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Goliath frogs build nests for spawning – the reason for their gigantism?

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ABSTRACT

In contrast to its popularity, astonishingly few facts have become known about the biology of the Goliath Frog, *Conraua goliath*. We herein report the so far unknown construction of nests as spawning sites by this species. On the Mpoula River, Littoral District, West Cameroon we identified 19 nests along a 400 m section. Nests could be classified into three types. Type 1 constitutes rock pools that were cleared by the frogs from detritus and leaf-litter; type 2 constitutes existing washouts at the riverbanks that were cleared from leaf-litter and/or expanded, and type 3 were depressions dug by the frogs into gravel riverbanks. The cleaning and digging activities of the frogs included removal of small to larger items, ranging from sand and leaves to larger stones. In all nest types eggs and tadpoles of *C. goliath* were detected. All nest types were used for egg deposition several times, and could comprise up to three distinct cohorts of tadpoles. Nests seemed to be clustered. Camera trapping revealed that nests are guarded by adult frogs at night. The breeding nests may allow the frogs to deposit their eggs away from the torrent rivers, and potential egg and tadpole predators. As nest construction, at least in some cases, requires the removal of large and heavy items, we hypothesize that this can only be achieved by decent sized frogs, possibly explaining the unique size of the species.

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Introduction

Amphibians have evolved the most diverse reproductive strategies of all terrestrial vertebrates (Duellman and Trueb 1986; Haddad et al. 2005; Wells 2007), and new reproductive modes are still discovered (e.g. Iskandar et al. 2014; Kusrini et al. 2015). One of the most famous frogs is the largest living species, the Goliath Frog, *Conraua goliath* (Boulenger, 1906), reaching more than 34 cm snout-vent-length and occurring along streams in lowland and mid-altitude rainforest from southwestern Cameroon into Equatorial Guinea (IUCN 2019; Figure 1). In contrast to its degree of popularity, astonishingly few facts have become known about its biology. Previous studies address the taxonomy of the species (Lamotte and Perret 1968), the tadpoles (Lamotte et al. 1959), gut parasites (Daniel et al. 2015),

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Figure 1. Adult *Conraua goliath* from Cameroon (a) and different sections of one of its habitats, the Mpoula River, Littoral District, western Cameroon (b, c).

locomotion (Herrmann and Edwards 2006), attempts to keep it in captivity (Gewalt 1977, 1996), and its consumption as bush meat (Gonwouo and Rödel 2008), but very little is known about its reproductive biology and behavior. One study, Sabater-Pi (1985), reported details concerning the larval development and some aspects of the species' reproduction; however, without mentioning any kind of parental care. During recent field work, we have been repeatedly informed by local Goliath Frog hunters, that this species constructs nests for egg deposition and guards the tadpoles. We thus decided to improve knowledge surrounding the reproductive biology of *C. goliath* and investigate whether these frogs exhibit nest construction and parental care.

Material and methods

From February to May 2018 we repeatedly searched a 400 m long section (4°38′15″N, 9° 43′07″E to 4°38′25″N 9°43′9″E) along the Mpoula River near the city of Penja, Littoral District, western Cameroon (app. 200 m a.s.l.), for Goliath Frog nesting sites (Figure 2). Mpoula River comprises very different habitats. Very turbulent rocky sections of the river, not wider than 5 m with cascades and small waterfalls of 20 to 120 cm height, could be followed by calm sandy areas of more than 50 m width and less than 10 cm water depth; or deep (> 1.5 m) stagnant, muddy sections. Most of the original gallery forest has been converted into small plantations and gardens, and a banana plantation nearly reaches the riverbed. Only on very steep sections of the river bank, gallery forest still persists. During our survey we witnessed ongoing slash and burn clearing of remaining forest parts, as well as pesticide spraying by airplane (plantation) and hand-pumps (villagers).

In total we surveyed this section on 12 days, searching for new breeding sites and assessing the use in already known sites. During four nights we focused on behavioral observations. Searching for breeding sites was conducted by two people, wading in parallel along both banks. Potential nests were initially identified by the presence of *C. goliath* tadpoles or eggs (Figure 5(b,c)). After we learned what to look for, we identified and registered all similarly structured sites, regardless of eggs or tadpoles' presence. In order to distinguish nests from non-nests; i.e. when concerning rock pools and water-filled depressions in sandbanks, we checked if these places had been apparently cleared from leaf-litter and other detritus, and if the excavated material piled up at the edges (and looked different to what would be expected to be caused by the water current). The structure, position, diameter and maximum depth of any potential nest was recorded. During each visit of the area each nest was checked for the presence of eggs, tadpoles, distinct tadpole size classes, predators, water depth and temperature. For spatial analysis of nest clusters, GPS coordinates were Z transformed and the k means clusters computed using R software version 3.4.3.

