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ASPECTS OF THE REPRODUCTIVE BIOLOGY OF *AUBRIA SUBSIGILLATA* (ANURA, PYXICEPHALIDAE) HARVESTED FOR FOOD IN WEST AFRICA

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Abstract.—**The West African Brown Frog (*Aubria subsigillata*) is highly valued in the diet of people in Benin Republic, but it is subject to uncontrolled harvesting. Herein, we characterize some aspects of the reproductive biology of the frog to facilitate the development of sustainable management practices for the West African batrachofauna. We purchased specimens of *A. subsigillata* monthly from commercial frog catchers in the Commune of Dangbo, Ouémé Department, Benin Republic, from June 2021 to May 2022. We instructed collectors to collect all sizes of frogs. We measured snout-vent length and mass of the intact frog, liver, gonads, and carcass. We computed a gonadosomatic index (GSI) and hepatosomatic index (HSI). We found that the sex ratio of collected frogs was significantly female biased (1.0 M:2.4 F), females were generally larger than males, and size at first maturity was greater in females than in males. We analyzed the ovarian structure of females, which revealed an asynchronous development of oocytes with a mean absolute abundance of 1,517 oocytes/female and a relative fecundity of 39.81 oocytes/g of body mass. The GSI of males and females showed a strikingly similar pattern of dramatic increase between April and June and diminishing progressively thereafter. The HSI for females also peaked in June, whereas males peaked in July. This period of gonadal maturation occurred early in the period of increasing rainfall. Females with mature oocytes (available for oviposition) predominated from July through November, which corresponded with the period of greatest rainfall and high river water levels.**

Key Words.—breeding season; conservation; first maturity size; Ouémé Valley; ovarian structure; West African Brown Frog

INTRODUCTION

Studying the reproductive biology of anurans is essential for understanding their life history (Hirschfeld and Rödel 2011). The reproductive biology of anurans depends on both endogenous and exogenous factors (Schalk and Saenz 2016). Endogenous factors are linked to internal processes that contribute to regulating gametogenesis, whereas exogenous factors relate to external factors such as temperature cycles, hydroperiod, photoperiod, and food availability (Schalk and Saenz 2016). Reproductive function in frogs is regulated by mechanisms involving different organs, including the hypothalamus, the adenohypophysis, and the gonads, all of which contribute to hormonal regulation of reproductive cycles by regulating gonadal growth and the production and release of gametes during reproductive activities (Rastogi et al. 2011). In many cases, exogenous or environmental factors result in differences in reproductive cycles among temperate versus tropical dwelling species (Byrne and Roberts 1999; Iela et al. 1986; Rastogi et al. 2011). Many frog species living in temperate regions have a discontinuous reproductive cycle due to the seasonality of environmental factors; thus, a substantial change is generally observed during the year in the maturity of the gonads in these temperate frog species. In tropical regions, by contrast, climatic variation is low throughout the year, allowing continuous maturation of the gonads of tropical species (Rastogi et al. 2011).

Due to the poikilothermic nature of frogs, temperature represents the main environmental variable affecting frog reproductive phenology (Rastogi et al. 2011). Temperature affects gonad growth in both sexes, with higher temperatures stimulating the growth of ovarian follicles in females and upregulating spermatogenesis in males. Temperatures typically peak at the end of the dry season in West Africa and are responsible for maturation of gonads in the Crowned Bullfrog (*Hopplobatrachus occipitalis*),

Figure 1. Dorsal view of an adult female West African Brown Frog (*Aubria subsigillata*) in the Commune of Dangbo, Ouémé Department, Republic of Benin. (Photographed by Houénafa A. C. Gansa).

a species that is commonly eaten by humans (Tohé et al. 2016). Additionally, hydroperiod can serve as a signal for the start of reproduction (Rastogi et al. 2011; Brum et al. 2022) and, as for many other anurans, is responsible for triggering mating and egg-laying in *H. occipitalis* at the start of the rainy season (Channing 2001; Tohé et al. 2016). Also, photoperiod is known to promote thermal absorption during frog reproduction; it contributes to the regulation of gonadotropic hormones and influences the regulation of biological rhythms (Brum et al. 2022). Finally, the availability of food in the environment allows the mobilization of energy reserves which are used during reproduction (Chaves et al. 2017). The effects of this suite of endogenous and exogenous factors are well-studied in several frog species throughout the world; however, many frogs native to Africa are little studied on this subject.

