



A nursery behind the waterfall – life-history and reproductive ecology of West African Sabre-toothed Frogs (Anura: Odontobatrachidae) in torrent streams

MARVIN SCHÄFER¹, DAVID SYDOW², JOSEPH DOUMBIA^{1,3} & MARK-OLIVER RÖDEL¹

¹) Museum für Naturkunde Berlin – Leibniz Institute for Evolution and Biodiversity Science, Invalidenstr. 43, 10115 Berlin, Germany

²) Department of Animal Ecology and Tropical Ecology, University of Würzburg, Biozentrum Am Hubland, 97074 Würzburg, Germany

³) ONG EnviSud Guinée, Quartier Kipé T2 commune de Ratoma, 530 BP 558 Conakry, Republic of Guinea

Corresponding author: MARVIN SCHÄFER, e-mail: marvin.schaefer@mf.n.berlin

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Abstract. Sabre-toothed Frogs (Odontobatrachidae) were only recently identified as the first vertebrate family endemic to West Africa. However, beyond their distribution in, and preference for, torrential rivers in forests, most of the biology of the five *Odontobatrachus* species remain unknown. Herein, we have summarized various field data from several years to present the first insight into the life-history of the Odontobatrachidae, with emphasis on *O. arndti* and *O. ziama*. We highlight differences in microhabitat use between sexes and ages, territorial behaviour with indications of intraspecific combats, identify the breeding habitat, and describe their unusual tadpole development. Tadpoles start off as troglodyte non-feeding, lentic larvae and subsequently shift to a torrenticolous morphology. Oviposition sites seem to be situated in narrow crevices filled with little water behind cascades and waterfalls. Spawning and fertilization may take place separately and not in amplexus. Scarcity of suitable breeding sites could be an explanation for territoriality and fighting of Sabre-toothed Frogs. These descriptive data provide the first detailed life-history account for several rare species and can be leveraged to improve their future conservation outlook.

Key words. Amphibia, *Odontobatrachus*, morphological change, non-feeding, tadpole, territorial behaviour, troglodyte.

Introduction

Data deficiency (DD) has been acknowledged as a serious threat to animal and plant species, including anurans (STUART et al. 2008, HOWARD & BICKFORD 2014). This is simply due to the fact that without data, species-specific threats cannot be evaluated, and conservation measures cannot be planned and executed accordingly. Of particular concern are newly described species, as the knowledge on their biology is usually the most incomplete, or in other words, data deficient. Whilst several authors have suggested new assessment tools and novel approaches to assess DD anuran species, such as machine learning (HOWARD & BICKFORD 2014) or using data from the fossil record (TIETJE & RÖDEL 2018), the optimal way to overcome knowledge deficiency is researching the respective species in the wild.

Although described more than a century ago (BOULENGER 1905), little more than a preference for forest streams (GUIBÉ & LAMOTTE 1958, BÖHME 1994, RÖDEL 2003, RÖDEL & BANGOURA 2004) has become known about West African torrent frogs. Initially a single West African species was assigned to the predominately Central Afri-

can genus *Petropedetes*. BAREJ et al. (2010a) summarized what was known about it and discovered that the West African populations should be placed in a genus of its own, *Odontobatrachus*, and a separate family, Odontobatrachidae (BAREJ et al. 2014, 2015a), and subsequently described four new species (BAREJ et al. 2015b). All but one *Odontobatrachus* species, *O. natator* (Least Concern), which is distributed from Guinea via Liberia to Sierra Leone, have very limited geographical distributions within Guinea and adjacent Ivory Coast (*O. arndti*) and first were classified as Data Deficient. It was only recently that their threat status was updated, ranging from Near Threatened (*O. arndti*) to Endangered (*O. fouta*) (IUCN 2019), however, so far this classification was based exclusively on range sizes.

The five species are reliably distinguishable only by their geographic origins and/or genetic data, rather than by phenotypic characters (BAREJ et al. 2015b; CHANNING & RÖDEL 2019). Morphological crypsis is also apparent in the *Odontobatrachus* tadpoles (LAMOTTE & ZUBER-VOGELI 1954, DOUMBIA et al. 2018), reflecting morphological convergence with many other torrenticolous tadpoles and frogs (INGER 1966, HEYER 1982, LAMOTTE & LESCURE 1988,

1989a, b, HODGKISON & HERO 2001, GAN et al. 2015). Very recently, the dietary preferences of the five species have been researched, revealing an opportunistic feeding pattern with an unexpected high extent of vegetal supplementation (SCHÄFER et al. unpubl. data). All other aspects of the biology and ecology of the genus *Odontobatrachus* remain unknown. Herein, we present a summary of numerous observations, collected throughout several field surveys, to describe aspects of the life-history of the Odontobatrachidae.

Material and methods

Most of the results presented in this paper were collected between December 2017 and July 2019 across the entire Guinean distribution of the Odontobatrachidae, however, with a special focus on the southeastern species, *O. arndti* and *O. ziama*. We collected data on sex-specific, spatial habitat use, the population structure in different habitat types, and early larval development. Frogs were also routinely checked for scars, injuries, and wounds. Some data were verified in specimens collected for the studies by BAREJ et al. (2015b) and DOUMBIA et al. (2018) and deposited at the Museum für Naturkunde, Berlin (ZMB; see these two papers for accession numbers). Some observations were also made in frogs held captive for acoustic recordings; these results will be published in a later paper. All data handling and analysis were computed with R software (4.0.0, R core team 2020). In general, most of our data did not meet with the assumption of normality, hence we compared groups by Kruskal–Wallis tests. As post hoc tests, we applied paired Wilcoxon rank sum tests, with Bonferroni corrections when doing multiple comparisons. We used Fisher's exact tests to determine proportional differences between groups. In general, we assumed that any $p < 0.05$ would define reasonably significant differences.

Habitat use

RÖDEL (2003) noticed a gender-dependent habitat segregation in what later turned out to be *O. arndti* in Mont Sangbé National Park, Ivory Coast. To evaluate this observation with data, we recorded the preferred perch sites of *O. arndti* along a 1000-m section of the Zougoué River (7.696337° N, 8.400049° W, Datum: WGS84) in the Mount Nimba Strict Nature Reserve (MNSNR), both in dry and wet season conditions. Sampling was conducted on three consecutive nights in December 2017 (dry season) and three nights in May 2018 (wet season). Searches started approximately 30 minutes after sunset, around 19.00 h, and comprised 300 m of riverine habitat that were examined by three researchers for three hours (nine person hours) each night. To avoid repetitive sampling, we never worked in the same area twice, but kept a buffer zone of about 25 m of unsearched area to the area sampled the previous day. We searched the riverbed and riverbanks upstream, and noted all sites where we spotted an *O. arndti*. We tried to capture the animals in or-

der to sex them. Males could be identified by the presence of femoral glands and an external vocal sac, both features are absent in females and juveniles. Animals smaller than 40 mm in snout–vent length (SVL) and/or weighing less than 4 g were classified as juveniles. We measured weight with a spring balance (range 0–100 g; precision ± 0.5 g), and took sizes as SVL with a vernier calliper (± 0.1 mm). Perch height was measured with a pocket ruler by measuring the distance to the water surface (± 0.5 cm). Whenever frogs were located right above the water, the distance was measured as the vertical line to the water level. Whenever frogs were not located directly above the water, we measured two distances: the vertical height over the water level and the shortest horizontal distance to this vertical. From this data we drew the shortest distance to the water by calculating the hypotenuse distance. To compare perches between sexes and seasons statistically, we applied Wilcoxon rank sum tests.

Site fidelity

To test if frogs exhibit some site fidelity, we marked six adult *O. arndti* from Zougoué River, three females and three males, displaced them from their perch sites and waited to see whether they would return to their original sites. We marked the frogs with elastic pearl collars around their waists (Fig. 1A, a method similar to attaching telemetry transmitters described by MUTHS 2003). The collars, consisting of natural latex, dissolve rapidly upon contact with water and will at the latest have ruptured after one week, thus ensuring that frogs lost their tags even if we could not recapture them. Two males and one of the females were released 15 m upstream; one male and the other two females were released 15 m downstream from their original sites. We searched the 15-m strip (between capture and release points) for the marked individuals or dropped waist-collars during the following four nights for 30 person-minutes each (two researchers searching for 15 minutes). After having identified a stationary male, we surveyed its perch site for three consecutive days with a 16-megapixel, low-glow infrared camera trap (BestoU®, Model 16) in time-lapse mode (1 picture every 45 seconds), to identify its movement radius (Fig. 1B).