For the nocturnal observations, we focused on the nesting site that showed the most recent changes between the last and the respective actual day visit. In particular, we decided to surveil one nest (#16; Figures 2 and 5(a)) with a 16-megapixel, low-glow infrared camera trap (BestoU®, Model 16). After realizing that the motion detector, 3 m from the nest, was not sensitive enough to record apparent frog activities, we decided to use the time-lapse option of the camera, taking pictures every 20 seconds, starting from shortly before nightfall for a duration of 11 h. The camera was positioned approximately 1.4 m above water level and 3 m from the nest.

In addition, we interviewed three local frog hunters and one frog hunter from the Nkongsamba region, as well as two villagers, having their gardens on the shore of the Mpoula River, for their knowledge on *C. goliath* breeding habits.

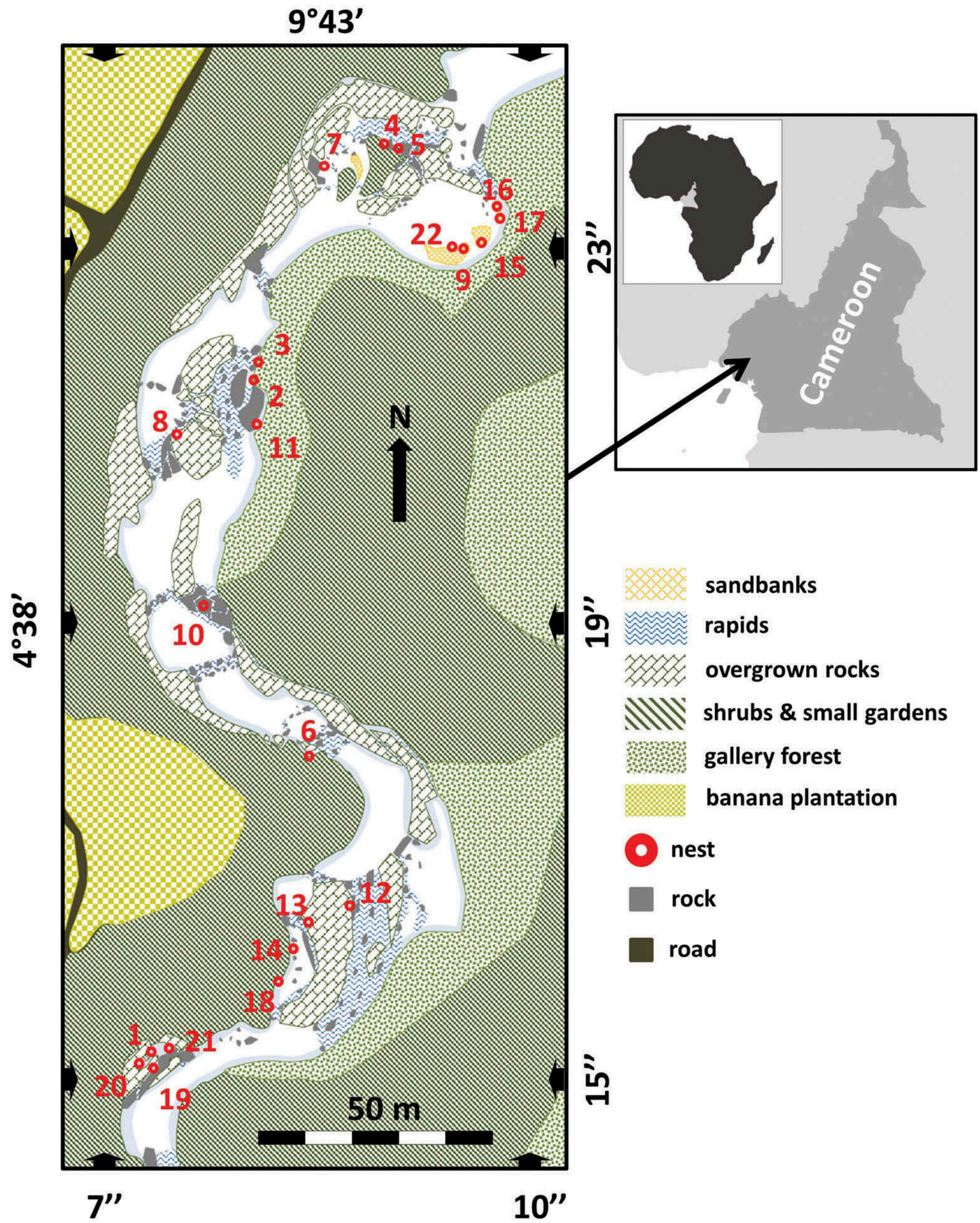

Figure 2. Study site at Mpoula River near Penja in West Cameroon (inset figure), and Goliath Frog nest sites (red dots) along the river; the river discharges southwards.

