Reproductive biology of the West African savannah frog
Hyperolius nasutus GÜNTHER, 1864
(Amphibia: Anura: Hyperoliidae)

Fortpflanzungsbiologie des westafrikanischen Savannenfrosches
Hyperolius nasutus GÜNTHER, 1864
(Amphibia: Anura: Hyperoliidae)

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KURZFASSUNG

Wir untersuchten das Paarungsgeschehen bei *Hyperolius nasutus* GÜNTHER, 1864 an einem temporären Savannentümpel im Comoé-Nationalpark, Elfenbeinküste. *Hyperolius nasutus* ist eine Art mit ausgedehnter Reproduktionszeit ('prolonged breeder'), die etwa 2-5 Monate nach dem Einsetzen der Regenzeit beginnt. Rufende Männchen saßen bevorzugt auf Seggen, die im Wasser wuchsen. Andere syntope Riedfroscharten wählten andere Rufwarten. Wir fanden Hinweise darauf, daß bei günstigen Wetterbedingungen innerhalb einer Regenzeit reproduzierende Männchen zweier aufeinanderfolgender Generationen zeitlich versetzt am Gewässer auftreten können. Die Größe (Länge und Masse) der Männchen erlaubte keine Vorhersagen über deren Paarungserfolg. Weibchen entschieden sich im Wahlversuch nicht bevorzugt für das größere Männchen. Im Durchschnitt betrug die Masse des Männchens 80% der Masse des laichreifen Weibchens, mit dem es verpaart war. Mögliche Erklärungen dafür, daß Weibchen nicht die größten Männchen wählten, werden diskutiert.

ABSTRACT

We studied the mating activities of *Hyperolius nasutus* GÜNTHER, 1864 at a temporary savannah pond in the Comoé National Park, Ivory Coast. *Hyperolius nasutus* is a prolonged breeder that started reproducing 2-5 months after the beginning of the rainy season. At that pond, males preferably called from sedges growing in shallow water, whereas other syntopic hyperoliid species chose different calling sites. We found evidence that two consecutive generations of reproducing male *H. nasutus* were sequentially present at the pond within one rainy season. Neither male body length nor mass predicted male mating success. Females did not preferentially select larger over smaller males. On average, a female mated with a male which had about 80% of her own body mass. We discuss possible explanations for this behavior.

KEY WORDS

Amphibia: Anura: Hyperoliidae: *Hyperolius nasutus*, female choice, reproduction, population ecology, behavior, savannah, Comoé National Park, Ivory Coast, West Africa

INTRODUCTION

Most West African savannah anurans seem to pursue one of two different reproductive strategies: species that spawn within one to three days after a rainfall event (explosive breeders) and species whose breeding period extends more or less continuously over weeks or even months (prolonged breeders; RÖDEL 2000). Under the climatic conditions of the study area, explosive breeding is largely restricted to the beginning of the rainy season (RÖDEL 1998, 2000). At this time both amount and temporal pattern of precipitation are highly unpredictable, however rainfall is essential for reproduction. In the explosive breeding species, the number of male and female individuals at a pond is more or less balanced or slightly male-biased. Anurans that mainly reproduce towards the middle and the end of the rainy season are almost exclusively prolonged breeders. At that time reproduction is less dependent on a definite rainfall event. The males congregate in large numbers almost every night in choruses around the breeding ponds while the number of females present is comparatively small. In some prolonged breeders calling and spawning sites are identical (RÖDEL 1998). In this case, female choice of the mat-

ing partner might be influenced by the quality of the site. In other species males call at some distance from potential spawning sites and do not offer any site information for females. If the male provides no direct benefits in terms of increased breeding success, we would expect females to select indirect benefits such as "good" genes (FISHER 1958) or high genetic variability (POMIANKOWSKI 1988).

Hyperolius nasutus GÜNTHER, 1864 is a common West African savannah frog. In southern Comoé National Park, Ivory Coast, *H. nasutus* is the last species to begin reproduction during the rainy season (RÖDEL 2000) in that larger choruses usually form during August / September in the second half of the regional rainy season. Since its reproductive period lasts several months, *H. nasutus* is a prolonged breeder. Eggs are attached to submerged vegetation (RÖDEL 2000). Little is known about the biology of the species. In this study, we aimed to gain general information on the reproductive biology of *H. nasutus* including data on the possibility of differential choice of males by females.