The West African Brown Frog (*Aubria subsigillata*; Pyxicephalidae; Fig. 1) is native to parts of western Africa where it lives in ponds and swamps containing permanent water (Perret 1994). This frog is highly valued nutritionally and economically in the human diet in Benin Republic and has a high market value (Gansa et al. 2021a); thus, it is subject to high and possibly unsustainable harvest rates that may lead to its disappearance (Gansa et al. 2021a,b). In addition, no local or regional laws or norms exist to curtail harvest during certain times and locations. Likely as a result, the harvested numbers of *A. subsigillata* are trending downward and catch per unit effort is decreasing (Gansa et al. 2021a). Gravid females are the most prized in harvesting due to their large body size, and this preference may have a pronounced impact on the reproductive output of an *A. subsigillata* populations (Gansa et al. 2021a). Furthermore, there are no regulations governing frog harvesting in Benin as well as in some other West African countries, in part due to the lack of information on the reproductive biology of the species (Mohneike 2011; Tohe et al. 2016). Despite the diversity of species representing the Beninese batrachofauna and the multiple anthropogenic threats to the fauna in Benin Republic (Gansa et al. 2021a), the reproductive biology of only two frogs has been studied, Accra Snake-necked Frog (*Phrynomantis microps*; Hirschfeld and Rödel 2011) and Crowned Bullfrog (*Hoplobatrachus occipitalis*; Godome et al. 2020). The reproductive phenology, demographics, and ecology are unknown for *A. subsigillata* despite its commercial and cultural importance. This information is needed to understand the life history and population dynamics of this species to aid in cultivating sustainable harvest practices. Furthermore, the growing human population of Benin has resulted in expanded development of butcheries (Institut Nationale des Statistiques et de l'Analyse Economique [INSAE] 2016), and growing demand for frog meat in West Africa (Mohneke et al. 2011), including in neighboring Nigeria, which has created a large export market for Benin (Mohneke et al. 2011; Gansa et al. 2021a). With harvesting practices intensifying, further information on the reproductive biology of *A. subsigillata* is essential for informing regulatory action in the development of sustainable harvesting regimes.

We characterized several aspects of the reproductive biology of the species to facilitate better management of *A. subsigillata* populations. To this end, we counted the number of male and female *A. subsigillata* individuals in monthly samples of the population to determine the sex ratio of collected frogs. Determining this ratio will facilitate the development of regulations to direct protection measures towards the less abundant sex. We also collected monthly data on the size of individuals and additionally weighed the gonads, liver, and carcass to identify timing of reproduction and determine the size of frogs at sexual maturity. This study is a contribution to the body of knowledge of harvested

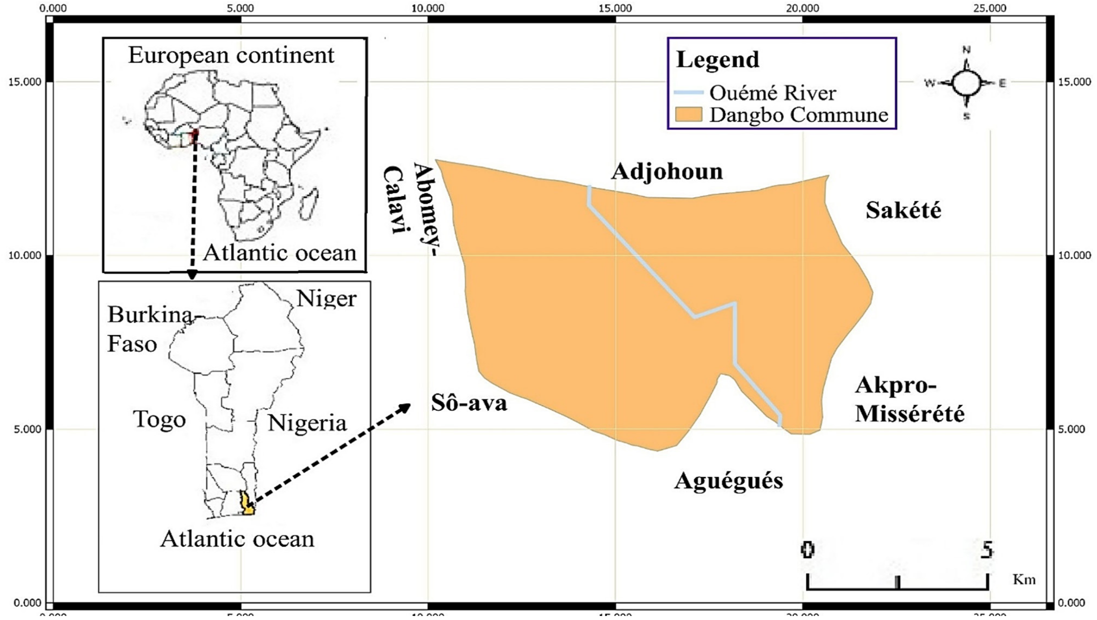

Figure 2. The sampling area of the West African Brown Frog (*Aubria subsigillata*) was the Commune of Dangbo (shaded polygon), Ouémé Department, Republic of Benin (inset map). Labels adjacent to Dangbo Commune refer to adjacent communes. Map border labels refer to UTM, Zone 31 projection.

anurans that can aid conservation efforts.