Population structure

After realizing that population composition (sex and age) as well as perching preferences of *O. ziama* might differ across microhabitats, we conducted a capture-mark-recapture study over 12 consecutive nights in three different sections on the Véré River in the Zيامa Massif Strict Nature Reserve (ZMSNR), Guinea, to estimate local population sizes and compositions. The three 30 by 10 m plots (~ 300 m²) represented typical microhabitats in which *Odontobatrachus* are usually found. The first plot (8.35699° N, 9.30552° W), referred to as 'cascade', was characterized by several consecu-

tive waterfalls and cascades (Fig. 2A), resulting in a drop of about 6 m over the 30-m sector of the stream (20% slope). Here, many cracks and crevices provided abundant hiding spots for the frogs. The second plot (8.35748° N, 9.30343° W), referred to as ‘plain’, was characterized by a rather level section, moderately swift water current, and many boulders surrounded by partly deeper pools (Fig. 2E). Here, the terrain dropped by about 1 m over 30 m (3% slope). The last plot (8.35733° N, 9.30483° W) was a bare granite slope, forming one large cascade after rain, referred to as ‘slope’ (Fig. 2C). This open habitat drops by more than 9 m over the 30-m section (30% slope). Potential frog retreats were largely absent on this massive rock. These microhabitats were chosen because, although *O. ziama* were abundant in all three of them, they exemplified major differences in water current and the presence/absence of potential shelters. We started shortly after nightfall by searching the first plot for frogs for one person-hour (two people searching for 30 minutes each). Searching and handling frogs mirrored the procedure during the surveys for measuring weight and body length, as described in the habitat use section. Captured frogs were released prior to our heading to the next plot. To avoid a potential time bias, the sequence of sampling the three plots was alternated each night. All frogs were marked by toe clipping, following the recommendations by GRAFE et al. (2011). A photograph of the back was taken in order to test if colour pattern could be used for individual identification. As plots were not equally readily accessible (i.e., we had to use belay equipment to be able to ascent the ‘slope’), we assumed that the individual numbers from time-constrained surveys would not be immediately comparable, however, that all animals would be equally difficult to catch in a plot. We thus continuously marked all newly captured frogs and calculat-

ed a Lincoln-Peterson index (PETERSON 1895) for each of the capturing days and every sex independently, in order to estimate the sex ratio on each plot. We then averaged the indices over all capturing days to correct for newly arrived animals (no closed population) for each sex, respectively. Body sizes were compared between the plots by Kruskal–Wallis tests and subsequent paired Wilcoxon rank sum tests, with Bonferroni corrections.

Larval development

Surveying the *O. ziama* population around the Vère River, we detected a clutch in a small crevice. We gently washed it out of the crevice into a plastic bag and took it to our hostel. The eggs were transferred into a plastic container, filled with 100 ml of river water and stored under a couch, the coolest and darkest place available (~ 24°C). At least every other day we exchanged half of the water with fresh water from the river. To observe the developmental progress, we regularly transferred 10 tadpoles into a petri dish, took photos and measured their total lengths (body and tail) on scale paper (± 0.5 mm). When the tadpoles had assumed their known torrenticolous phenotype (see DOUMBIA et al. 2018), we released them at the original site of capture. We calculated Kruskal–Wallis tests to compare their growth at different larval stages.

Anecdotal observations

Some results described below are based on non-quantified observations. However, our respective interpretations are

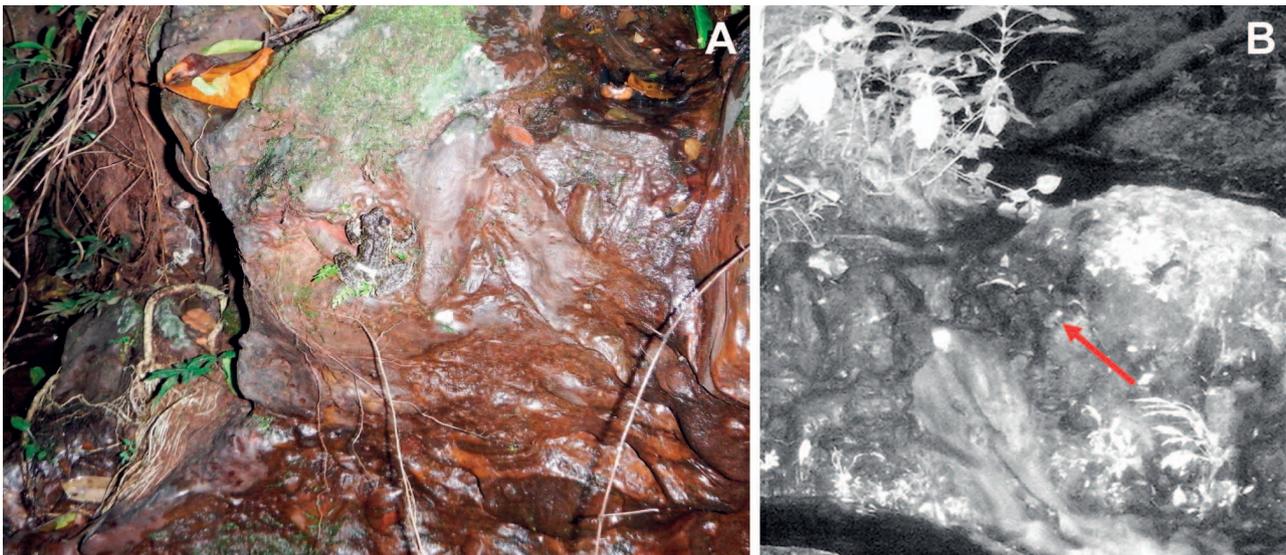


Figure 1. Site fidelity in a male *Odontobatrachus arndti* from the Zougoué River, Mount Nimba Strict Nature Reserve, Lola Province, Guinea; (A) marked with a waist pearl collar, found back at its original perch after displacing it 15 m downstream; (B) the same animal (red arrow) in the subsequent nights recorded by an infrared camera trap. Different patterns of black and white pearls on the collar allowed remote identification (~ 5 m distance), of individual frogs without the need to capture them. The used latex string dissolved and ruptured at the latest after a week and ensured that animals automatically lost the marker.

based on our combined experience of many years of field-work. We have little reason to presume that behavioural expressions differ between species. We specify anecdotal observations in the text by adding 'an. ob.'. These ob-

servations were made (but not counted) in several or all *Odontobatrachus* species. Other, quantified, species-specific observations are always reported with mentioning the respective species names.

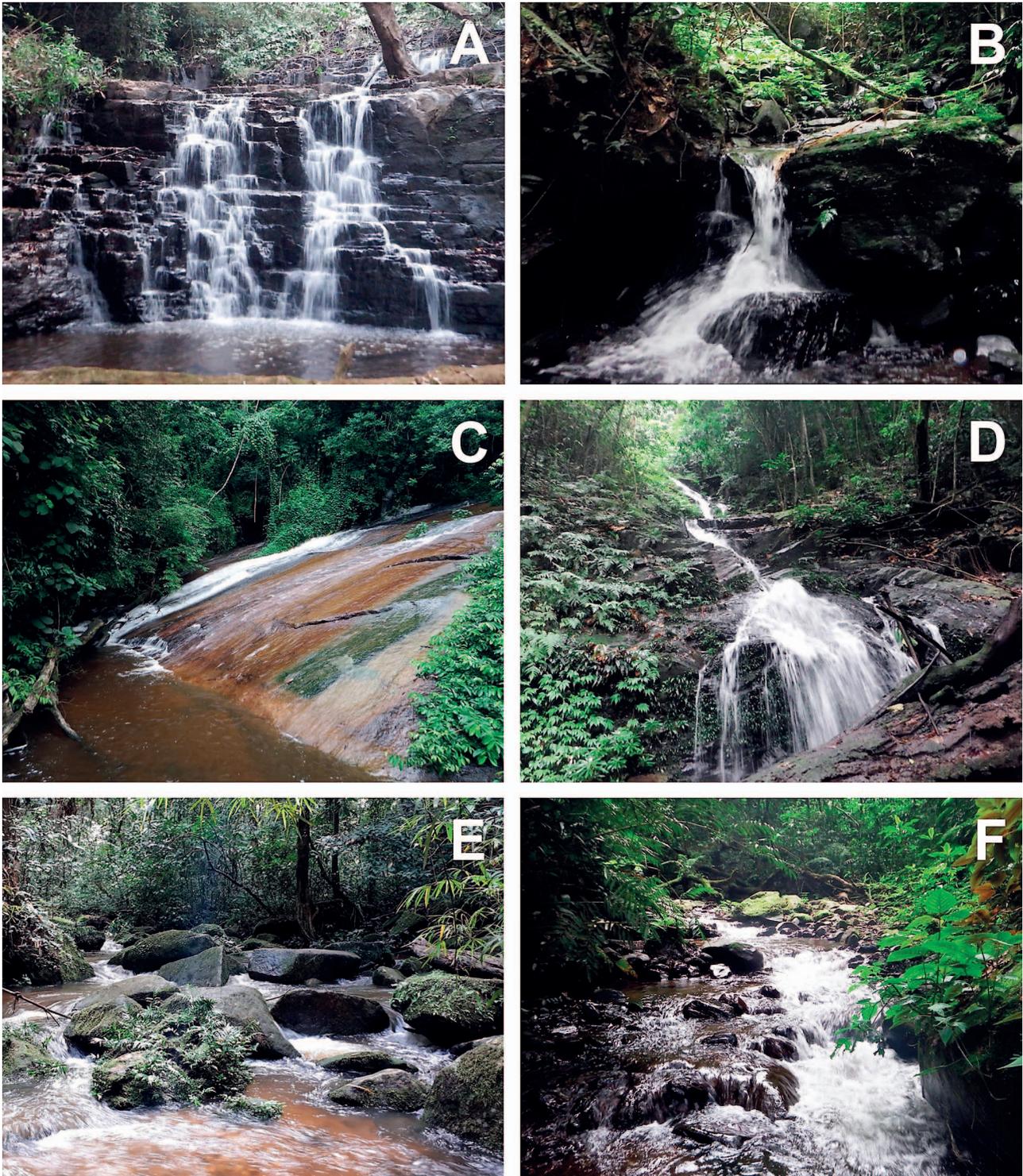


Figure 2. Three different typical microhabitats used by *Odontobatrachus*: (A, C, E) the Vère River near Sérédou, Ziama Massif Strict Nature Reserve, Macenta Province, Guinea; (B, D, F) Mandey River, Nimba Mountains Strict Nature Reserve, Lola Province, Guinea. (A, B) 'cascade': cascading river sections; (C, D) 'slope': steep granite slopes; and (E, F) 'plain': relatively flat river sections.