MATERIALS AND METHODS

Study site

The study was conducted in the rainy seasons of 1996 and 1999 in the Comoé National Park (CNP, 3°07' - 4°26' W, 8°30' - 9°37' N), Ivory Coast. The CNP comprises different vegetation zones from the Guinea to the Sudan savannah. Our study site was within open tree savannah (POILECOT 1991) in the northern part of the Guinea savannah. During the dry period (November to March / April), open water normally persists only within the river beds. During the rainy season (mean annual precipitation: 900-1,100 mm) a large number of ephemeral savannah ponds form. Our specimens all originated from the 'Hyperolius pond' (HP) appr. 5 km North of the Comoé Research Station (8°45,1'N, 3°49,0'W). This pond was chosen because, based on our previous knowledge, this pond seemed to very well reflect a typical breeding site for West African *H. nasutus* populations (RÖDEL 1998, 2000; K. P. LAMPERT, K. E. LINSENMAIR & M.-O. RÖDEL unpubl. data). The HP is a large savannah pond of approximately 50 m x 15 m surface and a maximum water depth of one meter. Two to three months after the onset of the rainy season it harbors a rich vegetation that is mainly made up of different grass species and water lilies. A more detailed description, including the amphibian species breeding in this pond is given by RÖDEL (1998). POILECOT (1991) provides more information on geography, geology and vegetation of the CNP.

Study animals

Hyperolius nasutus was believed to be a widespread African savannah frog, ranging from West into southern Africa (SCHIØTZ 1999; RÖDEL 2000). Recently CHANNING et al. (2002) revised the sharp-nosed reed frogs on the basis of advertisement calls. They concluded that two species occur in West Africa: a forest dwelling species (*H. nasutus*) and a savannah form that they assigned to *H. acuticeps* AHL, 1931. The latter species which should include *H. lamottei* LAURENT, 1958 was believed to occur in CNP. However, we never found any *H. nasutus* like frog in more than 20 West and Central African forest sites, which we investigated between Guinea and Central African Republic. All *H. nasutus* specimens recorded by us were exclusively found in savannah habitats. *Hyperolius lamottei*, although, having a call very similar to that of *H. nasutus* from CNP, is clearly a morphologically distinct species (RÖDEL & ERNST 2003) that is not closely related to *H. nasutus* (samples from various West African localities; J. KOSUCH and M.-O. RÖDEL unpublished data from mitochondrial 16S rDNA). We agree with CHANNING et al. (2002) that the name *H. nasutus* (sensu SCHIØTZ 1999; RÖDEL 2000) probably comprises several cryptic species. However, as long as the systematics of this species group is not sufficiently

elucidated we continue to refer to CNP frogs as *H. nasutus*. Voucher specimens from CNP are stored in the collection of the Staatliches Museum für Naturkunde, Stuttgart (SMNS 8968.1-2, 9679.1-11), the research collection of the senior author (MOR 9678) and the Institute of Zoology at Mainz University (tissue samples).

Other syntopic hyperoliid frogs recorded in this study with activity times that match those of *H. nasutus,* are either typical savannah species: *Hyperolius nitidulus* PETERS, 1875, *Afrixalus vittiger* (PETERS, 1876) and *A. weidholzi* (MERTENS, 1937), or normally inhabit forested and farmbush habitats: *Hyperolius concolor* (HALLOWELL, 1844). For more detailed descriptions of these species see SCHIØTZ (1999) and RÖDEL (2000).

Field data

Hyperolius nasutus were observed and measured at the HP between 19:00 – 22:00 (22 May to 27 September 1996; 20-26 July and 22-24 October 1999). Measurements were taken with dial callipers to the nearest 0.1 mm (snout-vent length, SVL) and with a laboratory balance (Ohaus CT 10 ®, precision 0.01 g). It was not always possible to obtain all individual data from a particular frog. Sample size therefore differs among analyses.

