodactylus knudseni</i>	1	1		1	1		1		1		1		1		
<i>Leptodactylus mystaceus</i>	1			1			1		1		1				
<i>Leptodactylus petersii</i>	1						1		1		1				
<i>Leptodactylus rhodomystax</i>	1	1					1		1		1		1		
<i>Lithodytes lineatus</i>	1						1	1			1				
<i>Physalaemus</i> sp.	1				1		1			1?	1		1		
Microhylidae															
<i>Ctenophryne geayi</i>	1			1			1	1			1				
<i>Synapturanus mirandaribeiroi</i>		1						1			1	1			
Pipidae															
<i>Pipa aspera</i>	1			1			1			1	1				
<i>Pipa pipa</i>	1			1			1		1		1	1			
Ranidae															
<i>Rana palmipes</i> [*]								1			1				
total	36	14	6	11	11	2	40	10	20	11	40	3	19	2	

Tab.3. Presence, distribution, habitat association, and conservation status of the anurans of the MHFR. BT = drift fences with bucket traps; FS = Field Station; Access-Rd = White Sand access road to field station; SA = South America; AM = Amazonia; GU = Guianan Region; F = forest; S = savannah; D = disturbed habitats; additional site abbreviations and detailed descriptions see study sites, 1^a = range extends SA; * = recorded at Pibiri only.

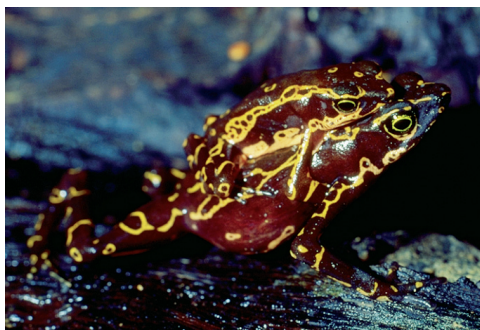


Fig. 10. Amplexant pair of *Atelopus spumarius*.

tion. The Guyanan records hence do not confirm this assumption. The actual pattern may be more complex than previously assumed.

Effects of logging

Preliminary results of the analyses of anuran community patterns in primary versus exploited sites indicate a general decrease in species richness (Tab. 1) and species diversity (Tab. 2) with increasing disturbance, i.e. moving from primary to old secondary (logged in 1988) and more recently disturbed (logged in 1992) forest sites. Assemblages in these habitats have been subjected to a different disturbance regime due to logging, generally producing more restrictive environments, especially with respect to microclimatic parameters. As species generally do not occur in areas that tax their physiological limits, the number of potential "true" forest species that can successfully colonize is a priori being reduced. The remaining set of species thus consists of either highly adapted species, resulting in stronger species-habitat relations than would be detected in primary forest habitats, or it consists of species that exhibit a broad-scale physiological tolerance. Increases in abundance after disturbance regularly occur among those species with wide ecological tolerances and large geographical ranges (HAMER

et al. 1997, SPITZER et al. 1997). In a study on small mammals and bats in a fragmented landscape in French Guiana, generalists were found to be the best survivors (GRANJON et al. 1996).

In case of the anuran communities of the MHFR, those species that had the highest abundance levels in exploited forest sites, exhibited specialized reproductive modes, i.e. the majority belonged to groups that are independent of open water (direct developers, e.g. *Eleutherodactylus marmoratus* or phytotelmata breeders, e.g. *Osteocephalus oophagus*). These specializations enable these species to cope with conditions, and to colonize habitats, not suitable for other species.

A transition from stochastically organized communities in primary forest sites to deterministically organized communities in secondary forest sites, as has recently been observed in west African anuran leaf litter communities (ERNST & RÖDEL in press), was also observed in the MHFR communities (R. ERNST unpubl.). This transition in predictability patterns indicates that logging not only affects system descriptors, such as species richness, abundance, and diversity, but may also alter the system's dynamics.