Table 1. Sex-specific population properties in different microhabitats of *Odontobatrachus ziama*, based on a 12-day capture-mark-recapture study in three plots of approximately 300 m² each (compare Fig. 1) on the Vèrè River near Sérédou, Ziama Massif Strict Nature Reserve, Macenta Province, Guinea. Given are mean ± SD for size and weight, total number of individuals caught, number of individuals caught only once (non-recaptured) and percentage of recaptured individuals, mean number of recaptures per individual and the maximum number of individual recaptures, as well as an averaged estimate of total individuals based on the Lincoln-Peterson index (see M&M section for details) for each sex and plot, respectively.

| | cascade (N = 118) | plain (N = 70) | slope (N = 129) |
|--|-------------------|----------------|-----------------|
| caught individuals | 45 | 42 | 71 |
| non-recaptured individuals (recapture rate%) | 34 (24%) | 24 (42%) | 53 (25%) |
| recaptures per individual (max number of recaptures) | 0.27 (3) | 0.60 (3) | 0.31 (3) |
| estimated individuals | 92 | 51 | 169 |
| SVL (mean ± SD) [mm] | 31.42±5.25 | 32.28±3.36 | 29.4±5.24 |
| weight (mean ± SD) [g] | 3.38±1.52 | 3.30±1.13 | 2.89±1.41 |
| caught individuals | 43 | 4 | 29 |
| non-recaptured individuals (recapture rate%) | 20 (53%) | 2 (50%) | 13 (55%) |
| recaptures per individual (max number of recaptures) | 0.98 (4) | 1.25 (4) | 0.86 (3) |
| estimated individuals | 53 | 5 | 44 |
| SVL (mean ± SD) [mm] | 45.59±2.69 | 38.9±4.05 | 44.69±2.97 |
| weight (mean ± SD) [g] | 9.67±1.31 | 4.75±0.87 | 9.5±1.89 |
| caught individuals | 30 | 24 | 29 |
| non-recaptured individuals (recapture rate%) | 7 (77%) | 9 (63%) | 13 (55%) |
| recaptures per individual (max number of recaptures) | 0.93 (5) | 1.08 (3) | 0.86 (3) |
| estimated individuals | 48 | 24 | 45 |
| SVL (mean ± SD) [mm] | 51.84±5.35 | 45.67±9.44 | 48.23±7.14 |
| weight (mean ± SD) [g] | 13.23±3.69 | 10.08±5.43 | 11.72±4.77 |

Results

Population composition of *Odontobatrachus ziama* in different microhabitats

In March 2019, we recorded 315 individual *O. ziama* across 12 consecutive days along the Vèrè River. In the ‘cascade’ section, we caught 118 individuals. On average, the total population at this site was estimated to comprise about 193 frogs (Table 1). Males, which slightly dominated this habitat were significantly larger ($p = 0.0015$, pairwise Wilcoxon tests, Bonferroni corrected; Table 1) and heavier ($p = 0.0008$) than males in the ‘plain’ section. ‘Cascade’ females tended to be larger and heavier than in the other plots investigated, however, the differences were not significant (Table 1). Juveniles from the ‘cascade’ site did not vary in size when compared to the ‘plain’ juveniles, but were heavier and significantly larger ($p = 0.0049$) than those on the ‘slope’ (Table 1). At the ‘plain’ site, we caught 70 individuals and estimated the population to comprise about 80 frogs. Males were rare in this habitat, and the few we caught were significantly smaller ($p = 0.0105$) and lighter ($p = 0.0018$) than males on the ‘slope’ (or the ‘cascade’; Table 1). Female dominated the ‘plain’, and on average were the smallest and lightest females across the three sites, although not significantly different. ‘Plain’ juveniles were significantly larger than those on the ‘slope’ ($p = 0.0048$), but not different in weight or size from juveniles from the ‘cascade’ (Table 1).

On the ‘slope’, observed and estimated population densities were highest: we caught 129 individuals, and the average estimate was 258 frogs. Here, males and females were captured equally often. Juveniles outnumbered adults by a

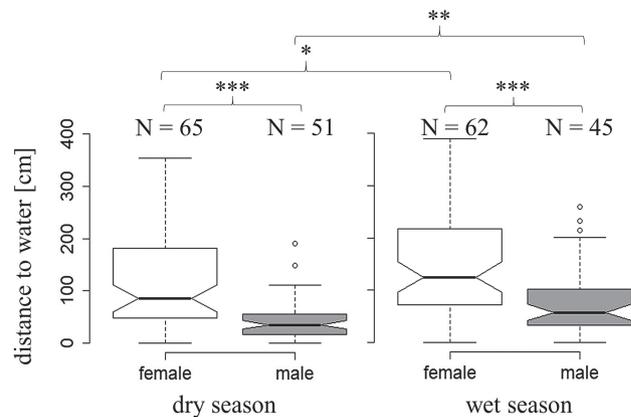


Figure 3. Perch site height of male and female *Odontobatrachus arndti* at the Zougoué River, Nimba Mountains Strict Nature Reserve, Lola Province, Guinea, during wet and dry seasons, measured as the shortest distance to the water surface. We found significant differences between males and females in both seasons as well as between the seasons for both sexes (* $p < 0.05$; ** $p < 0.01$; *** $p < 0.0001$); N = number of measured distances per season and sex, respectively.

factor of two. Juveniles on the ‘slope’ were the smallest and lightest in comparison to both other sites (Table 1).

Adult habitat use

On the Zougué River, we characterized the perch sites of 223 adult *O. arndti*, 96 males and 127 females. One-hundred sixteen frogs were recorded in the dry season and 109 in the wet season. Both females and males were observed at water level. Only females were also encountered at distances of more than 2 m from the water. During the dry season, females’ (N = 65) median distance to water (85.0 cm) was significantly greater than that of males (N = 51) (34.4 cm, Wilcoxon test: $W = 2609.5$, $p < 0.0001$). During the wet season both female (N = 62) (124.5 cm) and male (N = 45) (57.0 cm) frogs were perched significantly farther away from water

than during the dry season ($W = 1596$, $p = 0.0435$ and $W = 729.5$, $p = 0.0021$, respectively). The significant difference in distance to water between male and female perch sites persisted in the rainy season ($W = 2027$, $p < 0.0001$) (Fig. 3). In summary, female frogs were orientated closer to, or positioned on, the banks, and thus farther away from streams than males (Figs 4A, B). We frequently found females of all species on the riverbanks or in adjacent vegetation, often facing towards the interior of the forest (an. ob.). Juveniles, especially young and recently metamorphosed frogs, were often found in aggregations on small rocks close to the water, sometimes accompanied by tadpoles (Fig. 4C; an. ob.). Larger juveniles could be found perching on all sorts of objects near the water and on low vegetation, and some preference for moist rocks and trickling water was apparent (Fig. 4D; an. ob.). Juveniles seemed to stay more frequently in areas that were away from adult frogs (an. ob.).

