The amphibian fauna of the Kirindy dry forest in western Madagascar

JULIAN GLOS

Zusammenfassung

Die Amphibienfauna des Kirindy-Trockenwaldes in Westmadagaskar.

Die Amphibienfauna des Kirindy-Waldes in Westmadagaskar wurde über vier Jahre hinweg im Rahmen einer ökologischen Studie untersucht. Sie besteht aus 15 Arten aus vier verschiedenen Anurenfamilien (Mantellidae, Ranidae, Hyperoliidae, Microhylidae). Unter diesen Arten gibt es ein weites Spektrum von Explosionslaichern und solchen, die sich über die ganze Regenzeit hinweg fortpflanzen. In bezug auf die Wahl des Laichgewässers gibt es ähnlich viele Generalisten und Spezialisten. Vermutlich als Anpassung an die hohe Ephemeralität der Laichgewässer ist die larvale Entwicklungszeit einiger Arten sehr kurz. Zu den Arten des Kirindy-Waldes werden weitere Verhaltensbeobachtungen und ökologische Merkmale vorgestellt.

Schlagwörter: Madagaskar; Kirindy-Wald; saisonaler Trockenwald; Amphibien; Habitatwahl; Laichgewässerwahl.

Abstract

The amphibian fauna of the Kirindy forest in western Madagascar was analysed over the course of four years within the context of an ecological study. It consists of 15 species out of four anuran families (Mantellidae, Ranidae, Hyperoliidae, Microhylidae). There is a wide spectrum of explosive and prolonged breeders. About the same number of habitat specialists and generalists is present. Larval developmental time of several species is very short presumably as an adaptation to the high ephemerality of the breeding ponds. Further behavioural observations and ecological data are provided.

Keywords: Madagascar; Kirindy; dry forest; amphibians; habitat choice; breeding site choice.

1 Introduction

The diversity and uniqueness of its fauna and flora makes Madagascar one of the major hot spots of biodiversity (MYERS et al. 2000). Within Madagascar, amphibians are of special interest. Since the break-off of Madagascar from the African continent some 100 million years ago, the Malagasy amphibians evolved strictly separate from their continental counterparts. As a consequence, almost all frogs of Madagascar are endemics to this island (GLAW & VENCES 1994). Within Madagascar, the dry deciduous forest of the western part of the country stands out as it ranks among the most endangered ecosystems of the world (JANZEN 1992). However, very little is known about the fauna and flora present in that region as well as their biology and ecological interactions. In this paper I introduce the amphibian fauna of the Kirindy forest in western Madagascar, give an overview of its breeding sites and present further behavioural and ecological data.

2 Study site

The study site was the 'Forêt de Kirindy', a deciduous dry forest at the west coast of Madagascar, 60 km north of Morondava and about 20 km inland (44°39' E, 20°03 S; 18 - 40 m above sea level; SORG & ROHNER 1996; Fig. 1). The area of the Kirindy forest covers about 12.000 ha and thus may be among the largest remaining continuous forests in western Madagascar (NELSON & HORNING 1993, RAKOTONIRINA 1996). The forest

is intersected by the Kirindy river and is surrounded by a tree-shrub savanna of anthropogenic origin. This savanna is burned in regular intervals and grazed on by Zebu cows and goats. The Kirindy forest is managed by the 'Centre de Formation Professionelle Forestière' (C.F.P.F.) and is exploited by selective logging and eco-tourism. The Kirindy field station, supported by the German Primate Centre (DPZ, Göttingen), is located in the centre of the forest.

The climate is characterized by a marked seasonality. Almost all rain falls in the austral summer from November to March, followed by eight months of virtually no rain. Following SORG & ROHNER (1996), annual mean rainfall is 800 mm. Rainfall during the study was 803 mm in the rainy season 1998/99, 1265 mm in 1999/2000 and 874 mm in 2000/01 (own data). Temperatures during the rainy season range between 22 °C at night and > 40 °C during the day (SORG & ROHNER 1996, own data).

There are breeding sites for amphibians in three different habitat types: the closed forest (Fig. 2), the bed of the Kirindy river (before the river is running; Fig. 3), and the surrounding savanna (Fig. 4). All breeding ponds but a few pools in the river bed dry out completely during the dry season. They are successively filled with the onset of rain in November and December.