Conservation status of the amphibian fauna of the MHFR

The species richness of the region under investigation can be considered moderate, especially when compared to other neotropical sites. Endemicity on the other hand is comparatively high. Ten species can be considered Guianan Region endemics (sensu HOOGLMOED 1979, compare Tab. 3 and Appendix 2). *Atelopus spumarius* COPE, 1871 (Fig. 10) has recently been recognized as a species complex (LÖTTERS et al. 2002) and the status of the central Guyanan populations is currently the subject of a revision (S. LÖTTERS pers comm.). Individuals of the MHFR will likely prove to be distinct from those of central Amazonian populations. The number

of endemics would thus increase to 11. Except for one species just recently listed as vulnerable (the aforementioned *Atelopus spumarius*), none of the amphibian species recorded is currently considered threatened or included in the Red List 2001 (HILTON-TAYLOR 2001, CITES 2003, IUCN et al. 2004). Neither is their international trade monitored or regulated by inclusion in CITES appendices (one exception, see below). However, members of the genus *Phyllomedusa* are regularly caught for the pet trade and thus may be prone to severe population decreases. The same holds true for a number of dendrobatid frogs. Several species of this family are listed under CITES appendix II. Among them is one species (*Allobates femoralis*), recorded in the MHFR. The other species of the family Dendrobatidae that has been recorded during the study (*Colostethus* sp.) is currently not included in any of the lists. Recently, populations of several amphibian genera have been reported to undergo sudden and dramatic population declines or even to be facing extinction. In the Neotropics, this especially includes toads of the genus *Atelopus* (LIPS 1997, RON et al. 2003, LÖTTERS et al. 2004). This may be understood as part of a global biodiversity crisis affecting amphibians in general. Possible reasons include increased solar radiation, climatic change associated with El Niño southern oscillation (ENSO) events, but also environmental contaminations, the spread of the pathogenic chytrid fungus (*Batrachochytrium dendrobatidis*), the latter especially in higher elevation species that occur in undisturbed habitats (RON 2005), direct human impact, and habitat destruction, due to, for example logging. Almost all Andean *Atelopus* are now being grouped as “Critically Endangered” and two even as “Extinct” (IUCN 2003, IUCN et al. 2004). The status of lowland species’ populations, of which the only species of *Atelopus* (*Atelopus spumarius*) recorded at the MHFR is a member, has recently been defined as stable (LA MARCA et al. 2005) but the actual status of these populations has not yet been clarified. A

current study conducted in a comparable area in Suriname addresses these questions (W. HÖDL & M. LUGER pers. comm.). The sizable population (so far the largest population recorded within Guyana) at MHFR still seems to be stable, as indicated by the number of individuals recorded. However, reproduction was not confirmed and only two amplexant pairs were found during the entire study period. The loss of further habitat, especially permanent creek sites, may drastically affect these populations and eventually lead to their extinction. It is hence of utmost importance to preserve these pristine forest sites not only to guarantee the long-term viability of particular species or populations at risk, but also to maintain one of Guyana’s most precious resources as a whole, its biodiversity.

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Appendix 1

Description of particular sites surveyed. P = primary forest transect, S = exploited forest transect, BT = drift fences with bucket traps, FS = Field Station. GPS-coordinates for transects represent the respective south-east corner coordinate.