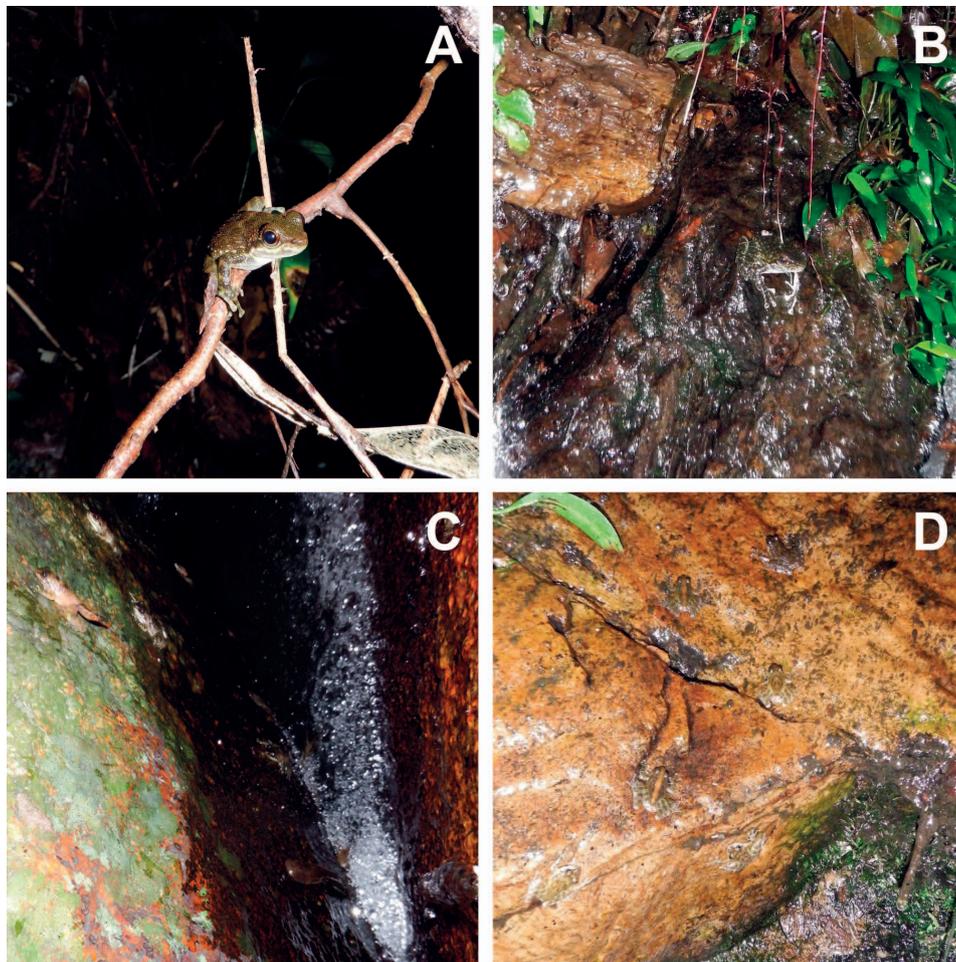


Figure 4. Typical perch sites of different *Odontobatrachus* species; (A) females (*O. ziamia*, Véré River, Sérédou, Ziamia Massif Strict Nature Reserve, Macenta Province, Guinea) often climb on vegetation on the riverbanks; (B) males (*O. arndti*, Guéguéblo River, Nimba Mountains Strict Nature Reserve, Lola Province, Guinea) predominately perch on rocky outcrops within small cascades; (C) metamorphs and juveniles (*O. natator*, Wosai River, Massadou, Ziamia Massif Strict Nature Reserve, Macenta Province, Guinea) congregate usually away from adult frogs; (D) congregation behaviour was also observable in slightly older juveniles (*O. smithi*, Ideta River, Mabhé, Télimélé Province, Guinea), photographed here are seven juveniles, two with very unusual reddish brown vertebral stripes. Note: The depicted behaviours are consistent throughout the genus, and these pictures therefore are representative of all five *Odontobatrachus* species.

Tadpole habitat use

Tadpoles of all species were observed only during the night, when they left their daytime hiding spots and congregated on submerged rocks (an. ob.). They were only rarely found singly (Fig. 5A), but usually had formed groups comprising a wide range of sizes and developmental stages (an. ob.). In fast-flowing water, the tadpoles usually were found close together whereas in less torrential sections, they were spread out, keeping some distance to the next individual (Figs 5B, C; an. ob.). Tadpoles usually climbed upstream grazing the surface of rocks. They even climbed very steep, bare rock slopes only covered by a thin film of water, with most parts of their body sticking out of the water (Figs 5A, C; an. ob.). When disturbed, tadpoles simply let go of their adhesion and were washed back downstream into pools, where they immediately sought shelter underneath rocks or in small crevices (an. ob.). We found that it was especially tadpoles of more advanced developmental stages that

were foraging outside the water (an. ob.). Very young tadpoles (see below) were never observed on the rocks or in open water (an. ob.).

Translocation and site fidelity of adults

In the *O. arndti* tagging experiment, frogs were translocated either up- or downstream by 15 m. We could only recapture one of the three females within 5 m of her original perch site. In contrast, all three male frogs returned to their original perch sites (< 1 m distance) within one night, regardless of whether they had been released up- or downstream. The IR videos confirmed for one of the returned males that it perched in the exact same spot for at least three subsequent nights (Fig. 1B). Each night, shortly after dusk, this frog emerged from behind a rock commanding his preferred perch. The frog stayed there for the entire night, never moving away for more than 1.5 m. Short-



Figure 5. Typical encounter situations for *Odontobatrachus* tadpoles; (A) *O. smithi* metamorph in the aquatic-terrestrial contact zone of the Ideta River, Mabhé, Téliélé Province, Guinea; metamorphs can sometimes also be observed in these positions during the day; (B) congregation of *O. fouta* tadpoles of different developmental stages in the torrential waters of the Ditiwol River near Din Tin in Dalaba Province, Guinea (water flow was temporarily blocked in order to take the photo); (C) widely spaced *O. arndti* tadpoles in a less rapidly flowing water film at night in the Zougé River, Nimba Mountains Strict Nature Reserve, Lola Province, Guinea. Note: The depicted behaviours are consistent throughout the genus, and these pictures therefore are representative of all five *Odontobatrachus* species (see also DOUMBIA et al. 2018).

ly before dawn, the frog headed back to the rock and disappeared. We subsequently searched this daytime shelter and found a rock crevice, which was occupied by that very male. All species used rock crevices (Fig. 6A), hollow trees and branches, small caves (Figs 6B, C), and exposed roots along the riverbanks as daytime shelters, sometimes sharing them with several other individuals (Fig. 6D; an. ob.). On the 'plain' plot, where frog abundance was comparatively low (Table 1), we could reliably and repeatedly – over the 12 survey days – retrieve the same individuals ($N > 20$) in the same area (roughly within a 5-m radius around a hiding spot). Frogs also tried to reach and hide in these spots when we approached them without the necessary caution (an. ob.). While the latter observations indicate a distinct site fidelity, other observations confirmed movement between sites. For instance, at least three females appeared in the 'plain' plot after heavy rains. They were subsequently recaptured like all other previously observed individuals. During other fieldwork, we found single females

of *O. arndti* ($N = 2$) and *O. ziama* ($N = 1$) up to 100 m away from the rivers when it was raining. We never encountered animals far from rivers without ongoing or preceding precipitation (an. ob.).

Territoriality

Although we never directly observed fighting, we noticed fresh and older injuries, especially in the gular region of male frogs of all species (an. ob.). During the dry season (February–March), between 72 (*O. ziama*) and 88% (*O. fouta*) of the screened males and between 11 (*O. ziama*) and 21% (*O. natator*) of the females exhibited injuries and scars (Table 2). These injuries comprised cuts, lacerations (more common in males; Figs 7A, B) or scars (Fig. 7C), always aligned parallel at distances of about 5 to 8 mm, thus mirroring the distance between the tusk-like fangs present in the genus (Fig. 7D). Injuries were present in all species

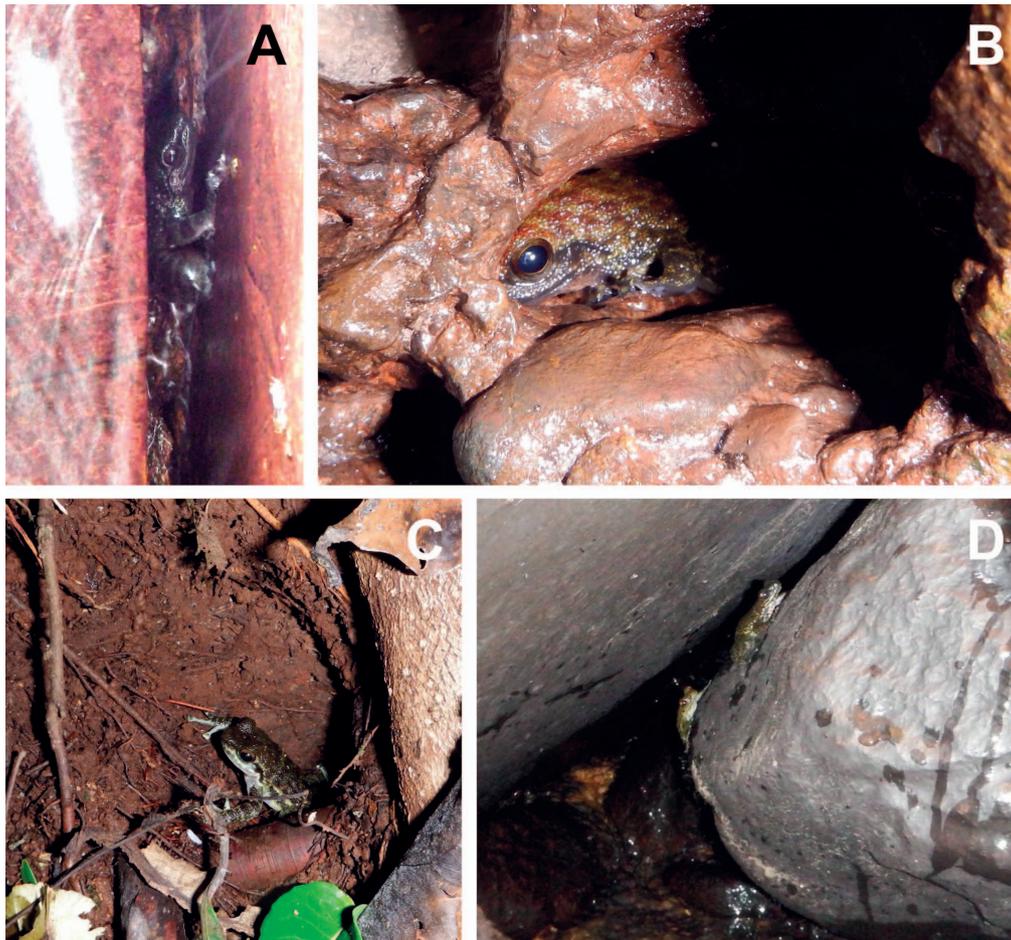


Figure 6. Daytime shelters of *Odontobatrachus*: (A) *O. smithi* in a rock crevice on the Ideta River, Mabhé, Téliimélé Province, Guinea; (B) *O. arndti* in a rock cave, and (C) emerging from an subterranean cave on the Zougoué River, Nimba Mountains Strict Nature Reserve, Lola Province, Guinea; (D) Two *O. ziama* emerging from between rocks at dusk on the Vère River, Sérédou, Ziama Massif Strict Nature Reserve, Macenta Province, Guinea. Note: The depicted behaviours are consistent throughout the genus, and these pictures therefore are representative of all five *Odontobatrachus* species.