The first waters that are used by amphibians for spawning usually arise in the rocky parts of the Kirindy river bed. As a rule, these ponds offer a low risk of desiccation and a low density of invertebrate predators. During the course of the rainy season, these waters connect with each other and eventually fish emigrate from the few permanent

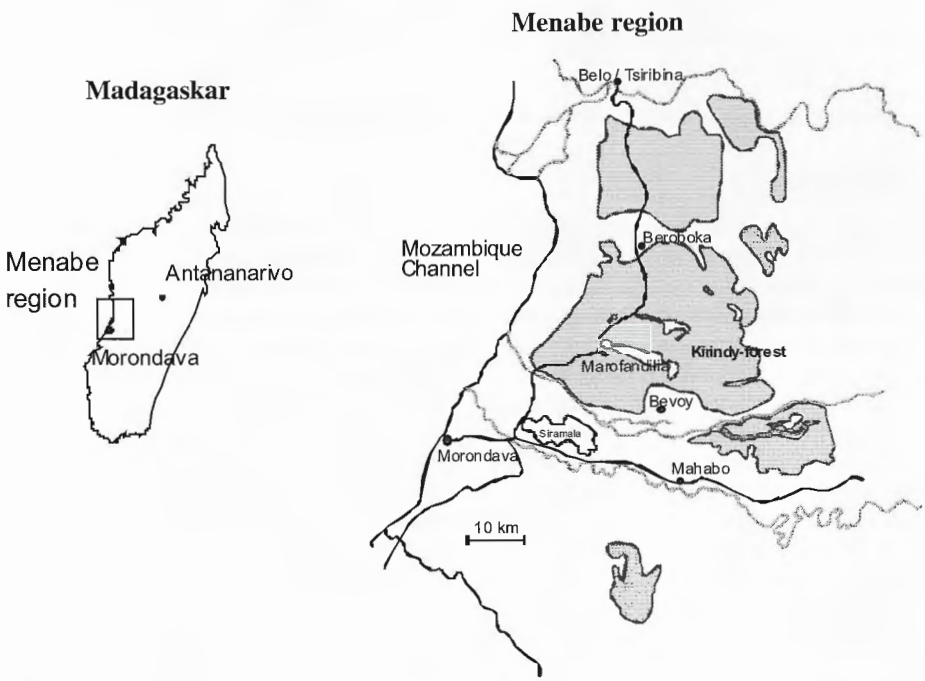

Fig. 1. Map of Madagascar (left) with the Menabe region (Box), precise location of the Kirindy forest (right).

Lage der Region Menabe innerhalb Madagascars (links), genaue Lage des Kirindy-Waldes in der Region Menabe (rechts).

Fig. 2. Larger breeding pond within the closed forest.

Größerer Laichtümpel innerhalb des geschlossenen Waldes.

Fig. 3. Rock pool in the Kirindy river bed with breeding *Aglyptodactylus securifer*.

Felstümpel im Bett des Kirindy-Flusses mit sich paarenden *Aglyptodactylus securifer*.

Fig. 4. Savanna habitat of human origin surrounding the Kirindy forest.

Savannenhabitat anthropogenen Ursprungs außerhalb des geschlossenen Waldes.

pools in the river bed, representing then a very high predation risk for amphibian larvae.

Usually in December, the first breeding ponds arise in the closed forest. Depending on amount and distribution of precipitation and habitat parameters of the ponds themselves, the persistence of these waters varies from three days to five months.

In the savanna, breeding ponds for amphibians arise only after heavy rainfalls. They are fully sun-exposed and often dry out very quickly.

3 Methods

The study was conducted in the respective rainy seasons of four years (Dec 1998 to April 1999, Dec 1999 to April 2000, Nov 2000 to June 2001, Nov 2001 to Feb 2002). The activity data are based upon vocal and sight control walks. For that purpose, the study ponds were visited in regular intervals (day and night) and checked for species and number of frogs as well as their calling activity. Additionally, the use of breeding ponds was checked by analysing tadpole communities. This was done by standardized dip-netting and the box-method (RÖDEL 1998). In total, calling activity and tadpoles communities were analysed at 191 breeding sites (65 forest ponds, 111 river bed ponds, 15 savanna ponds).

Snout-vent length of frogs was measured to the nearest 0.1 mm using callipers. Systematics follow VENCES & GLAW (2001).

4 Results and discussion

4.1 General aspects

In total, the amphibian fauna consists of 15 species representing four anuran families. Snout-vent length data to the most abundant species in Kirindy gives Table 1. The