All hyperoliid species were registered along 10 line transects, equally placed around the HP (12 June to 22 August 1996). Approximately half of each transect reached into the water. Each transect was 10 m long. Transects were intensively patrolled at a constant speed, thereby recording all calling hyperoliid frogs on either side of the path within a distance of 100 cm. Frogs were assigned to 2 m² sample units (SU; 10 SUs per transect). Calling sites were defined as: 1) shrubs and trees (only *Nauclea latifolia*), 2) Cyperaceae (*Eleocharis acutangula*, stalk without ramification, stiff and triangular), 3) different Poaceae (stalk without ramification, flexible and round), 4) different herbs (stalk flexible, round and with ramifications) and 5) water lilies (*Nymphaea lotus*). Stands of *Eleocharis* were always close to or within water whereas Poaceae and different herbs dominated the areas off the water.

In addition, two 8 m x 8 m sampling plots were searched for calling sites three times (28 and 30 May, 4 June 1996). In the first plot, one quarter was covered with *E. acutangula*, the other three quarters were covered with various Poaceae, and a medium sized tree (4 m high, crown diameter: 3 m). Plot 2 was half grown over with *E. acutangula* and half with various Poaceae and other herbs. In these plots all *H. nasutus* males were registered including data on their density, type of calling site, its height and distance to the edge of the pond. Additionally, we measured the straight-line distance to the nearest conspecific male. The nearest neighbors could be outside the plot. During the night we marked all calling sites with colored plastic tape. The measurements were taken the following morning. For abundance estimates we additionally performed T²-sampling at 21:00 of 5 June 1996 (50 *H. nasutus* males; see KREBS 1999). Random points were marked with plastic tape the day preceding T²-sampling.

Experiments

From 28 August to 27 September 1996 we caught 68 *H. nasutus* pairs and 214 single, calling males. Within two hours after capture, pairs were separated by us, measured and weighed. Subsequently, the frogs were transferred to 23 cm x 15 cm x 15 cm aquaria with 5 cm of water. Submerged vegetation was provided as spawning substrate. Each female was placed together with its original mate and a randomly chosen calling male. Both males typically started calling within a few minutes after being placed in the aquarium. After one hour all females were in amplexus. After two hours, the males not in amplexus were caught and measured again. Differences in size and/or mass of both males in a treatment were used for individual recognition. All females were measured and weighed again the following morning and all oviposited eggs were counted. In 1999 (22-24 October) additional 58 *H. nasutus* amplectant pairs were caught and measured. All frogs were released the evening after being captured. Statistical analysis was performed with the SPSS (6.0 and 7.0) for Windows.

Table 1: Spearman rank correlation (r_s) of snout-vent-length and body mass in *Hyperolius nasutus* Günther, 1864 as well as sex dependant size and mass differences (Mann-Whitney U test, see text). Samples of 1996 and 1999 were analyzed separately; m - male, f - female, SVL - snout-vent-length (mm), w – body mass (g), n - sample size.

Tab. 1: Korrelation von Kopf-Rumpflänge und Körpermasse (Spearman Rangkorrelation, r_s) bei männlichen und weiblichen *Hyperolius nasutus* Günther, 1864 sowie geschlechtsspezifische Größen- und Masse-unterschiede (Mann-Whitney U Test, siehe Text). Daten aus 1996 und 1999 wurden getrennt ausgewertet; m - Männchen, f - Weibchen, SVL - Kopf-Rumpflänge (mm), w – Körpermasse (g), n - Stichprobengröße.

| | | SVL / mass correlation Längen / Gewichts-Korrelation | | | Sex dependant size and mass differences / Geschlechtsspezifische Größen und Gewichtsunterschiede | | | | |
sex	year	r_s	p	n	year	measure	Z	p	n
m	1996	0.7061	< 0.001	282	1996	SVL	-2.764	0.006	350
m	1999	0.8545	< 0.001	57	1999	SVL	-5.8485	< 0.001	115
f	1996	0.5957	< 0.001	68	1996	w	-8.7252	< 0.001	350
f	1999	0.3850	0.003	58	1999	w	-8.8353	< 0.001	115