Life-history and reproductive ecology of Sabre-toothed Frogs

Table 2. Injuries on male and female *Odontobatrachus* during the dry season. Analyzed frogs were collected from the Ditiwol River near Din Tin in Dalaba Province (*O. fouta*), Wosai River near Massadou, Ziama Massif Strict Nature Reserve, Macenta Province (*O. natator*), Ideta River, Mabhé, Téliélé Province (*O. smithi*), and Vère River near Sérédou, Ziama Massif Strict Nature Reserve, Macenta Province (*O. ziama*), all Guinea. Displayed numbers and percentage for *O. fouta*, *O. natator*, *O. smithi* and *O. ziama* individuals, showing gular wounds (male and female), number and percentage of gravid females, number of females after oviposition (aft. ovi), and females that had deposited the eggs of only one ovary (half-ovi.), as well as numbers and percentages of females after full and partial oviposition with ventral lacerations. Fisher-tests were performed to compare the frequency of gular wounds between male and female frogs of the respective species.

| | <i>O. fouta</i> | | <i>O. natator</i> | | <i>O. smithi</i> | | <i>O. ziama</i> | |
|---------------------|-----------------|------------|-------------------|------------|------------------|------------|-----------------|------------|
| | male | female | male | female | male | female | male | female |
| N | 8 | 15 | 12 | 19 | 12 | 21 | 11 | 18 |
| gravid | | 80% (12) | | 74% (14) | | 72% (15) | | 83% (15) |
| aft. ovi. | | 3 | | 4 | | 5 | | 2 |
| half-ovi. | | - | | 1 | | 1 | | 1 |
| ventral lacerations | | 100% (3) | | 67% (3) | | 67% (4) | | 67% (2) |
| gular wounds | 88% (7) | 20% (3) | 83% (10) | 21% (4) | 75% (9) | 19% (4) | 72% (8) | 11% (2) |
| fisher test | OR = 0.2398 | p = 0.1264 | OR = 0.2608 | p = 0.0573 | OR = 0.2621 | p = 0.0560 | OR = 0.1605 | p = 0.0310 |

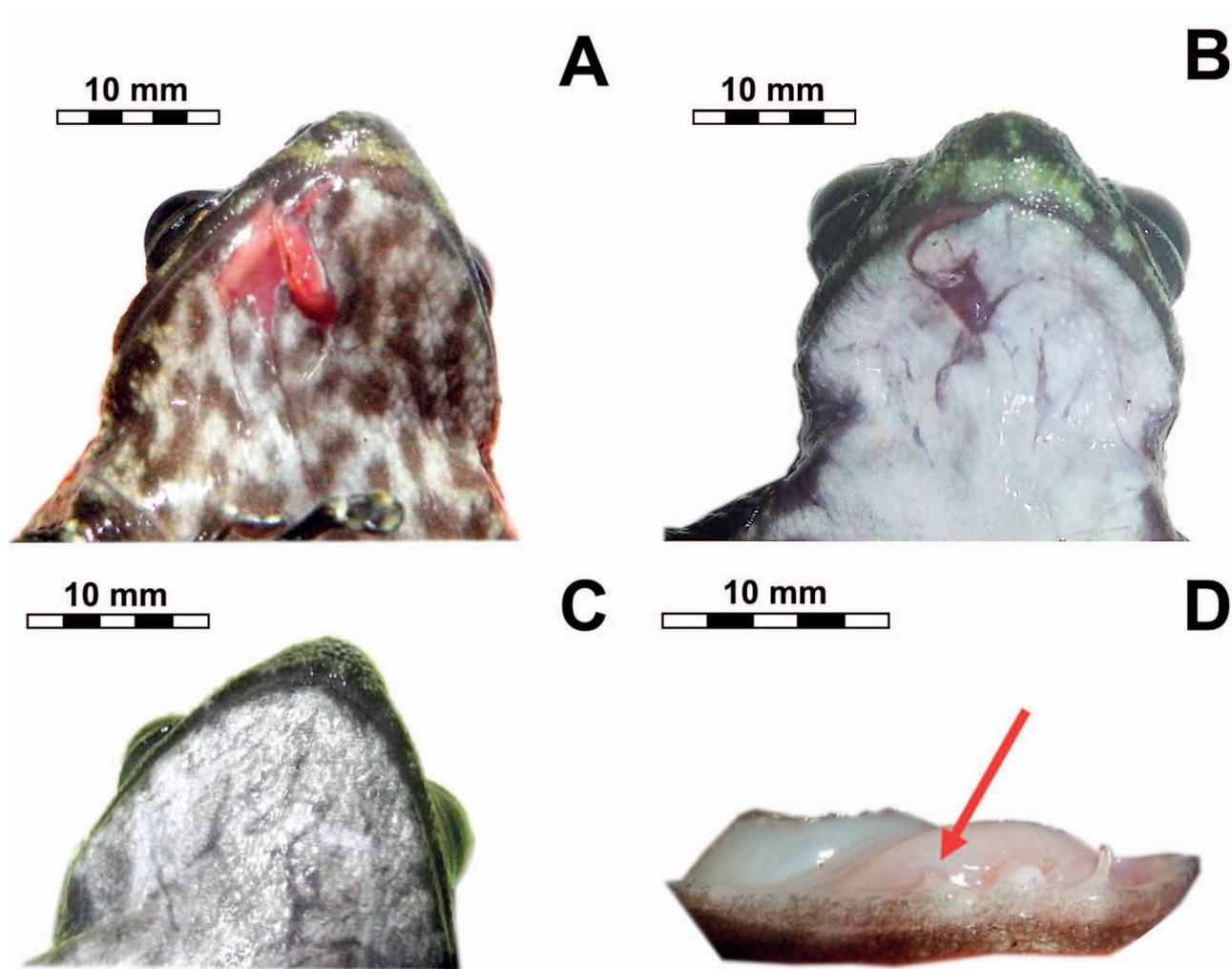


Figure 7. Injuries from presumed intraspecific fights in *Odontobatrachus*: (A) fresh throat injuries on a male *O. fouta* (note: the jaw-bone of this individual is fractured) and (B) *O. smithi*; (C) older, healed injuries in an *O. natator* male; (D) lower jaw with a broken fang (red arrow) in an *O. arndti* male. Important to note: the distance between the two parallel cuts (A, B and C) is in the range of the distance between the fangs.

and in two observed cases even involved broken mandibular bones (Fig. 7A). We also found broken fangs in male frogs (Fig. 7D; an. ob.).

Reproduction

We never directly witnessed mating or spawning. However, a combination of anecdotal observations and direct assessments of reproductive status provide insights into reproduction behaviour of *Odontobatrachus*. We observed once what looked like an amplexus in *O. arndti* in June 2018 on the River Ya in the MNSNR. A male frog was found half perched on a female. He had grabbed the female above the waist, slightly shifted to the left (Fig. 8A). The frogs quickly disappeared, not allowing further observation. However, we repeatedly found females with conspicuous marks in a mid-lateroventral position that seemingly matched the observed grabbing position by the above-mentioned male (Fig. 8B, Table 2).

During the dry season, between 72 and 80% of *O. fouta*, *O. natator*, *O. smithi*, and *O. ziama* females were carrying mature eggs (Table 2). A similar rate was found in *O. arndti* during the wet season. Of 42 female *O. arndti*, 12 apparently had deposited eggs already (71% were still gravid). From these 12 females, eight showed the ventrolateral scars (67%; between 67 and 100% in the other four species; Table 2). Of these eight females, three had open wounds, two exhibited fresh but healed ones, and in three females the flanks showed scars in the mid-lateroventral section. In five females, the wounds/scars had reddish to pink mites at-

tached (Fig. 8B), which would otherwise usually be present on the webbings or around the thighs or cloaca (an. ob.). In six of the wounded females, the lacerations were visible on both sides of the abdomen and in two cases only on one side. We found three females where one flank was swollen with ripe eggs, while the other flank was sunken and no eggs were visible through the thin skin of the inguinal region (ratio of females that we found after oviposition and females with only one empty ovary = 4:1). Similar rates of females that had deposited the eggs of only one ovary were noticeable in the dry-season comparison (3:0 in *O. fouta*, 5:1 in *O. natator*, 6:1 in *O. smithi*, and 3:1 in *O. ziama*; Table 2). During our recapture study on *O. ziama* (see above), we found females before, between, and after oviposition, as was apparent by the size of the abdomen and the weight differences. A female with ripe eggs weighed 18 g, then lost 2 and 1.5 g (3.5 g: ~ 20% of initial bodyweight) within the two consecutive recaptures, after depositing the eggs of the first and the second ovary, respectively (Fig. 9, 10B).