	Males / Männchen				Females / Weibchen			
Species / Art	ME ± SD	N	Min	Max	ME ± SD	N	Min	Max
Aglyptodactylus securifer	3.58 ± 0.25	78	3.00	4.45	4.29 ± 0.56	44	3.24	4.85
Aglyptodactylus laticeps	4.35 ± 0.28	74	3.25	4.91	5.90 ± 0.30	43	5.44	7.20
Laliostoma labrosum	4.89 ± 0.32	9	4.37	5.65	6.18 ± 0.47	9	5.59	6.83
Ptychadena mascareniensis	3.24 ± 0.15	4	3.14	3.49	3.63 ± 0.09	4	3.55	3.78
Boophis doulioti	3.85 ± 0.26	8	3.40	4.24	4.83 ± 0.41	7	3.93	5.24
Boophis xerophilus	3.60 ± 0.44	32	2.93	4.36	4.13 ± 0.56	6	3.39	4.88
Heterixalus luteostriatus	2.86 ± 0.19	11	2.56	3.16	3.09 ± 0.22	5	2.85	3.35
Heterixalus tricolor	2.78 ± 0.17	110	2.02	3.32	3.18 ± 0.19	32	2.88	3.59
Heterixalus carbonei	2.60 ± 1.09	9	2.41	2.80	2.59 ± 0.11	6	2.45	2.81
Dyscophus insularis	3.78 ± 0.39	26	3.44	5.21	4.19 ± 0.25	14	3.78	4.65
Scaphiophryne calcarata	2.84 ± 0.30	15	2.39	3.45	2.98 ± 0.22	7	2.55	3.30
Scaphiophryne brevis	3.81 ± 0.23	3	3.49	4.01	4.03 ± 0.43	3	3.55	4.60

Tab. 1. Adult snout-vent lengths (cm) of most abundant amphibian species at the Kirindy forest. ME = mean, Max = maximum, Min = minimum, N = number of measured specimens, SD = standard deviation. Included are only animals that actively participated in mating.

Kopf-Rumpf Längen (cm) der häufigsten Amphibienarten des Kirindy-Waldes. ME = Mittelwert, Max = Maximum, Min = Minimum, N = Anzahl gemessener Tiere, SD = Standardabweichung. Aufgeführt sind nur Tiere, die aktiv am Fortpflanzungsgeschehen teilgenommen haben.

anuran community of the Kirindy forest covers a wide spectrum of explosive breeders, reproducing only after heavy rainfalls, and prolonged breeders that are found reproducing over large parts of the rainy season (Tab. 2). In this study, explosive breeding was defined as breeding exclusively in the first two nights after rainfalls of > 30 mm. Apart from *Mantella betsileo*, which is calling regularily both at day and night time, all species are primarily nocturnal. After heavy rains that are creating new breeding sites, however, breeding activity in *Aglyptodactylus* spp., *Boophis* spp. and *Dyscophus insularis* can extend for several hours after sunrise. While *Heterixalus* spp. lay their

Species / Art	Embryonic development	Breeding strategy	Diurnal/ nocturnal	Spawn characteristics	Pond use	Habitat use
Aglyptodactylus securifer	< 24 h	EB	D / N	SUR	S	RB
A. laticeps	< 24 h	EB	N	SUR	S	FO
Laliostoma labrosum	< 24 h	EB	N	SUR	G	FO / RB / SAV
Ptychadena mascareniensis	no data	PB	N	SUR	G	FO / SAV
Mantella betsileo	no data	PB	D / N	TER	G	FO / RB
Boophis doulioti	< 24 h	PB	N	SUR	G	FO / RB / SAV
B. xerophilus	< 24 h	PB	N	SUR	(S)	FO / RB / SAV
Heterixalus luteostriatus	~ 3 days	PB	N	SEP	(G)	FO / RB / SAV
H. tricolor	~ 3 days	PB	N	SEP	S	FO
H. carbonei	~ 3 days	PB	N	SEP	S	FO
Dyscophus insularis	< 24 h	EB	N	SUR	G	FO / RB / SAV
Scaphiophryne calcarata	< 24 h	EB	N	SUR	G	FO / RB / SAV
S. brevis	< 24 h	EB	N	no data	G	FO

Tab. 2. Summarized ecological characteristics of the most abundant amphibians of the Kirindy forest. D = diurnal, EB = explosive breeder, FO = closed forest, G = generalist, N = nocturnal, PB = prolonged breeder, RB = ponds in the river bed, S = specialist, SAV = savanna, SEP = submersed egg packets, SUR = eggs as surface film, TER = terrestrial nest. Data in parentheses indicate that there are rare exceptions from the rule.

Zusammenfassung ökologischer Charakteristika der häufigsten Amphibien des Kirindy-Waldes. D = tagaktiv, EB = Explosionslaicher, FO = geschlossener Wald, G = Generalist, N = nachtaktiv, PB = Brutaktivität über lange Zeit hinweg, RB = Tümpel im Flußbett, S = Spezialist, SAV = Savanne, SEP = Eipakete unter der Wasseroberfläche, SUR = Eier als Oberflächenfilm, TER = terrestrisches Nest. Angaben in Klammern beziehen sich auf seltene Beobachtungen, die von dem Angegebenen abweichen.

Fig. 5. Amplectant pair of *Aglyptodactylus securifer*.
Paar von *Agylptodactylus securifer* im Amplexus.