RESULTS

Snout-vent length, body mass and clutch size

We measured 339 males (SVL: mean ± SD = 22.1 ± 0.7 mm, range = 18.4-25.5 mm; mass: mean ± SD = 0.51 ± 0.06 g, range = 0.32-0.73 g) and 126 females (SVL: mean ± SD = 22.9 ± 0.7 mm, range = 18.9-25.2 mm; mass before spawning: mean ± SD = 0.64 ± 0.01 g, range = 0.42-0.77 g; mass after spawning: mean ± SD = 0.56 ± 0.04 g, range = 0.39-0.71 g) of *Hyperolius nasutus*. Male and female SVL and mass were correlated in both sexes and differed between sexes (table 1). Female mass (before spawning) and SVL were not correlat-

ed with clutch size. Female mass loss after spawning was correlated with clutch size (1996: r_s = 0.3172, p = 0.014, n = 63; 1999: r_s = 0.4582, p = 0.002, n = 44). Clutch size (1996: x̄ = 161.6, 1999: x̄ = 158.9, range: 60-271, n = 107) and female mass loss after spawning (1996: x̄ = 12.1 %, 1999: x̄ = 14.2 %, range: 2.7-27.4 %, n = 107) did not differ between the two years.

In 1996 reproducing *H. nasutus* were observed at first towards the end of May. During mid-September we observed that the mean size of newly arriving frogs decreased (fig. 1). Males measured during period one (P1, 28 August to 2 September 1996) (see table 2) were significantly larger and heav-

Table 2: Snout-vent-length (mm) and body mass (g) of male and female *Hyperolius nasutus* Günther, 1864 captured during period one (P1, 28 August to 2 September 1996) and two (P2, 18-27 September 1996) and the differences observed (Mann-Whitney U-test, MWU); sample size in parentheses. SVL - snout-vent-length (mm), w – body mass (g), eggs - clutch size.

Tab. 2: Kopf-Rumpflänge (mm) und Körpermasse (g) männlicher und weiblicher *Hyperolius nasutus* Günther, 1864 aus Sammelperiode eins (P1, 28. August bis 2. September 1996) und zwei (P2, 18.-27. September 1996) und die beobachteten Unterschiede (Mann-Whitney U-Test, MWU); Stichprobengröße in Klammern. SVL - Kopf-Rumpflänge (mm), w – Körpermasse (g), eggs - Gelegegröße.

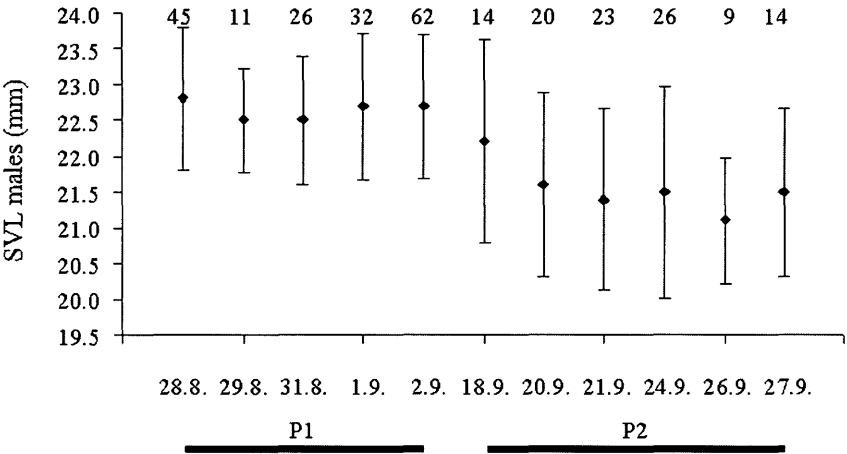| | Males / Männchen | | | | Females / Weibchen | | | | | |
| | P1 (176) | | P2 (106) | | P1 (20) | | | P2 (48) | | |
	SVL	w	SVL	w	SVL	w	eggs	SVL	w	eggs
mean	22.7	0.54	21.5	0.47	22.8	0.65	198.5	22.6	0.60	150.4
SD	1.0	0.07	1.3	0.07	0.9	0.05	30.1	1.0	0.07	31.5
MWU	Z		p		Z			p		
SVL	- 7.2109		< 0.001	-	0.4080			0.683		
w	- 7.502		< 0.001	-	2.3655			0.018		
eggs					- 4.2382			< 0.001		