Results

Nest numbers, sites and characteristics

From February 27 to May 5, we recorded a total of 22 sites along the river (Figure 2), which were used by Goliath Frogs as breeding sites. Identification of these sites was due to the

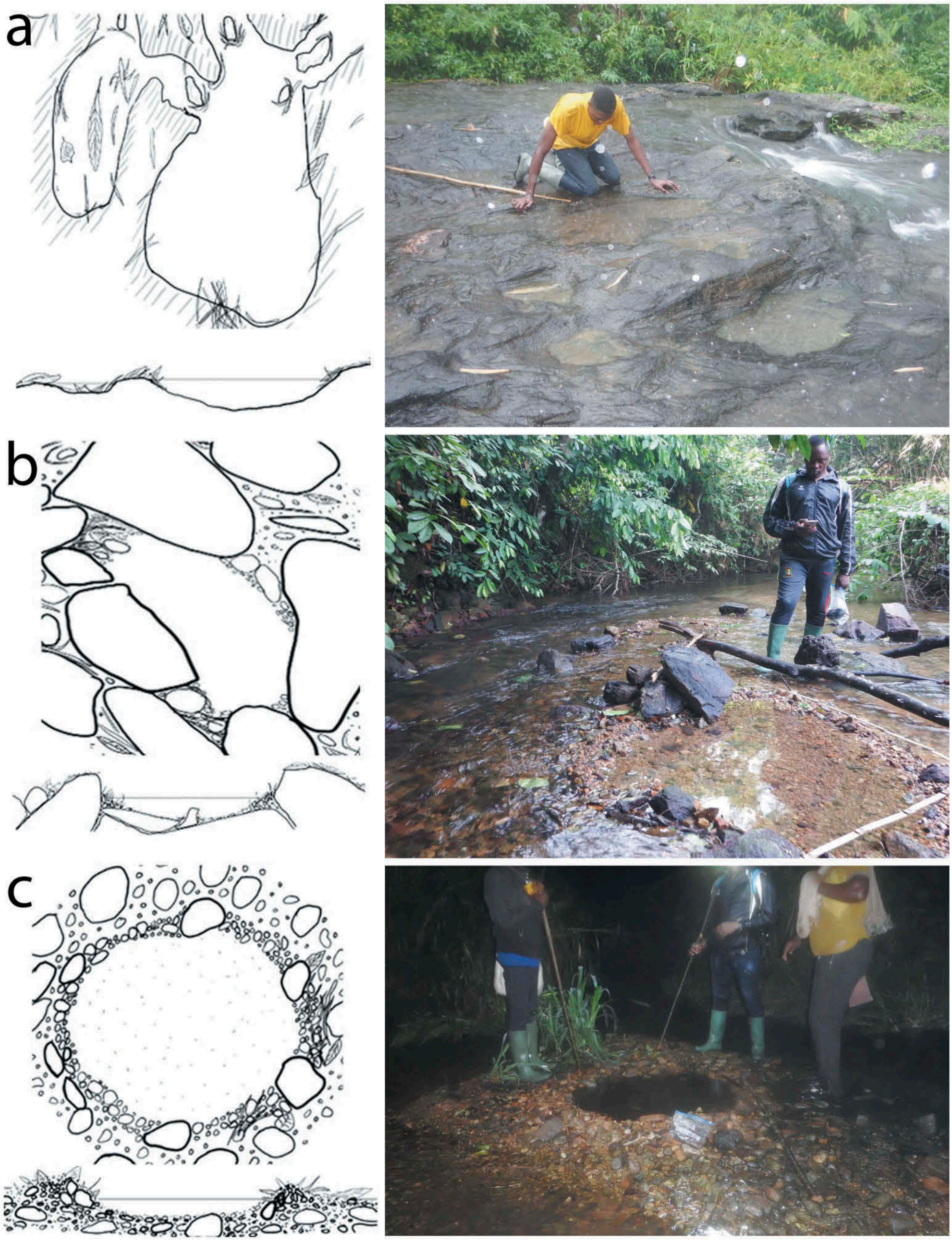

Figure 3. Different *Conraua goliath* nest types. On the left side nest types 1 (a), 2 (b) and 3 (c) are sketched in top view and in cross section, respectively; on the right side examples for each nest type are illustrated; compare text for further details.