Fig. 6. *Aglyptodactylus laticeps* female/Weibchen.

eggs in small packets under water and *Mantella betsileo* has terrestrial clutches, most of the species deposit their eggs as surface layers in stagnant waters. The embryonic and larval development is generally very fast, presumably as an adaptation to the unpredictability of rainfall and subsequent high ephemerality of the breeding ponds.

Fig. 7. Predation of *Boophis doulioti* by the iguanid *Oplurus cuvieri* (GRAY, 1831).

Der Dornschwanz *Oplurus cuvieri* (GRAY, 1831) beim Fressen eines *Boophis doulioti*.

Fig. 8. *Boophis xerophilus* female/Weibchen.

Accordingly, embryonic development in the majority of species is < 24 h, in *Heterixalus* about three days (Tab. 2). Moreover, larval development in some species (*Aglyptodactylus laticeps*, *Scaphiophryne calcarata, S. brevis*) can be as short as 10 days and is therefore among the fastest known for amphibians (compare RÖDEL 1998 for *Bufo pentoni* ANDERSSON, 1893). Seven species are specialists in respect to breeding site choice, eight species are generalists in this matter (Tab. 2). Specialists are defined as species using breeding ponds with biotic and abiotic parameters of only a small range, e.g. only small, ephemeral ponds without any water vegetation and low canopy cover. In contrast, generalists use breeding ponds with pond characteristics of a wide range.

4.2 Species accounts

Mantellidae

Laliostominae

Aglyptodactylus securifer GLAW, VENCES & BÖHME, 1998

This species was described first from the Kirindy forest (GLAW et al. 1998). It is known only from the type locality and another area further north (Berara; ANDREONE et al. 2001). *Aglyptodactylus securifer* is an extreme explosive breeder, reproducing almost exclusively in the rock pools of the Kirindy river while the river is not yet running. These are the only open waters at that time of the season. This narrow spatial niche is accompanied by a very narrow temporal niche. Breeding takes only place in the first days after the very first heavy rains, generally in mid November to early December (1.12.1998, 8.12.1999, 13.11.2000, 16.11.2001). At this time up to several hundreds of calling males and amplectant pairs can be observed at one single pond of < 20 m^2. Calling starts early at night, but the breeding activity can extend to the next mid-day. During immediate breeding activity there is a clear sexual dichromatism. While females and non breeding males are uniformly brown coloured, calling males and those in amplectant pairs have yellow lateral bands if breeding occurs at night (Fig. 5), or are bright yellow if breeding during daytime. Amplectant males detached from their females change from yellow to brown within a few minutes. However, it is not known whether the conspicuous yellow colour serves in the context of sexual selection or is simply a non-adaptive by-product of hormonal changes during breeding. When threatened, some individuals of *A. securifer* reacted with death-feigning behaviour. They turn actively on their backs, laying motionless with spread out legs. This behaviour was observed in both adult and freshly metamorphosed individuals. After breeding took place, adults of *A. securifer* were found feeding in the forest throughout the rainy season more than 1 km away from the river bed. The developmental time of the tadpoles is fast. Tadpoles raised in the field camp (density: 10 tadpoles / 15 l) reached GOSNER (1960) stage 42 in 21.5 ± 1.7 days (mean ± SD; range 19 - 32, n = 208). Tadpoles tend to form large aggregations as a reaction to an immediate predation risk.

Aglyptodactylus laticeps GLAW, VENCES & BÖHME, 1998

This species is only known from the Kirindy forest so far (GLAW et al. 1998). It is found almost exclusively in the closed forest. Preferred spawning sites are freshly arisen small and medium sized forest ponds, more rarely small puddles on forest roads. *Aglyptodactylus laticeps* (Fig. 6) is an explosive breeder that reproduces usually only after

rainfalls that exceed 30 mm of precipitation. In contrast to *A. securifer*, the breeding season starts later and extends over the whole rainy season. First calling activity in the study period was recorded on 23.12.1998, 13.12.1999, 25.12.2000 and 18.12.2001. Calling males form choruses of up to 80 individuals that are initiated by single males starting to call. The choruses fade out together and set in again after a few minutes. The members of these choruses are evenly spaced around the breeding pond, 0.3 to 3 m from the water edge. When captured, *A. laticeps* utters distress calls that are fairly different from their mating calls. Larval development is very short (minimum of 10 days in the field). Tadpoles raised in the field camp (density: 10 tadpoles / 15 l) reached GOSNER (1960) stage 42 in 17.1 ± 3.8 days (mean ± SD; range 10 - 29, n = 391).