Fig. 1: Snout-vent-length (SVL [mm]; mean value ± standard deviation) of male *Hyperolius nasutus* GÜNTHER, 1864 from Comoé National Park, Ivory Coast. Numbers on top of error bars indicate sample size. Compared are SVL of males captured during period one (P1, 28 August – 2 September) and two (P2, 18-27 September), respectively ($Z = -7.2109$, $p < 0.001$; compare table 2).

Abb. 1: Kopf-Rumpflänge (SVL [mm]; Mittelwert ± Standardabweichung) männlicher *Hyperolius nasutus* GÜNTHER, 1864 aus dem Comoé Nationalpark, Elfenbeinküste. Die Zahlen über den Fehlerbalken bezeichnen die Stichprobengröße. Verglichen wurden die Kopf-Rumpflänge von Männchen aus Sammelperiode eins (P1, 28 August - 2 September), mit denen aus Sammelperiode zwei (P2, 18-27 September; $Z = -7,2109$, $p < 0,001$; vergleiche Tabelle 2).

ier than males measured during period two (P2, 18-27 September 1996). During P1, females were, on the average, heavier and laid more eggs but did not show statistical differences in SVL from females caught during P2 (table 2).

Calling sites of *H. nasutus* and other hyperoliid species

We registered the calling sites of 94 *H. nasutus* males within the two 8 x 8 m sampling plots. Significantly more males used *Eleocharuis acutangula* (84) than other plants (10; herbs: 6 , shrub: 2, *Nymphaea lotus*: 2) as calling sites ($X^2 = 116.51$, $p < 0.001$). Most *H. nasutus* calling sites were plants emerging from the water (65), while 29 males were calling from plants that grew on land ($X^2 = 26.34$, $p < 0.001$). Out of 354 *H. nasutus* males that we registered during our transect walks, 276 were calling from *E. acutangula*, 78 used other plants ($X^2 = 221.49$, $p < 0.001$). While walking along the transects, we also registered *H. nasutus* pairs. Nineteen pairs were encountered on the pond edge, 11 near the

center of the pond ($X^2 = 4.27$, $p = 0.045$). We randomly collected 33 calling males from the pond's edge and 29 calling males from the center of the pond. We found no difference in SVL ($Z = -1.0118$, $p = 0.312$) or in mass ($Z = -0.6572$, $p = 0.511$).

All other reed frogs at HP, except *Hyperolius concolor*, called mainly from plants growing on land (table 3). In addition, we found differences in height of calling sites (Kruskal-Wallis; $X^2 = 73.35$, $df = 4$, $p < 0.001$), distance to nearest conspecific male ($X^2 = 38.79$, $df = 4$, $p < 0.001$) and distance to the pond's bank ($X^2 = 45.41$, $df = 4$, $p < 0.001$) between the five hyperoliid species (n = 323). Calling height of *H. nasutus* males, however, only differed from *H. nitidulus* (Scheffé post-hoc test: $p < 0.001$) and *Afrixalus vittiger* ($p < 0.001$) that both called from higher positions (table 4). The distance of a calling male to its nearest conspecific neighbor and to the pond's bank differed only between *A. weidholzi* and all other species ($p < 0.001$). In *Afrixalus weidholzi* the distance between calling conspecific males and to the water line was much

Table 3: Number of calling sites of five hyperoliid species (sample size in parentheses) on two 8 m x 8 m plots at the 'Hyperolius pond', Comoé National Park, Ivory Coast. Nal - *Nauclea latifolia*, Ea - *Eleocharis acutangula*, Po – Poaceae, Nyl - *Nymphaea lotus*, cord - transect line (compare text), Σ water – calling sites over water, Σ land – calling sites over land.