above-mentioned criteria. Seven sites were found on the first day, and another nine on the second visit. Two more sites were detected on the third visit and another three on the fourth. Lastly, one site was identified on the eleventh visit (Table 1). Nineteen of these sites were round to oval water-filled depressions (mean maximal depth 9.1 ± 2.1 cm) not

Figure 4. *Conraua goliath* is heavily hunted in the region, either using fishhooks set above breeding habitats (a, c) or with traps (b).

exceeding 140 cm in diameter (mean diameter 102.8 ± 14.5 cm). Three sites were smaller, measuring <60 cm in diameter (Table 1), showing all above mentioned features, but were never (during our survey) completed or used as nests.

The origin and structure of the nest sites allowed them to be grouped into three types (Figure 3). Type 1 (Figure 3(a)) comprised rock-pools (N = 2), situated on larger rock faces within the river bed. Thus frogs were using pre-existing structures for breeding. Eggs or tadpoles revealed the identity as nest; however, the lack of leaf-litter and other organic sediments, especially in respect of the near surrounding, was striking. Type 2 nests (N = 14; Figure 3(b)) were naturally existing washouts or shallow pools close to the river bank, which seemed to have been enlarged by the frogs and again were cleared from sediments such as leaf-litter. Similarly, type 3 nests (N = 6; Figures 3(c)) and 5(a)) were shallow water filled depressions with gravel or sandy ground, encircled by larger stones and rocks. The uniform structure of small gravel or sand in the center, lacking any other larger stones (only massive rocks remained) but surrounded by large stones, some of them quite apparently being

Table 1. Consecutive observations of 22 *Conraua goliath* nesting sites over 12 survey days: no = nest number, t = nest type (see text for definitions), Ø = maximum diameter [cm], d = maximum depth [cm], green cells: nests being usable (water depth > 4 cm); red: nests not usable (water depth < 4 cm); blue: nesting site incomplete; white: no observation. Capital letters refer to present fauna: - = nest empty, E = eggs, T = tadpoles, S = shrimp; du = dried up, sm = submerged (former boundaries under water not clearly defining the nest any longer), so = spilled out (no eggs or tadpoles detectable, sometimes remaining egg capsules), oc = ongoing construction; red capital letters refer to events were eggs were eaten or rotting; green capital letters refer to new clutch.

				February	March						April				May
no	t	Ø	d	27/28	3/4	8	12/13/14	17	25	31	9	15	21	29	5
1	2	96	10	E, T	T	T	E, T	T	T	T	T	T	T/*oc*	E, T	T
2	2	98	11	E	T	T, S	T	T	T	T, S	T, S	T, S	S	S	S
3	2	90	11	E	S	-	-	*sm*	*sm*	*sm*	*sm*	*sm*	*sm*	*sm*	*sm*
4	2	107	7	E	T	T, S	T	T	T	T	T, S	E, T	T, S	S	S
5	2	115	9	E	S	-	-	-	-	E	T	-	*sm*	*sm*	*sm*
6	2	117	12	T	E, T	T	T	T	E, T	T	T	T	T	E & T	T
7	3	-	-	*oc*	-	-	-	*sm*	*sm*	*sm*	*sm*	*sm*	*sm*	-	-
8	2	97	9		*oc*	-	-	-	-	-	-	-	-	-	-
9	3	119	6		E	*du*	E	T	T	T	*du*	*du*	*du*	*du*	*du*
10	1	111	7		E	-/*so*	-	E	-/*so*	-	-	-	-	-	-
11	2	93	-		*du*	*du*	*du*	*du*	*du*	*du*	*du*	*du*	*du*	*du*	*do*
12	2	100	8		-	-	-	*sm*	*sm*	*sm*	*sm*	*sm*	*sm*	*sm*	*sm*
13	2	86	10		-	-	-	-	-	-	-	-	*sm*	*sm*	*sm*
14	2	92	8		-	-	-	-	-	-	-	-			
15	3	-	-		*oc*	-	-	-	-	-	-	*sm*			
16	3	101	7		*oc*	E	T	-/*so*	-	-	-	-	-	-	-
17	3	-	-			*oc*	-	-	-	-	-	-			
18	2	80	10			E	T	T	T	T/*sm*	T	S	-	-	-
19	1	92	10				E	E	-/*so*	-	-	-	-	-	-
20	2	119	14				E	E, T	T	E, T	T	T	T	T	T/*sm*
21	2	100	7				E	T	T	*so*	E	T	T	E, T	E, T
22	3	140	7											E	T