Laliostoma labrosum (COPE, 1868)

This species (formerly *Tomopterna labrosa*) together with *Aglyptodactylus* was recently assigned to the new subfamily Laliostominae (VENCES & GLAW 2001). *Laliostoma labrosum* is widely distributed throughout western Madagascar (GLAW & VENCES 1994). In Kirindy, it is an explosive breeder, reproducing only after heavy rainfalls. It uses ponds of a wide variety of sizes and structures for breeding. Males generally call from the water edge and do not form choruses but are distributed over the breeding ponds. It is found in the closed forest and the river bed as well as in the savanna and in surrounding villages and towns. Tadpoles of *L. labrosum* were observed to be facultative carnivorous and preyed actively (and successfully) on smaller tadpoles (10-15 mm total length) of *Heterixalus* sp., *Boophis* sp. and *Dyscophus insularis* GRANDIDIER, 1872. However, their main food source was dead plant material. Larval developmental time is about one month.

Boophinae

Boophis doulioti (ANGEL, 1934)

This species was resurrected from the synonymy of *Boophis tephraeomystax* (DUMÉRIL, 1853) by VENCES & GLAW (2002). It is clearly adapted to anthropogenic altered habitats. It is found in the villages around the forest and even in the town of Morondava. In Kirindy, it uses all pond types for reproduction and is found in all major habitat types. Its breeding activity is relatively independent of rainfall and time within the rainy season. It calls from the ground, evenly spaced around the breeding pond, as well as from perches at the water edge (> 200 observations). When individuals that were originally calling on the ground were disturbed, they flew into the bushes and continued calling from higher perches within a few minutes. On one occasion, a successful predation event on *B. doulioti* by *Oplurus cuvieri* (GRAY, 1831) (Iguanidae) was observed (Fig. 7).

Boophis xerophilus GLAW & VENCES, 1997

This frog (Fig. 8) was described by GLAW & VENCES (1997) from the Kirindy forest. It is known from the type locality and Berenty in southern Madagascar. It resembles superficially the syntopic *Boophis doulioti*. However, it is different ecologically in respect to a more specialized use of breeding sites. *Boophis xerophilus* generally uses larger and more permanent waters as breeding ponds. On rare occasions, however, *B. xerophilus* was observed to breed in small ephemeral puddles. It is found primarily in the closed forest, only rarely in the river bed and the savanna. Breeding activity

Fig. 9. Male *Heterixalus tricolor* in typical calling position during night time.
Heterixalus tricolor-Männchen in typischer Rufposition während der Nacht.

Fig. 10. Male *Heterixalus tricolor* in resting position during daytime.
Heterixalus tricolor-Männchen in Ruhestellung während des Tages.

Fig. 11. Calling male *Heterixalus carbonei*.
Rufendes *Heterixalus carbonei*-Männchen.

Fig. 12. Green colour morph of *Scaphiophryne calcarata*.
Grüne Farbvariation von *Scaphiophryne calacarata*.

Fig. 13. *Scaphiophryne* cf. *marmorata* male/ Männchen.

stretches over the whole rainy season. However, activity peaks after heavy rainfalls. *Boophis xerophilus* males are about evenly spread around the breeding pond and mostly call from the ground not more than 2 m from the water edge (> 200 observations). Often two males form calling duets alternating their calls.

Mantellinae

Mantella betsileo (GRANDIDIER, 1872)

This species was recorded for this region by KUCHLING (1993). *Mantella expectata* BUSSE & BÖHME, 1992 was not recorded for the Kirindy forest as it could be expected following BUSSE & BÖHME (1992). Colouration of *M. betsileo* of the Kirindy forest ranges from bright red to ochre-yellow. However, the characteristic diamond shaped markings were present in all recorded individuals (n > 100). It stands out ecologically from all other species by its cathemerality and terrestrial breeding site choice. Individuals were found calling and foraging both during day and night (n > 300). Highest levels of calling activity were recorded at night near relatively permanent pools, which is unusual for *Mantella* species (STANISZEWSKI 2001). Breeding activity was independent of rainfall. On 9 January 1999, one clutch of *M. betsileo* containing 35 yellow eggs was found under a fallen log about two meters next to a forest pond (500 m^2).

Mantidactylus cf. *wittei* GUIBÉ, 1974

This species is the only member of the very specious genus *Mantidactylus* in the Kirindy forest. A final species affiliation of two voucher specimens and call is in progress. It is morphologically similar to *M. wittei*. *Mantidactylus* cf. *wittei* is very rare in the Kirindy forest. In four years and almost 200 ponds studied, it was found only in two nights at one pond. This pond was one of the largest (about 8000 m^2, depth up to 165 cm) and one of the most permanent (up to five months) ponds in the Kirindy forest. There, males called at night from a bush at the water edge about 1 to 4 m above ground. At Andrakata, GLAW & VENCES (1994) found egg clutches of *M. wittei* attached to leaves 1 to 1.5 m above water surface. No egg clutches or tadpoles of this species were found in the Kirindy forest.