Tab. 3: Anzahl der Rufwarten von fünf Riedfroscharten (Stichprobengröße in Klammern) auf zwei 8 m x 8 m Untersuchungsflächen am 'Hyperolius-Tümpel', Comoé-Nationalpark, Elfenbeinküste. Nal - *Nauclea latifolia*, Ea - *Eleocharis acutangula*, Po – Poaceae, Nyl - *Nymphaea lotus*, cord - Transektschnur, Σ water – Rufwarten über Wasser, Σ land - Rufwarten über Land.

species / Art	Nal	Ea	Po	Nyl	herbs	cord	Σ water	Σ land
Hyperolius nasutus (94)	2	84	6	1	1	0	65	29
Hyperolius concolor (15)	3	10	2	0	0	0	8	7
Hyperolius nitidulus (107)	45	30	22	0	5	5	21	86
Afrixalus vittiger (91)	27	10	53	0	0	1	3	88
Afrixalus weidholzi (20)	0	3	16	0	0	1	0	20

greater than in any other species investigated. *Hyperolius nasutus* males sitting on different plants but as close as 4-5 cm from each other uttered typical advertisement calls, but immediately defended the calling sites when another male climbed up the same plant.

Abundance

In 1996, we counted between 28 - 54 *H. nasutus* males per night along the 10 transects, which was 0.14 to 0.27 frogs per square meter. T²-sampling revealed a frog density of 0.14 frogs per m². Calling *H. nasutus* males were not randomly distributed along the pond's edge [Hines-test for random distribution pattern (Krebs 1999): $H_{(T)} = 2.100$, $p < 0.05$; values higher than 1.338 represent non random distribution]. Based on T²-sampling and transect counts we calculated 170-328 calling *H. nasutus* males per night at the 'Hyperolius pond'.
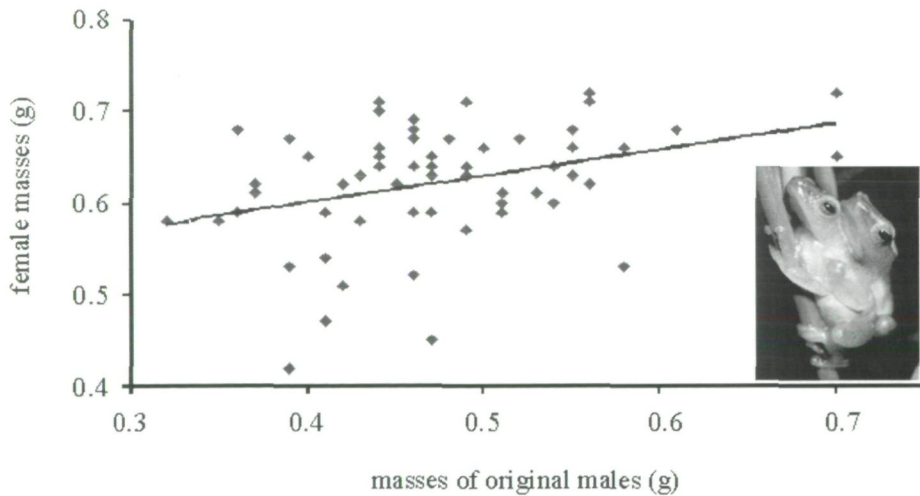

Fig. 2: Correlation between body masses of pairs of *Hyperolius nasutus* Günther, 1864. Data from 1996 (n = 68) (Spearman rank correlation: $r_S = 0.3461$; $p = 0.008$).

Abb. 2: Korrelation der Körpermassen bei Paaren von *Hyperolius nasutus* Günther, 1864. Daten aus 1996 (n = 68) (Spearman Rangkorrelation: $r_S = 0,3461$; $p = 0,008$).

Do females pick males randomly or are they choosy?

We separately compared SVL and body weight (mean ± SD) of amplectant (n = 55) and solitary (n = 227) males, respectively. These two types of males differed significantly in SVL ($Z = -3.892$, $p < 0.001$) and body weight ($Z = -3.788$, $p < 0.001$). Amplectant males were lighter ($\bar{x} = 0.48 \pm 0.08$ g) and smaller ($\bar{x} = 21.6 \pm 1.4$ mm) than solitary males ($\bar{x} = 0.52 \pm 0.08$ g; $\bar{x} = 22.4 \pm 1.2$ mm).