Example how to read the table: on March 3 a new clutch was found in nest 10 (type 1 nest, rock pool); the following observation (March 8) revealed no eggs, tadpoles or egg capsules. Water level after excessive rainfalls in the days between 3 and 8 March presumably had been spilled out the eggs.

moved recently (stones turned up-side-down as visible from surfaces apparently being formerly in the ground and now exposed and vice versa) indicated that these nests had been created by the frogs, pushing the stones to the edges (some of the moved stones having a weight of up to 2 kg).

One main aspect that all nests had in common was that the substrate seems to have been cleaned, because leaf-litter and other detritus were absent from these sites. Other similarly sized puddles and rock pools along the river, which were not being used as nests, contained these elements. This suggests the items had been actively removed from the nests. Particularly in type 2 and 3 nests (see below) these sediments, leaf-litter and gravel, had been pushed to the edges of the nest, there forming a dam like structure, being most obvious in type 3. All nests could be completely isolated from the river (at least until water level rises) or were connected by shallow in- and outflow. Type 3 nests allowed a kind of 'filtered' in- and outflow of water due to the stone and gravel barrier.

Nest site use

In 14 nests we found *C. goliath* eggs, attached to the ground (solid rock, stones, pebbles, branches or leaves; Figure 5(b)), scattered or clustered (numbers usually varied between 20–150 eggs per 100 cm^2) but always spread across the entire area of the nests. Exact clutch size could not be recorded as eggs, especially older ones, merged to a grey mass with sand and other material sticking to the egg capsules, making it impossible to identify the individual eggs without destroying them. Based on what was countable we estimated for most nests that egg numbers varied from 150 to 350. However, in two cases we counted 709 and 678 eggs in one quarter of a nest. In those two nests the eggs were more or less homogenously scattered across the nest sites. We therefore estimate that each nest comprised about 2700–2800 eggs, respectively. Four nests did not show recent traces of breeding activity but had been defined as nest sites due to their structure (typical type 2 nests, see above). Nest 11 was dried up, nests 6, 12 and 13 showed signs of traps that local poachers typically use to catch *C. goliath* (elastic branches tied together to form a tennis racket like frame, to which 15 to 25 fishhooks are attached on 20 to 30 cm long fishing lines; Figure 4). Nests 7, 8 and 17 showed recent frog activity, i.e. the ground cleared; however, it seemed that we and/or poachers scared off the frogs, which subsequently did not come back. In one case (nest 15) the frogs seemed to have terminated the construction work. We thereafter found a new nest (nest 16) 2.5 m apart (Figure 5(a)).

Several nests were repeatedly used (Table 1), indicated by up to three distinctly different sized cohorts of tadpoles. Heavy rainfall could trigger raising water levels that lead to spill-outs of eggs and tadpoles in all three nest types. Dropping water level after a period of five days without rainfall resulted in the drying up of one nest (nest 9, type 3). Later this nest dried out permanently and a new nest was constructed in close vicinity (nest 22, type 3). One nest was permanently dry (nest 11, type 2). Small shrimp (*Caridina evae* 2009) and fish were observed in some type 2 nests connected to the river. Nest sites were clustered, not evenly distributed, along the river bank, i.e. six clusters best explained the distribution of the spatial data (>98%, based on k means; see Figure 2).

In the 14 active nests, defined as tadpoles or eggs being present at least once during our study period (Figure 5(b,c)), we recorded a total of 27 clutches (all eggs of identical age, found at one site, were defined as belonging to the same clutch). In nine cases eggs disappeared within one or two days. Three clutches were spilled out due to heavy rainfall, one dried out and three clutches were eaten by the shrimp. Two clutches decayed for no obvious reason. In 12 consecutive visits we made 195 single observations in 19 nests (red and green cells; Table 1). In 156 cases (80%) we identified the nest as functional, based on water being present in the nest (green cells; Table 1). In 82 (52%) of these 156 events the nests were in use, i.e. eggs and/or tadpoles present (Table 1).