In March 2019, we detected a clutch of *O. ziama* on a tributary of the Vère River in a small rock crevice behind a cascade. The clutch comprised 146 eggs. The eggs had been laid in a puddle of approximately 50 ml of water. There was no continuous water inflow; however, water dropped occasionally from the wall and spray-water from the cascade refilled the puddle. The single eggs were loose, not attached to the ground or the walls (Fig. 10A). The crevice measured 12 mm in width, 60 mm in depth, and approximately 120 mm in length. Two unfertilized clutches were laid under similar conditions by a captive *O. ziama* female in January and December 2020, respectively. These eggs had



Figure 8. Possibly mating-related observations in *Odontobatrachus*: (A) possible amplexus in *O. arndti*, observed on the Ya River, Nimba Mountains Strict Nature Reserve, Lola Province, Guinea; (B) mite-infested lacerations on the flanks of an *O. smithi* female from the Naremba River near Kindia in Téliélé Province, Guinea. This female had already deposited the eggs of her left ovary, while eggs could still be seen shining through the right flank.

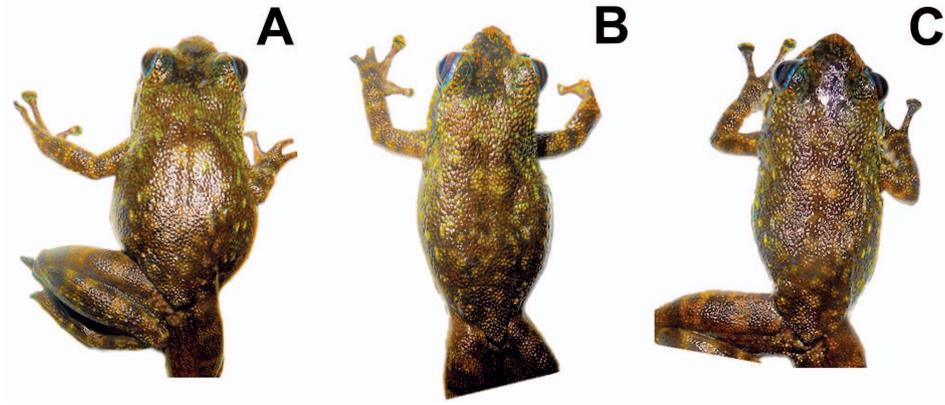


Figure 9. *Odontobatrachus ziama* female on the Vèrè River, Sérédou, Ziama Massif Strict Nature Reserve, Macenta Province, Guinea before, during and after oviposition; (A) captured first on 15th March 2019, weighing 18.0 g, both ovaries with ripe eggs; (B) recaptured on 20th March 2019, weighing 16.5 g, left ovary empty; (C) second recapture four days later on March 24th 2019 with a weight of 14.5 g, both ovaries empty.

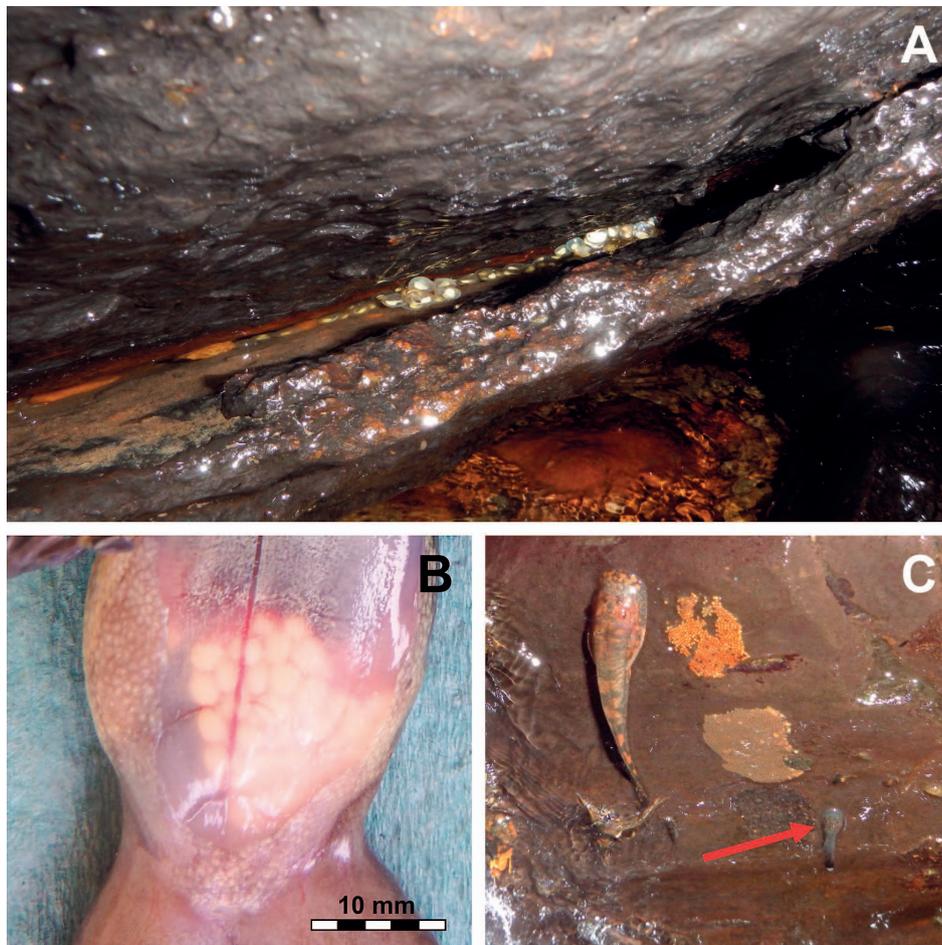


Figure 10. Indications of *Odontobatrachus* breeding activities: (A) Clutch of *O. ziama* found in March (late dry season) on a tributary of the Vèrè River, Sérédou, Ziama Massif Strict Nature Reserve, Macenta Province, Guinea; the crevice measured 12 mm in width, 60 mm in depth and approximately 120 mm in length. (B) dissected *O. ziama* female from the Vèrè River, with the ventral skin removed: ripe eggs in the left ovary, right ovary apparently empty. (C) Two tadpoles of *O. arndti* found in December (mid dry season) on the Zougoué River, Mount Nimba Strict Nature Reserve, Lola Province, Guinea; the tadpole marked with a red arrow is the earliest larval stage (appr. Gosner stage 25) ever found in the open.

been laid in an artificial cave behind a waterfall, a place these frogs usually use to hide at during daytime. A second clutch of about 150 eggs was deposited in very shallow, slow-flowing water below a piece of cork.

Especially on large permanent streams, tadpoles of different developmental stages, of all five species, could be found all year round (Fig. 10C). Tadpole abundances did not show apparent peaks in any month or season, indicating a continuous or at least prolonged breeding season (an. ob.). Adult frogs of all species could be also observed along smaller rivers (Figs 2B, D, F) that partially dried up during the dry season (an. ob.).

Larval development of *Odontobatrachus ziama*

From a single *O. ziama* clutch with 146 eggs (egg diameter: mean \pm SD = 2.71 \pm 0.57 mm; diameter jelly: 5.20 \pm 0.64 mm; eggs uniform yellowish), 144 bulky, unpigmented embryos hatched within two days after our discovery of the clutch. These hatchling larvae were at a late embryonic stage, about Gosner 18 (GOSNER 1960), just occasionally showing any muscular response. Except for the deep yellow, ball-shaped yolk, the larvae were entirely pale. They mostly rested on the ground, tilted to one side, showing no movement other than occasional tail flipping. These embryos did not develop any pigmentation until the fifth day after hatching, when the first indication of eyespots became visible. During this time, the larvae remained very

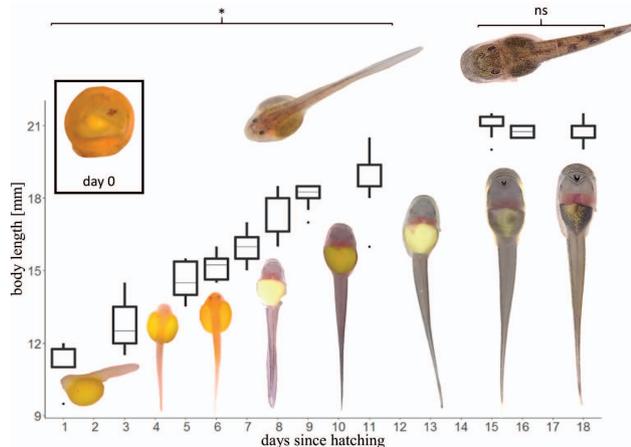


Figure 11. Embryonic and early larval development in *Odontobatrachus ziama* from the Vère River, Sérédou, Ziama Massif Strict Nature Reserve, Macenta Province, Guinea, raised in captivity at 24°C: Boxplots each show the total body lengths of ten randomly selected tadpoles one day after their respective hatching. Photographs of tadpoles show shape, granulation of yolk, state of dentition, and ventral (above boxplots) and dorsal (below boxplots) pigmentation one day after hatching; * = significantly different in body length; ns = no significant difference in body length: While we recorded a continuous longitudinal growth from the first day (Gosner 18–19) until the eleventh day after hatching (Gosner 25), growth ceased over the last four days in captivity (Gosner 26).

bulky. After Day 6, the bulky, yolk-filled body began to slowly flatten ventrally, yet the tadpoles still barely moved at that stage. The eyespots now became more pronounced and on Day 7, the first dorsal pigmentation appeared. By Day 8 (Gosner 22), a flagellum had formed on the tail and the tadpoles were clearly more agile. By Day 9 (Gosner 23), a sucker-like oral flap had formed, and the tadpoles started sucking on the stones and bottom substrate of their container. By Day 10 (Gosner 23–24), their yolk reserves had been very much reduced, and instead of a uniform yellow mass, a roughly spiral-shaped gut became discernible; the tadpoles now exhibited dorsal pigmentation and were flattened ventrally. Their initial, bulky appearance had vanished, and they had turned into very agile swimmers.