Materials and Methods

Study area.—The study area was the Commune of Dangbo, Ouémé Department, Republic of Benin (Fig. 2), which is located in the lower valley of the Ouémé River. The Commune of Dangbo covers an area of 149 km^2, the soil is ferralitic on the plateau (districts of Dangbo, Hozin, and Zounguè), and vertisol descending into the valley (districts of Dêkin, Gbékô, Houédomey, and Kessounou; INSAE 2016). The climate of the Commune of Dangbo is subequatorial, with mean annual ambient temperatures of 26.5° C (INSAE 2016; Zinsou et al. 2016). Annual rainfall is around 1,500 mm, and mean monthly relative humidity is 85% (INSAE 2016). Two main rainy periods and two main dry periods occur in the Commune of Dangbo. These are the major dry season (December to March/April), major rainy season (March/April to July), minor dry season (July/August to the beginning of September), and the minor rainy season (September to November; INSAE 2016). The Commune of Dangbo has vast plains flooded by the Ouémé River from August to November (Lalèyè et al. 2004).

The uncultivated vegetation in the region is dominated by species such as Gamba Grass (*Andropogon gayanus*), Mosquitofern (*Azolla pinnata*), Chaff Flower (*Centrostachys aquatica*), Hornwort (*Ceratophyllum demersum*), Water Fern (*Cyclosorus striatus*), Papyrus (*Cyperus papyrus*), Water Hyacinth (*Eichornia crassipes*), Cogongrass (*Imperata cylindrical*), Water Spinach (*Ipomea* aquatica), Marsh Taro (*Lasimorpha senegalensis*), Duckweed (*Lemna minor*), White Egyptian Lotus (*Nymphaea lotus*), Seashore Paspalum (*Paspalum vaginatum*), Water Lettuce (*Pistia stratiotes*), and Spotless Watermeal (*Wolffia arrhizal*; Gansa et al. 2023). Due to the high fertility of the soils of floodplain, numerous crops are grown by people whose dominant activity is agriculture, such as Bird Pepper (*Capsicum frutescens*), Oil Palm (*Elaeis guineensis*), Lady's Fingers (*Hibiscus esculentus*), Cassava (*Manihot utilissima*), Tomato (*Solanum lycopersicum*), and Maize (*Zea mays*; INSAE 2016; Gansa et al. 2023). This floodplain is also heavily fished in man-made depressions known as fish holes (i.e., 1.5-m deep, 4-m wide, and up to 20-m long hollows cut in the floodplain that are used by fish as a refuge during the flood season and where fish subsequently find themselves trapped when waters recede; Fig. 3) and ahlos (depressions dug in the floodplain, in which people lay tree branches to serve as food for