Ranidae

Ptychadena mascareniensis (DUMÉRIL & BIBRON, 1841)

This species is one of the few non-endemics to Madagascar. It is distributed throughout Madagascar and is one of the most abundant frogs (GLAW & VENCES 1994). While it is found only sporadically in the closed Kirindy forest, it is the dominant species in the savanna. This is consistent with the view that *P. mascareniensis* profits by anthropogenic disturbances and is rarely found in primary forests (GLAW & VENCES 1994).

Hyperoliidae

Heterixalus tricolor (BOETTGER, 1881)

This frog has a scattered distribution in northern and western Madagascar (GLAW & VENCES 1994). It is a prolonged breeder that starts its breeding activities not earlier than one month after the beginning of the rains. It uses only the most permanent ponds as breeding sites (> 500 m^2; e.g. Fig. 2) that are grown with submergent and emergent vegetation. Males are calling consistently throughout the rainy season from within the pond, either from the floating leaves of water-lilies or from reed grass stems (> 1000

observations; Fig. 9). The calling activity is relatively independent of rainfall. Individuals of this species spend the day sitting motionless on leaves of bushes or grasses not more than 1.5 m above ground level, mainly inside the pond and fully sun-exposed (> 30 observations). There, they face a considerable predation risk by spiders. On six occasions, large spiders (Pisauridae) were observed to suck out *H. tricolor* individuals. These spiders are quite abundant on the reed grass stems within the pond. The colouration of *H. tricolor* changes from yellow or brownish at night to bright white during the day (Fig. 10). A similar behaviour is found in West-African *Hyperolius nitidulus* (Rödel 2000). There, juveniles spend several months of the dry season on grass stems fully exposed to the sun (Spieler 1997; Rödel 2000). Several behavioural and morphological adaptations help to reduce the desiccation risk of these frogs (Schmuck et al. 1988, 1994; Kobelt & Linsenmair 1992, 1995; Linsenmair 1998). Parallel to *Hyperolius* (Grafe et al. 2002), *H. tricolor* individuals remain vigilant during their daily sunbath as they flee into the water or into bushes when disturbed.

Heterixalus carbonei Vences, Glaw, Jesu & Schimmenti, 2000

This frog was recently described by Vences et al. (2000) from the "Tsingy de Bemaraha". The Kirindy forest represents a further record for this species (Fig. 11). Males and females show the same colouration, with females being considerable larger (Tab. 1). In Kirindy, this species shares almost all habitats with *H. tricolor* (e.g. Fig. 2) and shows the same habitat choice and seasonal activity pattern. However, there is almost no overlap in calling activity between *Heterixalus tricolor* and *H. carbonei* during one night. While *H. tricolor* calls from sunset to about midnight, *H. carbonei* starts calling later at night, being rarely active before 11:00 p.m. (> 50 controls). In contrast to *H. tricolor*, males of *H. carbonei* call mainly from high perches at the pond edge (often > 3 m; n > 300). As *H. tricolor*, they spend the day fully sun-exposed mainly on leaves of bushes that surround the breeding pond (> 30 observations). In full sun, their colour is a shiny silver, and shows characteristic dark grey dorsolateral bands.

Heterixalus luteostriatus (Andersson, 1910)

The locally very abundant frog is found throughout all Kirindy habitat types as well as anthropogenic habitats (villages, rice paddies, towns). It is less pretentious compared to the two other *Heterixalus* species in respect to breeding sites, accepting also smaller (> 20 m^2) and less permanent ponds. It starts being active usually in mid December, later than most of the Kirindy amphibians but earlier than *H. tricolor* and *H. carbonei*. The first calling activity in the study period was observed on 19.12.1998, 15.12.1999, 5.12.2000 and 18.12.2001. Highest calling activity is after larger rainfalls. Preferred calling sites are usually high perches (often > 2 m) at the water edge (< 100 observations), more rarely grass stems within the pond. On two occassions, two males of this species were observed wrestling for about 15 seconds, presumably fighting for preferred calling sites.

Microhylidae

Dyscophinae

Dyscophus insularis Grandidier, 1872

This species is widespread mainly over the western part of Madagascar (Glaw & Vences 1994) and is generalistic in respect to breeding site choice and habitat use. It is found

in all pond types and in all habitats, including villages and towns. These frogs are breeding only after heavy rains, calling in choruses aggregated within the pond while they are floating on the water surface. As in *Aglyptodactylus laticeps*, these choruses set in and fade out together. When threatened, *D. insularis* digs itself into the mud. When captured, it utters distress calls similar to its mating call. Tadpoles of this species form large aggregations as a reaction to the presence of predatory fish and birds.