Within eleven days post-hatching the tadpoles had steadily and significantly gained in body length (Gosner 24–25), starting off at about 11.15 \pm 0.74 mm (one day after hatching), they now measured 18.70 \pm 1.23 mm (mean \pm SD; Kruskal-Wallis test: $X^2 = 71.994$, $df = 7$, $p < 0.0001$). In the following week, their longitudinal growth came to a hold. Measuring 21.00 \pm 0.47 mm on Day 15, no changes became apparent until the end of our observation period on Day 18 post-hatching (mean \pm SD = 20.85 \pm 0.47 mm; Kruskal-Wallis test: $X^2 = 2.4731$, $df = 2$, $p = 0.2904$). In the meantime, the tail had become more muscular, the dentition more refined (with the keratodont formula changing from 1–3/1 to 4/3), and their dorsal and ventral pigmentation became denser (Fig. 10). The tadpoles now had a fully developed sucker and all keratodonts, scraping on the stones and walls in their container (Gosner 26), fitting the descriptions by LAMOTTE & ZUBER-VOGELI (1954) and DOUMBIA et al. (2018). When we released the tadpoles at that stage, their developmental stage and size matched the smallest tadpoles we could detect in the open water (red arrow in Fig. 9A).

Discussion

Torrential streams are extreme habitats, requiring specialized inhabitants. Adult and larval torrent anurans of non-related taxa across the world often share a convergent morphology. In the West African *Odontobatrachus* species, the prominent sucker-mouth of tadpoles, with which they attach themselves to rocks below and above the water, has been already described by LAMOTTE and co-workers (LAMOTTE & ZUBER-VOGELI 1954, LAMOTTE & LESCURE 1988, 1989a, b, LAMOTTE 1985) and more recently by DOUMBIA et al. (2018), who did not detect major, phenotypical differences between the five species. Adults, that are likewise cryptic, have characteristic, T-shaped, adhesive fingertips, and strongly muscled hind limbs (BAREJ et al. 2015b). Similar features have been reported from other torrent frogs, such as Asian *Amolops* (Ranidae) (INGER 1966), some Australian *Litoria* (i.e., *Litoria nannotis*, Pelodryadidae) (HODGKISON & HERO 2001), *Petropedetetes*, Petropedetidae, in Central Africa (BAREJ et al. 2010a), and South American *Hylodes*, Hylodidae (HEYER 1982). Besides mor-

phological features, behavioural adaptations to the torrent environment have evolved, such as unusual forms of communication, including ultrasonic calls in *Amolops tormotus* (FENG et al. 2006), foot flagging in *Staurois*, Ranidae (GRAFE et al. 2012), *Micrixalus*, Micrixalidae (VASDEVAN 2001) and *Hylodes*, Hylodidae (HADDAD & GIARETTA 1999), or other visual cues in *Sachatamia orejuela* (BRUNNER & GUAYASAMIN 2020). Site fidelity, while not exclusive to torrent habitats, is another common if not ubiquitous behaviour in torrent frogs, and has been reported, for instance, from *Petropedetes* (BAREJ et al. 2010a), *Hylodes* (NARVAES & RODRIGUES 2005, ALENCAR et al. 2012), *Litoria nannotis* (HODGKINSON & HERO 2001), and *Amolops mantzorum* (LIAO 2011).

Some species of torrent frogs only inhabit certain parts of the torrent environments. Central African *Petropedetes* spp. for instance, mostly just avoid the torrents (SANDERSON 1936). *Petropedetes* oviposition sites have been reported to be situated on moist rocks in the splash zones of cascades and torrents, and are guarded by the adults (AMIET 1991, BAREJ et al. 2010a). The hatched tadpoles mostly stay outside the water until their metamorphosis (BAREJ et al. 2010a). They have been suggested to be poor swimmers, lacking well-developed fins, and show a rather early development of hindlimbs, needed to move about on the rocks (LAMOTTE et al. 1959, BAREJ et al. 2010a, CHANNING et al. 2012). In contrast, all *Odontobatrachus* species show a clear preference for torrents (BAREJ et al. 2015b), and their tadpoles can be observed even in the most torrential parts of their rivers (DOUMBIA et al. 2018). Our own data indicate that the slope and hence the velocity of a river, together with rocky substrate are a good proxy for *Odontobatrachus* occurrence. Within the geographic range of the genus, the presence of steep cascades and splashing water, at least within intact gallery forests, is a good indicator of their possible presence (GUIBÉ & LAMOTTE 1958, BÖHME 1994, RÖDEL 2003, RÖDEL & BANGOURA 2004).

However, *Odontobatrachus* spp. also inhabit calmer rivers, and there might be a sex-specific preference for different river parts. While males tended to be found frequently on lager waterfalls, and more than 200 frogs may sometimes be encountered in a place, moderately swift-flowing sections seemed to be favoured by females. At least at the sites we examined more intensively, frog densities were lower in the latter sectors. Males appeared to have a high site fidelity and associated territorial behaviour (i.e., they were calling in corresponding microhabitats), whereas females may have larger home ranges and seemed to migrate between different river sections. Sex-specific differences in habitat use persisted through the dry and wet seasons. One reason for larger home ranges and different microhabitat preferences might be that females have to forage more actively to maintain a positive energy balance (PRADO & HADDAD 2005). The higher diversity of food items found in females' diets supports this assumption (SCHÄFER et al. unpubl. data). Exceptionally, females of at least two species were found up to 100 metres away from their rivers, however, only under very humid conditions. That both sexes

depend on high humidity was visible under dryer conditions, when they occur closer to the river than in the rainy season. Females in non-breeding condition may as well choose different microhabitats to escape male harassment (see below).

Male *Odontobatrachus* preferred perching on exposed rocky outcrops at night, in close vicinity of cascades. They were absent from habitats lacking these features. Displaced males, but not females, returned to their original perches, which is a behaviour rarely documented in anurans, but known from other stream-breeding species (e.g., CRUMP 1986). Our camera-trap data also revealed that one male was very loyal to his preferred perch. Homing behaviour is especially well expressed when frogs are released in unsuitable habitats (WELLS 2007). However, NAVARRO-SALCEDO et al. (2021) reported pronounced homing in reproductive and territorial male glass frogs, *Centrolene savagei*. There is indirect evidence that male *Odontobatrachus* spp. may move through leaf litter at least sometimes. We observed exoparasitic mites on both males and females. The mites, tentatively identified based on morphology as members of the genus *Endotrombicula*, parasitize various African anurans (SPIELER & LINSSENMAIR 1999, WOHLTMANN et al. 2007, KPAN et al. 2019), have been reported mostly from species of the genus *Phrynobatrachus*. These mites are associated with moist terrestrial environments (KPAN et al. 2019). Mites are predominately found on the lower parts of thighs and around the cloaca, as these body parts are more commonly in contact with the leaf litter where the mite larvae wait for hosts (WOHLTMANN et al. 2007). However, we also observed mites on wounds on females' flanks.

We found tadpoles of all species at various stages all year round and thus have no indication of a defined breeding season. Likewise, we observed females with mature eggs in one or both ovaries in both the dry and wet seasons. However, we found dead tadpoles in dried-up pools, which demonstrated that breeding conditions are not always favourable, and an observation by RÖDEL & GLOS (2018), reporting on *O. natator* populations in dried-up rivers in Liberia, indicates that breeding activity is variable. An indication that some *Odontobatrachus* species have adapted to unpredictability is that females are able to deposit multiple clutches of eggs as has been observed in wild and captive specimens. Risk-spreading by increasing the number of independent reproductive events is a well-known strategy (STEARNS 2000) and often a consequence of unpredictable environments (SPIELER & LINSSENMAIR 1997, HIRSCHFELD & RÖDEL 2011, SIMONS 2011). While the breeding period seems not bounded, oviposition sites are probably chosen very thoroughly. Although still anecdotal, our observations of one clutch in an area with several male perches, as well as our female recaptures before and after oviposition in these microhabitats, indicate that *Odontobatrachus* spawning sites are rock crevices around cascades and waterfalls. Two clutches were also deposited under similar conditions in captivity (M. SCHÄFER pers. obs.). The predominance of large adult males of all five species in these microhabitats,

especially in contrast to smaller males in less rapid river sections, also suggests that male perch sites may be associated with breeding activity. Although we never saw a male calling on the rocks, we heard advertisement calls, as already described by RÖDEL (2003) and BAREJ et al. (2015), exclusively from these areas. We interpret the male-biased sex ratio around waterfalls as an indication that females may visit the breeding sites for oviposition only (RUSSEL et al. 2005). That females migrate between different river sections, up or down the river, was shown in our 12-day recapture study, where new females showed up in the 'plain' plot. In contrast, males seemed to stay at the breeding sites, have territories, and return to their places when displaced; most likely in order to wait for conceptive females and/or for guarding offspring. Even though we expect the sex-dependent habitat use and the respective behaviours around oviposition sites to be a genus-specific trait, it is important to notice that this assumption is mostly based on observations from two species, *O. arndti* and *O. ziama*. Nevertheless, less frequent observations in the other three species indicate the same.