In 58 mate choice experiments two males were presented to each female; the original and an alternative mate. Thirty-two females chose the lighter male, 25 the heavier one ($X^2 = 1.72$, $p = 0.190$), in one case the males were of equal weight. Twenty-four females chose the larger male, 28 the smaller one ($X^2 = 0.62$, $p = 0.433$), in six cases the males were of equal length. Thirty-nine females chose the original male, 19 females chose the alternative one ($X^2 = 13.79$, $p < 0.001$). We found a significant positive correlation between the body masses of the original males ($r_S = 0.3461$, $p = 0.008$) and the experimentally chosen males ($r_S = 0.2559$, $p = 0.049$) with the body masses of their respective females (fig. 2). There was no significant correlation between the SVLs of males and their respective females. There was a significant positive correlation between the number of eggs deposited and the mass of the original male in 1996 ($r_S = 0.3062$, $p = 0.021$, n = 39) and 1999 ($r_S = 0.6451$, $p < 0.001$, n = 44). In the 19 experiments where females chose an alternative male, we neither found a significant correlation between the female's body mass with that of the original male ($r_S = 0.3123$, $p = 0.193$), nor with the body masses of the alternative males ($r_S = 0.0892$, $p = 0.717$). The body masses of the 19 alternative and the 19 original males did not differ significantly ($Z = -1.4911$, $p = 0.136$). In the 39 experiments where the females mated again with their original males we found no significant correlation between the body masses of the rejected (alternative) males and the females ($r_S = 0.0632$, $p = 0.702$). On the average, in an amplectant pair of *H. nasutus*, the male weighed 81.7 % of the female.

Table 4: Perch height of male reed frogs calling from over land and over water, distance of calling male to the nearest conspecific male and the pond's bank (sample size in parentheses). All measures are given in cm. Data from two 8 m x 8 m plots at the 'Hyperolius pond', Comoé National Park, Ivory Coast and T²-sampling (50 *Hyperolius nasutus* males). SD - standard deviation.

Tab. 4: Rufwartenhöhen von Riedfroschmännchen (über Land und über Wasser), Entfernung zum nächsten Männchen der gleichen Art und zum Ufer (Stichprobengrößen in Klammern). Alle Entfernungen in cm. Daten von den zwei 8 m x 8 m Untersuchungsflächen am 'Hyperolius-Tümpel', Comoé-Nationalpark, Elfenbeinküste und vom 'T²-sampling' (50 *Hyperolius nasutus* Männchen). SD - Standardabweichung.

| Species / Art | Perch height (cm) / Rufwartenhöhe (cm) | | | | | | Distance to (cm) / Entfernung zu (cm) | | | | | |
| | over land / über Land | | | over water / über Wasser | | | conspecific male / artgleiches Männchen | | | bank / Ufer | | |
	mean	SD	range	mean	SD	range	mean	SD	range	mean	SD	range
Hyperolius nasutus (144)	68	75	0-265	156	63	20-315	96	104	4-606	129	78	0-315
Hyperolius concolor (15)	42	41	2-89	104	56	30-209	261	284	5-1000	75	58	2-209
Hyperolius nitidulus (107)	145	98	0-375	172	78	20-300	81	78	3-370	150	94	0-375
Afrixalus vittiger (91)	180	105	0-445	82	53	20-115	63	77	6-430	176	105	0-445
Afrixalus weidholzi (20)	1765.50	1672.32	0-8050	-	-	-	456.80	917.49	20-4015	1765.50	1672.32	0-8050