site	GPS-coordinate	description
P1	N 5° 09.2003'; W 58° 41.8590'	Mixed forest on gravelly clay laterite (Leptosols) hill slope, low lying segment touching Maiko creek.
P2	N 5° 09.2454'; W 58° 41.7921'	Mixed forest on gravelly clay laterite (Leptosols) hill slope, low lying segment riverine floodplain forest on alluvial soils
P3	N 5° 10.1231'; W 58° 41.5004'	Well-drained mixed forest on brown sand (ferralic Arenosols) hill slope
P4	N 5° 10.1334'; W 58° 41.5667'	Poorly drained mixed forest on brown sand (ferralic Arenosols) with pegasse (terric Histosols) and white sand (albic Arenosols) segments, dissected by small black water creek
P5	N 5° 10.0066'; W 58° 42.2536'	Palm-swamp forest on peaty soils (Histosols)
P6	N 5° 09.7131'; W 58° 41.7969'	Riverine floodplain forest on alluvial soils connecting with Maiko creek, transcending in well-drained mixed forest on brown sand (ferralic Arenosols) hill slope
P7	N 5° 09.4540'; W 58° 41.8928'	Riverine floodplain forest on alluvial soils connecting with Maiko creek, transcending in well-drained mixed forest on brown sand (ferralic Arenosols) hill slope
S1	N 5° 09.6484'; W 58° 42.7071'	Well-drained mixed forest on white sand (albic Arenosols), logged in 1992 with an extraction rate of 19.5 trees (app. 57 m ³) ha ⁻¹
S2	N 5° 10.6700'; W 58° 42.3685'	Well-drained mixed forest on white sand (albic Arenosols), logged in 1992 with an extraction rate of 19.5 trees (app. 57 m ³) ha ⁻¹
S3	N 5° 10.8805'; W 58° 42.1953'	Well-drained mixed forest on brown sand (ferralic Arenosols), transcending into poorly-drained mixed forest with ephemeral creek, logged in 1988 with an extraction rate of 19.5 trees (app. 57 m ³) ha ⁻¹
S4	N 5° 10.9712'; W 58° 42.1690'	Well-drained mixed forest on white sand (albic Arenosols) with ephemeral creek, logged in 1988 with an extraction rate of 19.5 trees (app. 57 m ³) ha ⁻¹
S5	N 5° 11.1096'; W 58° 42.1416'	Well-drained mixed forest on brown sand (ferralic Arenosols), transcending into poorly-drained mixed forest with ephemeral creek, logged in 1988 with an extraction rate of 19.5 trees (app. 57 m ³) ha ⁻¹
BT1	N 5° 09.2699'; W 58° 42.0025'	Riverine floodplain forest on alluvial soils connecting with Maiko creek
BT2	N 5° 09.3207'; W 58° 41.9494'	Riverine floodplain forest on alluvial soils connecting with Maiko creek
BT3	N 5° 09.7636'; W 58° 42.0145'	Mixed forest on gravelly clay laterite (Leptosols) hill slope
BT4	N 5° 09.4572'; W 58° 41.8574'	Riverine floodplain forest on alluvial soils connecting with Maiko creek
W-Fall	N 5° 09.3767'; W 58° 41.5587'	Waterfall and flood terraces, laterite bottom black water creek, plateau with dry evergreen low forest
FS	N 5° 09.3217'; W 58° 41.9826'	Large clearing near Maiko creek, at the southern side of the MHFR

Appendix 2

Summary of site records and geographic distribution of the amphibian species recorded during the study period at the MHFR. Nomenclature follows FROST (2002, with updates) and IUCN et al. (2004). Species names are followed by a list of localities from which they were recorded (see Appendix 1 for more details). Distributions according to IUCN et al. (2004).

Country Abbreviations: **AG**: Antigua and Barbuda ; **AR**: Argentina; **AU**: Australia; **BB**: Barbados; **BO**: Bolivia; **BR**: Brazil; **BZ**: Belize; **CO**: Colombia; **CR**: Costa Rica; **DO**: Dominican Republic; **EC**: Ecuador; **GD**: Grenada; **GF**: French Guiana; **GP**: Guadeloupe; **GT**: Guatemala; **GY**: Guyana; **HN**: Honduras; **HT**: Haiti; **JM**: Jamaica; **KN**: St. Kitts and Nevis; **LC**: St. Lucia; **MQ**: Martinique; **MX**: Mexico; **NI**: Nicaragua; **PA**: Panama; **PE**: Peru; **PR**: Puerto Rico; **PY**: Paraguay; **SR**: Suriname; **SV**: El Salvador; **TT**: Trinidad/Tobago; **UY**: Uruguay; **VC**: Saint Vincent & the Grenadines; **VE**: Venezuela; **VI**: U.S. Virgin Islands.