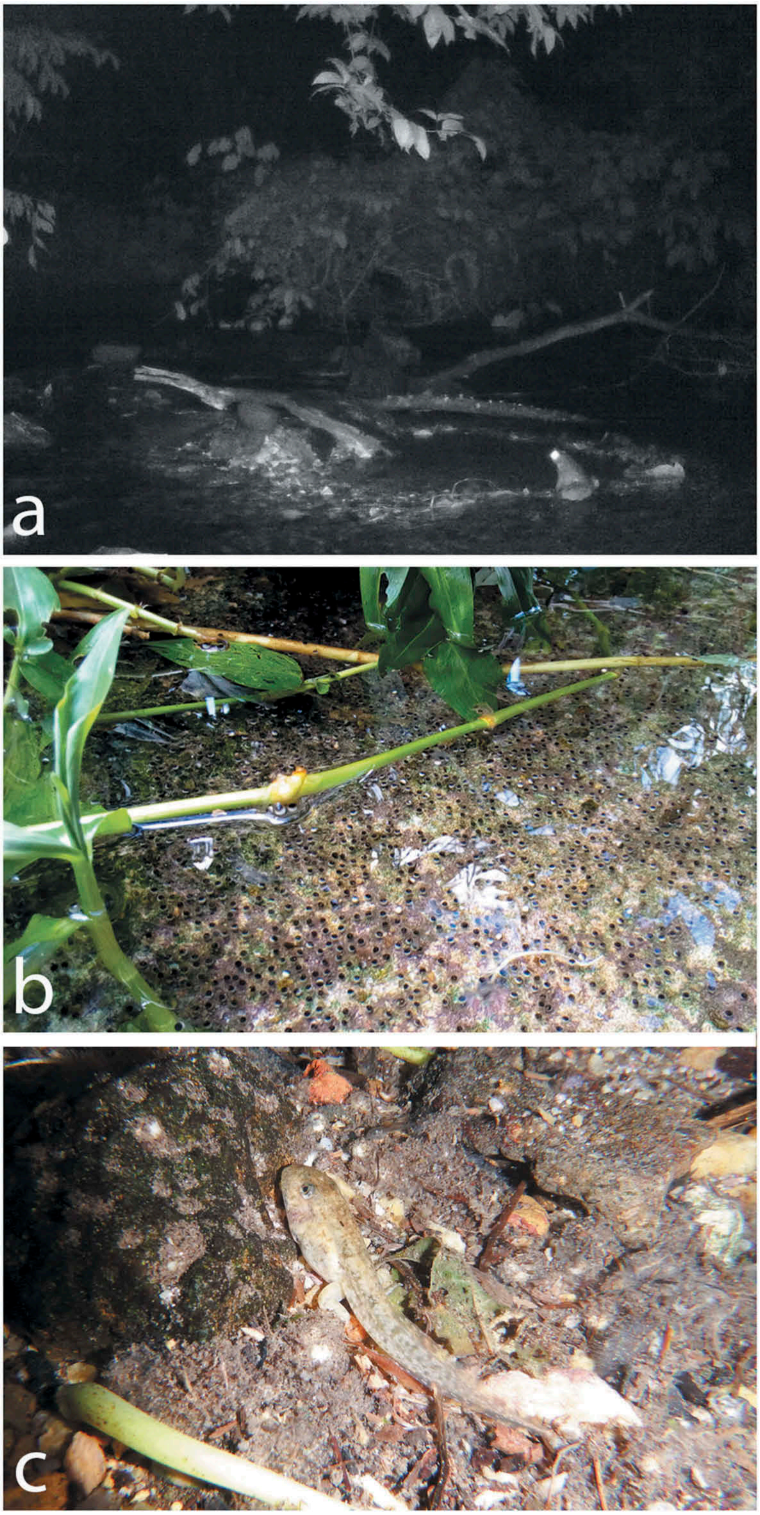

Figure 5. *Conraua goliath* at nest sites; (a) adult sitting at the edge of nest 16 (compare text and Supplementary Material); (b) eggs attached to cleaned nest ground; (c) tadpole in advanced developmental stage, the white dots above its head and at the left margin, are new eggs.