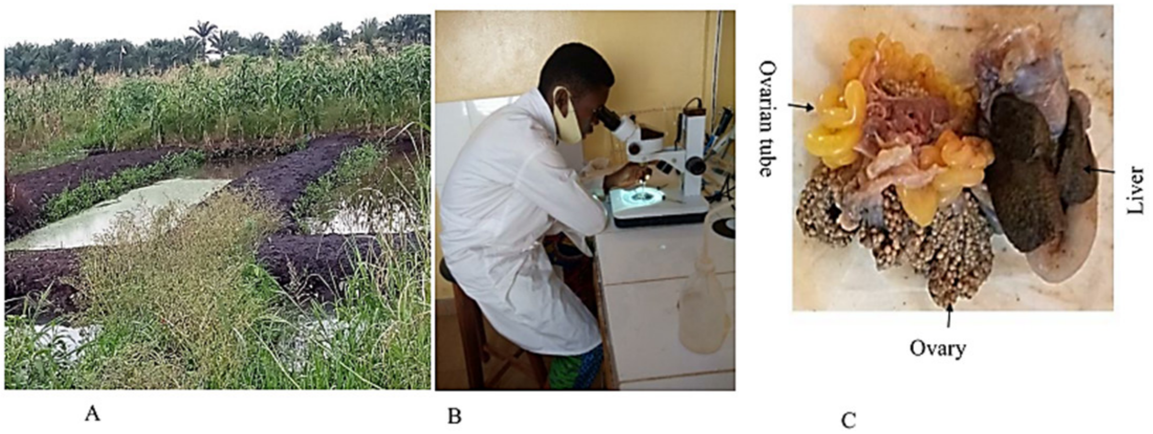

Figure 3. (A) An example of the type of marsh habitat sampled for West African Brown Frogs (*Aubria subsigillata*) in the Commune of Dangbo, Ouémé Department, Republic of Benin from June 2021 to May 2022. (B) Using a stereoscope to count oocytes from a female *A. subsigillata* in the oviposition phase (stage V; Table 1) (C) Organs extracted from the belly of a female *A. subsigillata* and weighed to derive reproductive metrics to determine fecundity. (Photographed by Houénafa A. C. Gansa).

the fish, which are harvested when the floodwaters recede). The ichthyofauna includes North African Catfish (*Clarias gariepinus), C. ebriensis* (No Common Name [NCN] in Benin)*, Heterobranchus longifilis* (NCN in Benin)*,* African Bonytongue (*Heterotis niloticus*)*,* Nile Tilapia (*Oreochromis niloticus*)*,* and Blackchin Tilapia (*Sarotherodon melanoteron*; Lalèyè et al. 2004; Chikou 2006).

The floodplain of the Ouémé River is also home to several species of anuran. In order of abundance, the anuran fauna includes western clawed frogs (*Xenopus tropicalis* and *X. fishbergi*)*,* Mascarene Ridged Frogs (*Ptychadena* cf. *mascareniensis*-complex), South African Sharp-nosed Frogs (*Ptychadena oxyrhynchus*)*, Hoplobatrachus occipitalis*, and Galam White-lipped Frogs (*Amnirana galamensis*; Gansa et al. 2023). Individual *A. subsigillata* are also present in these floodplains (Fig. 1), although their abundance is very low relative to the other species (Gansa et al. 2023). *Aubria subsigillata* individuals are commonly observed in human-made ponds (containing fish), natural ponds, and along river edges.

Sampling of *A. subsigillata* ***and environmental data.***—Between 1 June 2021 and 29 May 2022, we identified five frog collectors in the Commune of Dangbo to supply us with *A. subsigillata* frogs. We communicated that the aims of the study were to have a broad range of all sizes of frogs without preferences for sex, not just the more desirable large gravid females. As the sample of collected frogs was subject to the collection practices of the individual collectors, however, we do not assume that demographics of the collected frogs reflect the true size distribution

Table 1. Description of five stages of ovarian development in 278 female West African Brown Frogs (*Aubria subsigillata*) sampled in the Commune of Dangbo, Ouémé Department, Republic of Benin from 1 June 2021 to 29 May 2022. Values are mean ± standard deviation.

Maturity stage	Description
Stage I. Immature female	Ovary poorly differentiated; oocytes are barely visible to the naked eye and pasty. Numerous atretic oocytes are visible, resembling small black dots; n = six females.
Stage II. Female in early oocyte growth	Ovary differentiated, showing mostly reddish bloody oocytes with a small proportion of whitish and sometimes yellowish oocytes. For reddish oocytes mean mass = 0.21 ± 0.038 mg and mean diameter = 240.43 ± 7.49 µm; n = 48 stage II 48 oocytes from 35 females.
Stage III. Female in full oocyte growth or post oviposition phase	Ovary differentiated, with reddish, whitish, and yellowish oocytes. There is a high proportion of whitish oocytes with a pasty or sometimes yellowish appearance. For whitish oocytes mean mass = 0.53 ± 0.022 mg and mean diameter = 521.58 ± 13.39 µm; n = 185 stage III oocytes from 95 females.
Stage IV. Female in the final phase of oocyte enlargement or pre-spawn phase	Ovary differentiated, containing oocytes of variable size and color. The ovarian cavity contains reddish, whitish, and yellowish oocytes. Yellowish oocytes (mean mass = 0.71 ± 0.011 mg; mean diameter = 748.11 ± 10.62 µm) are the most abundant; n = 481 stage IV oocytes from 50 females.
Stage V. Mature female or oviposition phase	Ovary differentiated, occupying the entire ovarian cavity. The ovary contains reddish, yellowish-white, and dark yellow oocytes. Dark yellow oocytes (mean mass = 1.02 ± 0.027 mg, mean diameter = 996.16 ± 22.19 µm) are the most abundant; n = 803 stage V oocytes from 92 females.

or sex ratio of the sampled *A. subsigillata* population. *Over the 12-mo period, we* purchased dead frogs each month totaling 394 frogs for inclusion in this study. We weighed the specimens using an electronic balance (precision 0.001 g) and measured the snout-vent length (SVL) of each specimen using calipers (precision 0.1 mm). We fixed specimens in 5% formalin and transferred them to 70% ethyl alcohol after two weeks. At the end of each month, we transported all collected specimens to the laboratory for additional measurements.