Bufonidae: *Atelopus spumarius* COPE, 1871 (P1, P2, P6, P7). Distribution: BR, CO, EC, GF, GY, PE, SR; *Bufo guttatus* SCHNEIDER, 1799 (P1, P2, P3, P4, P5, S2, S4, P6, P7, W-Fall). Distribution: BO, BR, CO, EC, GF, GY, PE, SR, VE; *Bufo margaritifera* (LAURENTI, 1768) (P1, P2, P3, S1, S2, P6, P7). Distribution: BO, BR, CO, EC, GF, GY, PA, PE, SR, VE; *Bufo marinus* (LINNAEUS, 1758) (P1, P4, S1, S5, P6, P7). Distribution (Neotropical Realm only): AG, BB, BO, BR, BZ, CO, CR, DO, EC, GD, GF, GP, GT, GY, HN, HT, JM, KN, LC, MX, NI, PA, PE, PR, SR, SV, TT, VC, VE, VI; *Dendrophryniscus minutus* (MELIN, 1941) (P1, P2, P3, P4, P5, P6, P7, S1, S2, S3, S4, S5). Distribution: BO, BR, CO, EC, GF, GY, PE, SR. **Centrolenidae**: *Hyalinobatrachium* sp. 1 (P1, P2, P4, P6, P7); *Hyalinobatrachium* sp. 2 (W-Fall); *Hyalinobatrachium nouraguensis* LESCURE & MARTY, 2000 (P1, P2, P6, P7). Distribution: GF. **Dendrobatiidae**: *Allobates femoralis* (BOULENGER, 1884 “1883”) (P1, P2, P3, S3, P6, P7). Distribution: BO, BR, CO, EC, GF, GY, PE, SR, VE; *Colostethus* sp. (P1, P2, P3, P4, P5, P6, P7, S1, S3, S4, S5). Distribution: GF, GY, SR. **Hylidae**: *Hyla boans* (LINNAEUS, 1758) (P1, P2, P6, P7). Distribution: BO, BR, CO, EC, GF, GY, PA, PE, SR, TT, VE; *Hyla brevifrons* DUELLMAN & CRUMP, 1974 (P2, P7). Distribution: BR, CO, EC, GF, PE; *Hyla calcarata* TROSCHEL, 1848 (P1, P6, P7). Distribu-

tion: BO, BR, CO, EC, GF, GY, PE, SR, VE; *Hyla crepitans* WIED-NEUWIED, 1824 (FS). Distribution: BR, CO, GF, GY, HN, PA, SR, TT, VE; *Hyla geographica* SPIX, 1824 (P1, P4, P6, P7). Distribution: BO, BR, CO, EC, GF, GY, PE, SR, TT, VE; *Hyla granosa* BOULENGER, 1882 (P1, P2, P4, P5, S3, P6, P7). Distribution: BO, BR, CO, EC, GF, GY, PE, SR, VE; *Hyla minuscula* RIVERO, 1971 (P1, P7). Distribution: BR, CO, GF, GY, SR, TT, VE; *Hyla minuta* PETERS, 1872 (FS). Distribution: AR, BO, BR, CO, EC, GF, GY, PE, PY, SR, TT, UY, VE; *Osteocephalus leprieurii* (DUMÉRIE & BIBRON, 1841) (P1, P7). Distribution: BO, BR, CO, GF, GY, PE, SR, VE; *Osteocephalus oophagus* JUNGFER & SCHIESARI, 1995 (P1, P2, P3, P4, P5, P6, P7, S1, S2, S3, S4, S5). Distribution: BR, CO, GF; *Osteocephalus taurinus* STEINDACHNER, 1862 (P1, P2, P3, P4, P6, P7, S1, S2, S3, S4, S5). Distribution: BO, BR, CO, EC, GF, GY, PE, SR, VE; *Phrynohyas resinifictrix* (GOELDI, 1907) (P1, P2, P3, P5, P6, P7, S1, S2, S3, S4, S5). Distribution: BO, BR, CO, EC, GF, PE, SR, VE, *Phyllomedusa bicolor* (BODDAERT, 1772) (P1, P2, P6, P7). Distribution: BO, BR, CO, GF, GY, PE, SR, VE; *Phyllomedusa tomodon* (COPE, 1868) (FS). Distribution: BO, BR, CO, EC, GF, GY, PE, SR, VE; *Phyllomedusa vaillantii* (BOULENGER, 1882) (P1, P2, P3, P4, P6, P7). Distribution: BO, BR, CO, EC, GF, GY, PE, SR, VE; *Scinax ruber* (LAURENTI, 1768) (FS). Distribution: BO, BR, CO, EC, GF, GY, LC, MQ, PA, PE, PR, SR, TT, VE. **Leptodactylidae**: *Adenomera andreae* MÜLLER, 1923 (P1, P2, P3, P6, P7, S2, S3, S4, S5). Distribution: BO, BR, CO, EC, GF, GY, PE, SR, VE; *Eleutherodactylus marmoratus* BOULENGER, 1900 (P1, P2, P3, P4, P5, P6, P7, S1, S2, S3, S4, S5). Distribution: BR, GF, GY, SR, VE; *Eleutherodactylus zeuctotylus* LYNCH & HOOGMOED, 1977 (P1, P7). Distribution: BR, CO, GF, GY, SR, VE; *Leptodactylus bolivianus* BOULENGER, 1898 (P1, P4, P6, P7). Distribution: BO, BR, CO, CR, EC, GF, GY, NI, PA, PE, SR, TT, VE; *Leptodactylus knudseni* HEYER, 1972 (P1, P2, P3, P4, P6, P7, S1, S2, S3, S4). Distribution: BO, BR, CO, EC, GF, GY, PE, SR, VE; *Leptodactylus mystaceus* (SPIX, 1824) (P2, P7). Distribution: BO, BR, CO, EC, GF, GY, PE, PY, SR, VE; *Leptodactylus petersii* (STEINDACHNER, 1864) (P1, P2, P4, P5, P6, P7). Distribution: BO, BR, CO, EC, GF, GY, PE, SR, VE; *Leptodactylus rhodomystax* BOULENGER, 1884 “1883” (P2, P3, P4, P6, P7, S3, S4, S5). Distribution: BO, BR, CO, EC, GF, GY, PE, SR, VE; *Lithodytes lineatus* (SCHNEIDER, 1799) (P1). Distribution: BO, BR, CO, EC, GF, GY, PE, SR, VE;