Egg and tadpole predators and nest guarding and maintenance

Nests in use comprised all developmental stages, from eggs to froglets. If undisturbed, e.g. no spilling-over of the nests, tadpoles finished their development in the nests. *Conraua goliath* froglets were frequently observed near the nests. Several shrimp were repeatedly observed feeding on eggs (N = 3). In the presence of shrimp, tadpoles formed schools (N = 6), usually moving as far as possible from the shrimp. When visiting nests during the night, adult *C. goliath* were always (N = 16) recorded in close vicinity (~3 m) of active nesting sites. As any sound, movement, or the light of our torches triggered the frogs to escape, typically by jumping into the river (up to 5 m jumps), direct observations of the frogs were difficult. However, we once observed a frog sitting in a nest, partly cleared from organic sediments. Over five days, we were able to follow the construction of a nest, from the first apparent digging attempts to egg deposition. The frogs jumping away at our appearances indicated that they are usually present close to active nests. In order to check for such behavior, we installed a camera on nest 16. The images (Figure 5(a)) revealed that a large frog of unknown sex, sat or moved around the nest shortly after nightfall from 6:36 pm to 5:32 am, just minutes before dawn. The frog changed its position approximately every 30 to 90 minutes, sitting within the nest, on the edges of nests and sometimes up to 3 m from the nest. During this entire period, a second larger frog briefly approached as well, not triggering any notable reaction of the first frog (see video in Supplementary Material).

In most cases we have no evidence that active nests have been cleaned by adults, although they seemed to contain much less leaf-litter or detritus than non-active nests and similar structures along the river. However, some leaf-litter accumulated again while tadpoles developed. This was also the case in nests where new clutches were deposited in short sequence and tadpoles and eggs were present at the same time (see '*E, T*' in Table 1). In contrast, after longer periods without deposition of new clutches, we could observe repeated cleaning activity in existing nests (see *oc* in Table 1). In those cases where nests still contained tadpoles, tadpole numbers were reduced after cleaning, indicating that tadpoles were washed into the river due to the digging activity.

Observations by frog hunters and farmers

The digging behavior of Goliath Frogs was never directly observed by us. Our interpretation is based on indirect clues (the moved material and the structure of the nests) and respective reports by frog hunters (N = 4) and local farmers (N = 2). However, it was not certain how many of the interviewees have directly witnessed the behavior or have repeated secondary information to us. The most detailed description we got (from one frog hunter) was that the male would construct the nest while the female waits in proximity. Once the nest is finished, the male whistles to attract the female, which then is grasped by the male and eggs are deposited. Afterwards the female would guard the nest and subsequently open the nest towards the river.

Discussion

Our results confirmed the reports of local frog hunters that Goliath Frogs provide some parental care by (i) using nests for oviposition which are at least somehow cleaned (type 1 nests), or even constructed (type 2 & 3), and (ii) presumably guarding eggs and tadpoles. While nest construction has been known from several South American leptodactylids (Heyer 1978; Faggioni et al. 2017), various hylids from South America (Lutz 1960; Kluge 1981) and South East Asia (Dring 1979; Emerson 1992), as well as from a Bornean dicroglossid (Inger 1966), such behavior so far was unknown from African species. Although we are lacking direct observations of the nest construction, several facts indicate that the nests indeed were established and used by *C. goliath*. All three nest types showed a common feature: a ground cleaned from leaf-litter and debris, excavation piling up on the edges of the nests. This feature is particularly striking in comparison with the condition of surrounding puddles, which always have thick layers of leaves, debris and heterogeneous sand or gravel ground. That a 'clean' ground was due to the frogs' activity was underlined in a nest where a Goliath Frog apparently just had started with the cleaning process and continued the following days. The most convincing argument, that the frogs deliberately cleaned and/or constructed these sites, was due to the fact that eggs were deposited after a site had been established and cleaned, and that new nests were established in close vicinity to nests which became dysfunctional, i.e. which dried up or get submerged by raising water levels.

Attaching eggs to substrate is a well-known behavior in anurans to prevent the displacement of single eggs and clutches and thus is particularly often observed in stream breeders (Duellman and Trueb 1986). *Conraua goliath* attaches its eggs, under water, singly or in small groups to rocks, gravel or larger pieces of wood (Sabater-Pi 1985, this paper). The cleaning of the ground from leaf-litter and other debris may be in order to help preventing eggs from being attached to lose structure and thus potentially washed away. The preparation of such a nest site might also be meant to attract females to that site. However, apart from the observation of one frog hunter, telling us that females are close by when males are constructing nests, we have no observation supporting this assumption. Finally, a cleaned substrate may facilitate the monitoring of potential egg and larval predators. It is known that some frogs are able to detect the presence of predators and avoid those sites for spawning (Resetarits and Wilbur 1989; Kats & Sih 1992; Hopey & Petranka 1994; Spieler & Linsenmair 1997). However, whether *C. goliath* is able to judge breeding sites for the presence of predators or not, is unknown. The use of existing (type 1 & 2) or constructing (type 2 & 3) nests which are, at least partly, isolated from the river bed may help to reduce predators' presences (i.e. fish and shrimp), and prevent the eggs from being washed away. However, fluctuating water levels may bring in predators and/or spill out eggs and tadpoles, or result in total mortality when eggs and tadpoles, trapped within the nest, dry up. Roughly half of the recorded egg losses were caused by nests drying up or being over-flooded.