Site fidelity usually comes along with territoriality and conflicts (STAMPS 1994) and we found evidence for both. Frequent injuries and scars indicate that physical combat is common in all species of *Odontobatrachus*. On one occasion in June 2018, we observed possible male territorial behaviour in *O. arndti* on the River Veblo (MNSNR). We released a male that we had caught farther downstream, at another typical male perch site, not realizing that the perch site owner was sitting less than 50 cm away. The 'resident' male instantly gave off an aggressive series of calls towards the 'intruder', tensing its extremities into a body-raising posture, seemingly in an attempt to appear larger. However, our attempt of recording this behaviour irritated both individuals and triggered their seeking shelter in two different, nearby crevices. Although the observed behaviour was in response to a situation created by us, we often heard similar high-pitched calls in the field, especially near waterfalls and larger cascades that we knew to harbour large frog populations. The frequently observed parallel wounds and scars indicated biting with the tusk-like fangs, and the observed broken jaws and fangs suggests that fights may escalate into damaging combat. Potential bite-marks in the gular region and scars on the back were also described for *Petropedetes* spp., which lack tusks but in which the males possess carpal spines (SANDERSON 1936, GVOŽDÍK & KOPECKÝ 2011). BAREJ et al. (2010a) and GVOŽDÍK & KOPECKÝ (2011) also interpreted these wounds and scars as the results of territorial behaviour. While biting is a known anuran behaviour, especially in fanged frogs (BALINSKY & BALINSKY 1954, KATISKAROS & SHINE 1997, ORLOV 1997, TSUJI & MATSUI 2002, FABREZI & EMERSON 2003), severe injuries are scarce (WELLS 2007) even though they do occur. In several gladiator frogs (*Boana* spp.), severe injuries and even fatalities due to the usage of the sharp prepollical spines during fighting have been reported (KLUGE 1981, MARTINS et al. 1998). Injuries resulting from the usage of similar weapons against conspecifics were reported from *Lepto-*

dactylus spp. (SHINE 1979), or through maxillary spines in *Leptobrachium boringii* (ZHENG et al. 2011). The phalanges used for stinging in *Trichobatrachus robustus* and *Astylosternus* spp. (and some *Ptychadena*; M.-O. RÖDEL unpubl. data) are known to injure predators (i.e., human frog hunters) (BLACKBURN et al. 2008). *Trichobatrachus* males also use spines on their thumbs for fighting, as is evident from frequent scars on the backs and flanks of adult males (BAREJ et al. 2010b). In *Odontobatrachus* both sexes possess tusks (BAREJ et al. 2014), thus these wounds may result from fights with either sex, however it seems more likely that they had been inflicted by territorial males; maybe this is another reason why females would visit male areas only for mating and oviposition. Whether males and/or females guard and defend their clutches is unknown, but seems possible from what we observed in captive frogs. In contrast to what the scars indicate, we often made the observation that adult frogs congregated in their narrow daytime shelters. Outside these hiding places, adults usually kept some distance. In contrast, juveniles and metamorphosing frogs frequently perched closely together. These assemblages were usually at some distance from adult frogs. Potential cannibalism has been documented in all *Odontobatrachus* species (SCHÄFER et al. unpubl. data) and it may be that younger frogs try to avoid predation from adults. Given the obvious contrast between brutal wounds and the observed dense aggregations, we believe that detailed research on the social behaviour of *Odontobatrachus* might reveal further interesting details. Recently, a very complex breeding behaviour, including scarce breeding sites, clutch cannibalism, male aggression towards both male and female conspecifics, as well as female hierarchy and reproductive fidelity, was discovered in *Thoropa taophora*, Cycloramphidae, from the Brazilian Atlantic forest (DE SÁ et al. 2020).

For many of the outlined behaviours we unfortunately lack repeated or even direct observations. We for instance have no direct observation of the oviposition behaviour. Indirect evidence however indicates that the eggs may not have been deposited in the narrow crevice by an amplexant pair. We believe it to be more likely that females lay the eggs without the male where they are subsequently inseminated by the males, thus explaining why the clutches laid in captivity were not fertilized. Here, a constant water-flow may have prevented insemination. Similar egg-laying and fertilization behaviour is known from the terrestrial cave-breeding frog, *Eleutherodactylus johnstonei* (BOURNE 1997). However, the frequent and characteristic lacerations on females' flanks, which we only observed in females that had already deposited all or half of their eggs, as well as the presence of nuptial pads in males (BAREJ et al. 2015b), indicate some sort of clasping or transient amplexus. Maybe clasping serves as a stimulus inducing ovulation. While early works pointed out that a mechanical stimulus is not necessary for ovulation (WARING et al. 1940), more recent work highlights that transdermal chemical stimuli can be conveyed during amplexus (WILLAERT et al. 2013, LUNA et al. 2018).

The lack of any pigmentation in the early larval stages indicates that oviposition always occurs sheltered from direct insolation and that eggs, embryos and young tadpoles are troglodytic. This explains why these stages have never been recorded from open water in any of the five species. Normally, functional pigment cells are present already at a very early embryonic state in tadpoles (THIBAudeau & ALTIG 2012). That clutches are not supposed to be in open, flowing water, is also suggested by the fact that the eggs were not attached to substrate, which is another trait common to stream breeders (DUELLMAN & TRUEB 1986), but scattered loosely on the ground in a very thin film of water. Hatching larvae also lacked any of the morphological features older tadpoles have to withstand strong currents (i.e., flat body, muscular tail, and in particular a sucker mouth). Although cave-dwelling species, with pigment-free clutches, have been reported in some Brazilian hylids (HARTMANN et al. 2004, WELLS 2007) and the leptodactylid *Leptodactylus troglodytes* (ARZABE & DE ALMEIDA 1997), we are not aware of a comparable breeding behaviour in other stream frogs. However, MALAGOLI et al. (2021) very recently documented, that *Bokermannohyla astartea* tadpoles change from a lentic hatching site to the lotic waters of neighbouring streams, to complete their development.

Free-swimming *Odontobatrachus* tadpoles are morphologically well prepared for a rheophilic life and retain the sucker mouth even after the forelimbs are fully developed (Fig. 5C; DOUMBIA et al. 2018). Beside morphological adaptations, the observed aggregations may potentially be an adaptation as well. Usually, tadpole aggregations occur in species with toxic tadpoles such as bufonids (WELLS 2007), or tadpoles living in open water such as *Scaphiopus* spp. and *Spea* spp. (BRAGG 1968), *Xenopus* spp. (WASSERSUG & HESSLER 1971), *Phrynomantis* spp. (RÖDEL & LINSENMAIR 1997), or *Rhinophrynus dorsalis* (FOSTER & MCDIARMID 1982), and are formed as an anti-predator strategy (SPIELER 2003, 2005), or are simply a consequence of food availability (WATT et al. 1997). Aggregation would normally end when the tadpoles complete their metamorphosis (WASSERSUG & HESSLER 1971). The observed *Odontobatrachus* tadpole aggregations in calmer sections could be a consequence of food availability and/or anti-predator behaviour. However, the dense aggregations often found in rapids, comprising various developmental stages, might be formed for a different purpose. LAMOTTE (1985) classified *O. natator* tadpoles as “oro-adhesive”, meaning they may be permanently attached to a substrate. This is even true in dead tadpoles, whose sucker mouths will still hold on to a smooth surface. Still, strong currents will demand a more active attachment, and energy might be simply saved by forming the observed aggregations with tadpoles benefiting from each other’s slipstreams (WEIHS 1973, SFAKIOTAKIS et al. 1999, RIEUCAU et al. 2014). Alternatively, tadpoles may choose to be in closer contact in torrential waters where they cannot rely on their well-developed lateral line system (A. GUTSCHE & M.-O. RÖDEL unpubl. data), as turbulent water will reduce the effectiveness of hydrodynamic sensations (MOGDANS 2019). By keeping contact to

each other, tadpoles might increase their individual chances of survival by observing their neighbours and thus, indirectly, become aware of approaching predators. Especially the water snake *Afonatrix anoscopus* has been observed trying to approach tadpoles in the torrents, and freshwater crabs, which have been identified as potential predators (SCHÄFER et al. 2019), were often observed nearby. However, such speculations need further investigation.

Conclusion

Whilst generalizations across genera may lead to spurious conclusions, our data include multiple observations across species that exhibit similar behaviours. For *O. arndti*, we could identify that males perch closer to the water than the females, both in dry- and wet-season conditions. During the dry season, both sexes stay generally closer to their water course, however. Relocation experiments, although based on few individuals, indicated homing behaviour and site loyalty, especially in males. We also observed potential territorial behaviour. Isolated females were observed up to 100 m away from the rivers, and females migrated to plots where they had not been seen before. For *O. ziama*, we could demonstrate that population structure varied between microhabitats. Here, males dominated in cascading river sections. Non-breeding females may avoid these sections to evade male aggression. Oviposition sites seem to be narrow caves and crevices behind cascades and waterfalls. Tadpoles start off as troglodyte, non-feeding, lentic larvae and later shift to a torrenticolous lifestyle and morphology. We assume that intraspecific fighting is common in all five species. Based on the frequency of scars, males seem to fight more often than females. Year-round tadpole occurrences and rates of gravid females indicate that the breeding season is continuous or at least prolonged. Duration of reproduction periods might dependent on river properties and vary regionally.

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