Physalaemus sp. (P7; FS). Distribution: GY. **Microhylidae:** *Ctenophryne geayi* MOCQUARD, 1904 (BT1). Distribution: BO, BR, CO, EC, GF, GY, PE, SR, VE; *Synapturanus mirandaribeiroi* NELSON & LESCURE, 1975 (P7). Distribution: BR, CO, GF, GY, SR, VE. **Pipidae:** *Pipa aspera* MÜLLER, 1924 (P1; P2; P7). Distribution: GF, SR; *Pipa pipa* (LINNAEUS, 1758) (P1; P7; BT1; BT4). Distribution: BO, BR, CO, EC, GF, GY, PE, SR, TT, VE. **Ranidae:** *Rana palmipes* SPIX, 1824 (Pibiri). Distribution: BO, BR, CO, EC, GF, GY, PE, SR, TT, VE.

Note added in proof

The family Hylidae has recently undergone major systematic revision [see FAIVOVICH, J., C.F.B. HADDAD, P.C.A. GARCIA, D.R. FROST, J.A. CAMPBELL & W.C. WHEELER (2005): Systematic review of the frog family Hylidae, with special reference to Hyalinae: Phylogenetic analysis and taxonomic revision. – Bull. Amer. Mus. Nat. Hist., **294**: 1-240]. This work has been published too recently to be considered in our study. We therefore decided to retain the conventional nomenclature of FROST (2000) until taxonomic changes have been widely established. However, we provide a brief list of taxa (relevant to the present study) that underwent taxonomic changes (Table below).

Current name	New name	New group assignment
<i>Hyla boans</i>	<i>Hypsiboas boans</i>	<i>Hypsiboas semilineatus</i> group
<i>Hyla geographica</i>	<i>Hypsiboas geographicus</i>	<i>Hypsiboas semilineatus</i> group
<i>Hyla calcarata</i>	<i>Hypsiboas calcaratus</i>	<i>Hypsiboas albopunctatus</i> group
<i>Hyla crepitans</i>	<i>Hypsiboas crepitans</i>	<i>Hypsiboas faber</i> group
<i>Hyla granosa</i>	<i>Hypsiboas granosus</i>	<i>Hypsiboas punctatus</i> group
<i>Hyla brevifrons</i>	<i>Dendropsophus brevifrons</i>	<i>Dendropsophus parviceps</i> group
<i>Hyla minuscula</i>	<i>Dendropsophus minusculus</i>	<i>Dendropsophus microcephalus</i> group
<i>Hyla minuta</i>	<i>Dendropsophus minutus</i>	<i>Dendropsophus minutus</i> group
<i>Phrynohyas resinifictrix</i>	<i>Trachycephalus resinifictrix</i>	

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