Scaphiophryninae

Scaphiophryne calcarata (MOCQUARD, 1895)

This small, usually brown frog is found mainly in western Madagascar (GLAW & VENCES 1994). In Kirindy, it is an explosive breeder that colonizes freshly arisen ephemeral pools. Waters of all sizes in the closed forest, the river bed and the savanna as well as inside human settlements are used for breeding. After heavy rains, males call in great numbers from crevices and troughs at the edge of these ponds. As described by GLAW & VENCES (1994), a green colour morph exists (Fig. 12). In Kirindy, this colour morph was found in 5.8 % of freshly metamorphosed individuals (n = 104). One population consists of both morphs that were observed interbreeding. When threatened, this frog shows death-feigning behaviour by actively turning on the back, laying motionless and spreading apart its four legs. During the dry season, individuals of *S. calcarata* are found regularly buried in the ground (depth about 30 cm) by villagers digging their peanut fields. Larval developmental time is very short (10 – 11 days).

Scaphiophryne brevis (BOULENGER, 1896)

This species is found in south-western Madagascar (GLAW & VENCES 1994). As the considerably more abundant *S. calcarata*, it breeds primarily in freshly filled pools after heavy rainfalls, using all major habitat types including human settlements. Often, two males were found at a breeding pond forming alternating calling pairs. At the beginning of the dry season of 1999 (22.4.1999), one individual was dug out in the research camp in hard soil at a depth of 20 cm. This individual appeared to be very globular presumably because it stored water. Larval developmental time is very short (10 – 11 days).

Scaphiophryne cf. *marmorata* BOULENGER, 1882

A definitive determination of this species is in progress. This frog is a medium sized, brown marbled microhylid frog (Fig. 13) with enlarged toe tips. It was found in Kirindy only at three different ponds, all of them medium sized (~100 m^2), ephemeral forest ponds. It is an explosive breeder that breeds after heavy rainfalls (> 40 mm) and only a few times during the rainy season. Males are calling floating on the water exclusively at night.

Acknowledgements

I would like to thank K.E. LINSENMAIR for supporting my work, K. DAUSMANN for assisting in the field work, M.-O. RÖDEL for useful comments on the manuscript, F. GLAW for his help in species determination and geographic distribution, P. KAPPELER and the German Primate Center (DPZ) for logistic support and the Biology Departement, Antananarivo University, for their cooperation. Research permits were provided by the Ministère des Eaux et Forêts, Antananarivo. Financial aid was provided by the DAAD (German Academic Exchange Service).

Résumé

La faune d'amphibiens de la forêt sèche de Kirindy à Madagascar.

La faune d'amphibiens de la forêt de Kirindy à Madagascar d'Ouest était examinée pendant une analyse écologique. Elle se compose de 15 espèces de quatre familles différentes (Mantellidae, Ranidae, Hyperoliidae, Microhylidae). Parmi ces espèces il y'a un grand spectre de couvers explosives et couvers prolongés. Concernant la choix des eaux pour la reproduction, il y'a à peu prés la même nombre de generalists et specialists. Le développement larvaire de certaines espèces est très court, probablement une adaptation sur l'ephemeralité des eaux de reproduction. Autres observations de la comportement et caractères écologiques des amphibiens de Kirindy sont présenté.

Mot-Clés: Madagascar; forêt de Kirindy; forêt sèche saisonnière; amphibiens; choix d'habitat; choix des eaux pour la reproduction.

References

ANDREONE, F., M. VENCES, & J.E. RANDRIANIRINA (2001): Patterns of amphibian and reptile diversity at Berara Forest (Sahalamaza Peninsula), NW Madagascar. – Italian Journal of Zoology, **68**: 235-241.

BUSSE, K. & W. BÖHME (1992): Two remarkable discoveries of the genera *Mantella* (Ranidae: Mantellinae) and *Scaphiophryne* (Microhylidae: Scaphiophryninae) from the west coast of Madagascar. – Rev. franc. Aquariol., **19**(1/2): 57-64.

GLAW, F. & M. VENCES (1994): A fieldguide to the amphibians and reptiles of Madagascar. – Köln. (M. Vences & F. Glaw Verlags GbR).

— & — (1997): New species of the *Boophis tephraeomystax* group (Anura: Ranidae: Rhacophorinae) from arid Western Madagascar. – Copeia, **1997**(3): 572-578.

—, — & W. BÖHME (1998): Systematic revision of the genus *Aglyptodactylus* BOULENGER, 1919 (Amphibia: Ranidae), and analysis of its phylogenetic relationships to other Madagascan ranid genera (*Tomopterna*, *Boophis*, *Mantidactylus* and *Mantella*). – Journal of Zoological Systematics and Evolutionary Research, **36**: 17-37.

GOSNER, K. L. (1960): A simplified table for staging anuran embryos and larvae with notes on identification. – Herpetologica, **16**: 183-190.