DISCUSSION

Length measures in *Hyperolius nasutus* were within the known range of sharp-nosed reed frogs (see Rödel 2000; Channing 2001). However, in contrast to information in Schiøtz (1999), sexes showed small but significant sex-specific differences in body length. With a continuous reproductive time of several months *H. nasutus* belongs to the prolonged breeders (Rödel 2000). Density of reproducing *H. nasutus* was high during the second part of the rainy season in 1996 and in 1999. Males were preferably calling from one particular plant species, the sedge *E. acutangula*. This preference is consistent with what we observed in other West African sites, including other ponds in CNP. Whenever available, sharp-nosed reed frogs seem to prefer small, thin, stiff reed grasses that grow in water (Rödel 2000, Channing 2001; Burger et al. 2004; Lötters et al. 2004). *Hyperolius nasutus* thus selects different plant species and calling sites than other syntopic hyperoliid species. Calling males were clumped and defended a small territory (calling site plant), but no bias in male distribution could be found (e.g. larger males at the potentially more attractive pond edges, where most pairs formed). Calling and breeding sites were not linked spatially. Hence, males seem to offer no resources to females, and the mating system can be best described as a lek mating system (Bradbury & Gibson 1983; Höglund & Alatalo 1995; Sullivan et al. 1995).

The observed decrease in the average male size (SVL, body mass) towards the end of the rainy season in 1996 (P2) is indirect evidence for the emergence of another generation of *H. nasutus*. Lampert & Linsenmair (2002) found a similar decrease in size in the West African *H. nitidulus*. This decrease was correlated with the appearance of males that reproduced in the same rainy season they were born in (second generation per year). The exceptionally early start of the rainy season and, as a consequence, the early start of reproduction in 1996 (end of May; in other years larger choruses were not formed before August / September, Rödel 2000) might have enabled *H. nasutus* to produce a generation that did not have to aestivate before reproducing. In female *H. nasutus* the above decrease in SVL was not observed, although, they were heaviest and laid most eggs at the beginning of the study period. The absence of a decrease in SVL could indicate that female *H. nasutus* did not reproduce in the same year in which they had metamorphosed. This can be due to longer maturation times for females, i.e. females may depend on a certain body size/mass to spawn (but see Lampert & Linsenmair 2002). Decreased female mass and clutch size during the second period in 1996 may be due to the fact that females reproduce more than once per year and succeeding clutches are generally smaller (Davidson & Hough 1969; Grafe 1997).

The most interesting finding was that females did not prefer larger males and that we could not detect size assortative mating, instead, we found weight assortative mating. We had expected a female preference for larger males as amphibian body size seems to be a criterion of quality. Large individuals are thought to be more successful in terms of survival and reproductive success (e.g., Ryan 1980; Passmore et al. 1992; Castellano & Giacoma 1998; but e.g. see Stephenson & Verrell 2003 for a contradicting example). Size assortative mating has been reported for many anuran species and explained by an optimized fertilization rate, achieved by an optimal cloaca fit during spawning (Licht 1976; Davies & Halliday 1977; Bourne 1993). In this study mass assortative mating was found. The variability of male body mass explained by female body mass, however, was rather low compared to other studies where size assortative mating was found (Robertson 1986, 1990; Bourne 1993). A puzzling detail of our finding was that although mass of mating partners correlated significantly, length did not. Robertson (1986, 1990) reported the same for *Uperoleia*. According to this author, males that defend a territory loose mass but not length. Because females chose males for their mass, mates' lengths were not significantly intercorrelated.

Extraordinary high predatory pressure when spawning under water might explain why female *H. nasutus* do not chose the largest and heaviest males, as agility under water might be higher when the females carry a lighter male. The dense water vegetation and the high density of predators preying on adult frogs (giant water bugs, spiders, snakes, turtles, fishes and small crocodiles - RÖDEL 1998) possibly make female agility a limiting factor in mate choice.

It is noteworthy that in *H. nasutus* the original female mate choice was, to a considerable degree, reproducible in experiments. Significantly more females preferred the males they were originally paired with. Repeatability of female choice was also documented for other frog species (e.g. ROBERTSON 1990) including another *Hyperolius* species (JENNIONS et al. 1995b). However, it remains unclear which male traits *H. nasutus* females exactly prefer. Further investigations on mate choice in *H. nasutus* should include the analysis of various call parameters (e.g. MACNALLY 1981; DYSON & PASSMORE 1988a, 1988b; PASSMORE et al. 1992; JENNIONS et al. 1995a), duration of male presence at the breeding site, calling activity at the breeding site (JACOBSON 1985; CHERRY 1993; MURPHY 1994; DYSON et al. 1998) and/or particular genotypes and genetic diversity (ABT & REYER 1993).

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