Breeding activity of anurans is usually strongly influenced by environmental triggers, such as rainfall, influencing the availability and suitability of breeding sites (Wells 2007). By digging nests into the riverbed, Goliath Frogs are less dependent on existing structures suitable for egg deposition (presence of non-torrent water, absence of predators), both during the dry season when natural pools might be dry, and the wet season when the river bed is rising. Constructing (nest types 2 & 3) or modifying (types 1 & 2) suitable nest sites may thus allow the frogs to prolong the possible breeding season and increase the number of breeding sites that match their demands, e.g. concerning water presence and predator absence.

The different nest types may have different advantages and disadvantages. Nest type 1 was the 'easiest' to use, as only the cleaning of the substrate was required. However, these nests turned out to be the least reliable, as spilling over of the nests, usually positioned in the river bed or on the bank of the river, occurred frequently. Besides eggs, the young tadpoles may be vulnerable to (i) washing out of the nests by overflows and (ii) having predators enter the nests. Freshly hatched tadpoles lack several morphological adaptations for torrential lifestyles, including a streamlined body, muscular tail, and mouth sucker, which typically develop in Gosner stage 26 or 27 (Gosner 1960; Sabater-Pi 1985). Rock pools with smooth ground will certainly be the nest type that offers the least protection from being washed out, whereas coarse gravel nests, offering interstitial gaps, might enhance the chances for eggs and tadpoles to not be displaced. However, if the water level does not show major fluctuations, a rock pool might be a suitable nesting site, offering the advantage of requiring only minimal effort by the adults. In contrast type 2, and in particular type 3 nests were less likely to be over-flooded, but instead have a higher risk of drying up during periods of dropping water levels. In addition, they need much effort from the frogs to be established. We believe that the use of different nest types thus might reflect trade-offs between availability of sites, construction costs and survival probabilities of the offspring.

The clustered distribution of the nests indicates that Goliath Frogs may have territories. This has already been suggested by Sabater-Pi (1985). However, this needs further investigation, as we were not able to track the locations of individual frogs in our study. Additionally, it is unclear which sex is (i) responsible for the construction or cleaning of nest sites, and (ii) responsible for defending or guarding the nest sites. The relatively small clutch and egg size in most nests, compared to the frogs' body size, might indicate that females do not deposit all their eggs at once, but that several smaller clutches are placed in the same or different nest over a certain period (Wells 2007, and references therein). This could also explain the presence of different cohorts of tadpoles in the same nest.

Our new findings of the reproductive biology of *C. goliath*, i.e. the active establishing of nests, suggest as well an explanation for the question, why Goliath Frogs have become the biggest anuran species in the world. Digging out a nest that exceeds 1 m in diameter and 10 cm in depth, by moving coarse gravel and stones of several kilograms, is a serious physical task, and suggest a potential explanation for why Goliath frogs are among the largest frogs in the world. Other frog species that are known to conduct arduous labor when preparing spawning sites are as well at the upper limits of anuran body size range. Examples are male African Bullfrogs (*Pyxicephalus adspersus*) which guard tadpoles and are digging channels to allow tadpoles to escape drying pools (Balinsky and Balinsky 1954; Kok et al. 1989; Cook et al. 2001; Channing et al. 1994; Yetman and Ferguson 2011); or Gladiator Frogs (*Hypsiboas rosenbergi*; Kluge 1981; Höbel 2008; Luza et al. 2015) and the Bornean Giant River Frog (*Limnonectes leporinus*; Inger 1966) that construct nests. Another large African frog, *Aubria subsigillata*, also seems to guard tadpoles (Jongsma and Emrich 2012), but it is not clear which sex is performing this activity. Interestingly a close relative of the Goliath Frog, the much smaller *Conraua crassipes* (Buchholz and Peters, 1875) (maximum SVL 81 mm), has become known to build sandy heaps on which they sit, just above the water surface (Amiet 1990). Thus the capability to modify the environment to some extent might be a feature of this family of frogs.

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Disclosure statement

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