GRAFE, T.U., S. DÖBLER & K.E. LINSENMAIR (2002): Frogs flee from the sound of fire. – Proceedings of the Royal Society, London, **269**: 999-1003.

JANZEN, D. (1992): Tropische Trockenwälder: Die am stärksten bedrohten Ökosysteme der Tropen. – pp. 152-161 in: WILSON, E.O. (ed.): Ende der biologischen Vielfalt? – Heidelberg (Spektrum-Verlag).

KOBELT, R.F. & K.E. LINSENMAIR (1992): Adaptations of the reed frog *Hyperolius viridiflavus* (Amphibia, Anura, Hyperoliidae) to its arid environment: VI. The iridophores in the skin of *Hyperolius viridiflavus taeniatus* as radiation reflectors. – Journal of Comparative Physiology B, **162**: 314-326.

— & — (1995): Adaptations of the reed frog *Hyperolius viridiflavus* (Amphibia, Anura, Hyperoliidae) to its arid environment: VII. The heat budget of *Hyperolius viridiflavus nitidulus* and the evolution of an optimized body shape. – Journal of Comparative Physiology B, **165**: 110-124.

KUCHLING, G. (1993): Zur Verbreitung und Fortpflanzung von *Mantella betsileo* in Westmadagaskar. – Salamandra, Frankfurt/M., **29**(3/4): 273-276.

LINSENMAIR, K.E. (1998). Risk-spreading and risk reducing tactics of West African anurans in an unpredictably changing and stressful environment. – pp. 221-242 in: NEWBERRY, D.M., H.H.T. PRINS & N.D. BROWN (eds.): Dynamics of Tropical Communities. – London (Blackwell Science).

MYERS, N., R.A. MITTERMEIER, C.G. MITTERMAIER, G.A.B. DA FONSECA & J. KENT (2000): Biodiversity hotspots for conservation priorities. – Nature, **403**: 853-858.

NELSON, R. & N. HORNING (1993): AVHRR-LAC estimates of forest area in Madagascar, 1990. – International Journal of Remote Sensing, **14**: 1463-1475.

RAKOTONIRINA (1996): Composition and structure of a dry forest on sandy soils near Morondava. – pp. 81-88 in: GANZHORN, J.U. & J.-P. SORG (eds.): Ecology and economy of a tropical dry forest in Madagascar. Primate Report 46-1. – Göttingen (DPZ).

RÖDEL, M.-O. (1998): Kaulquappengesellschaften ephemerer Savannengewässer in Westafrika. – Frankfurt am Main (Edition Chimaira).

— (2000): Herpetofauna of West Africa. Vol. I. Amphibians of the West African Savanna. – Frankfurt am Main (Edition Chimaira).

SCHMUCK, R., F. KOBELT, & K.E. LINSENMAIR (1988): Adaptations of the reed frog *Hyperolius viridiflavus* (Amphibia, Anura, Hyperoliidae) to its arid environment: V. Iridophores and nitrogen metabolism. – Journal of Comparative Physiology, **158**: 537-546.

—, W. GEISE & K. E. LINSENMAIR (1994): Life cycle strategies and physiological adjustments of reedfrog tadpoles (Amphibia, Anura, Hyperoliidae) in relation to the environmental conditions. – Copeia, **1994**(4): 996-1007.

SORG, J.-P. & U. ROHNER (1996). Climate and tree phenology of the dry deciduous forest of the Kirindy forest. – pp. 57-80 in: GANZHORN, J.U. & J.-P. SORG: Ecology and economy of a tropical dry forest in Madagascar. Primate Report 46-1. – Göttingen (DPZ).

SPIELER, M. (1997): Anpassungen westafrikanischer Anuren an Austrocknungsrisiko und Räuberdruck in einem saisonalen Lebensraum. – Berlin (W & T Verlag).

STANISZEWSKI, M. (2001): Mantellas. – Frankfurt am Main (Edition Chimaira).

VENCES, M. & F. GLAW (2001): When molecules claim for taxonomic changes: New proposals on the classification of Old World treefrogs. – Spixiana, **24**(1): 85-91.

— & — (2002): Molecular phylogeography of *Boophis tephraeomystax*: a test case for east-west vicariance in Malagasy anurans. – Spixiana, **25**(1): 79-84.

—, —, R. JESU & G. SCHIMMENTI (2000): A new species of *Heterixalus* (Amphibia: Hyperoliidae) from western Madagascar. – African Zoology, **35**(2): 269-276.

Author: JULIAN GLOS, Lehrstuhl für Tierökolgie und Tropenbiologie, Biozentrum, Am Hubland, D-97074 Würzburg, Germany, E-Mail: glos@biozentrum.uni-wuerzburg.de.