We downloaded information on rainfall of Dangbo Commune over the sampling period from the website of the Benin Ministry of Livestock, Agriculture and Fisheries (MAEP; http://www.dsa.agriculture.gouv.bj) and obtained ambient temperature data from the meteorological service website of the Agence pour la sécurité de la navigation aérienne en Afrique et à Madagascar-Benin (https://fr.weatherspark.com/y/147923/M%C3%A9t%C3%A9o-moyenne-%C3%A0-Cotonou-Airport-B%C3%A9nin-tout-au-long-de-l'ann%C3%A9e#Figures-Temperature). Finally, we determined gauge water level in the aquatic environment multiple times each month from staff gauges installed in the plains bordering the Ouémé River in the Commune of Dangbo.

***Characterizing reproductive biology*.**—We classified female *A. subsigillata* by stage of ovarian development into one of five categories (Table 1). Additionally, we removed and separately weighed the liver, gonads, and carcass (i.e., the body with all viscera removed) of all frogs (female and male) as well as the ovarian tube (cavity that collects oocytes expelled by the ovary; Fig. 3) from females of the 394 specimens collected over 12 mo. To determine absolute fecundity (number of oocytes/female), we counted the oocytes in three mature female frogs (i.e., a female with an ovary with predominantly large-diameter oocytes [≥ 996 µm diameter], ovarian stage V; see Table 1) in each of the months of June, July, August, September, October, and November (n = 18). We used forceps to open the ovary, and we counted the number of oocytes in the ovarian cavity using a stereoscope to determine fecundity during each month (Fig. 3). We then calculated relative fecundity, expressed as the number of oocytes/body mass using all females. For this determination, we first counted the number of oocytes in 1 g of ovary and then multiplied this by the total ovarian mass to estimate the total number of oocytes. We then divided the count estimate by body mass to determine relative fecundity.

To determine the ovarian structure of *A. subsigillata*, we dissected one stage V female (see Table 1) and, using a micropipette, we removed all the oocytes contained in her ovarian cavity. We placed a petri dish on graph paper (millimeter squares) and placed the oocytes inside the petri dish. We projected the whole set (petri dish + graph paper) onto a computer using a micro capture digital microscope (AM300X, Ningbo Diamond Metal Products, Zhejiang, China). Using AMCAP Version 4.9 software (available from http://noeld.com) we photographed the oocytes and the graph paper. We then measured the oocyte diameter from the photographs using Camera Measure Version 1.0 software (CCD Digital Cameras, Titan Tool Supply, Inc, Buffalo, New York, USA). We then grouped the oocytes by size class using Sturge's formula (Scherrer 1984) to determine the number of classes. We calculated Sturge's formula as number of classes = 1 + 3.3 log10 (n), where n represents the number of oocytes in the sample. Then, we described the ovarian structure as the frequency of oocyte numbers by size class. To determine the ovarian stage frequencies among females, we determined the predominant ovarian stage (Table 1) for each female and calculated the relative frequency of females at a given stage for each month. The determination of ovarian stage frequencies is useful to help evaluate whether eggs are oviposited in a single or multiple spawns (Leivas et al. 2012).

We estimated the size at first maturity (L50) as the SVL at which 50% of males and females were mature (i.e., individuals reaching the size at which they are capable of producing offspring; Lévêque and Herbinet 1979; Légendre and Ecoutin 1996). We considered mature males to be those with gonads of high mass (i.e., > 0.04 g) and mature females to be those with an ovary with predominantly large-diameter oocytes (i.e., ≥ 996 µm; Stage V). First, we divided individuals into equal-interval size classes, with the number of classes determined using Sturge's formula as described above. We then plotted the median SVL of each class size on the X-axis of a graph, and the cumulative percentage of mature specimens for each size class on the Y-axis (i.e., the percentage of mature individuals for all sizes classes up to and including the one being plotted). Next, we fitted a curve to the points using the Scatter with Smooth Lines function in Excel (Microsoft Corp., Redmond, Washington, USA). To determine L50, we identified the point on the curve where 50% of individuals were mature (i.e., Y-axis value) and projected this onto the X-axis (SVL).

We calculated the gonadosomatic index (GSI) or gonadosomatic ratio as the ratio expressed as a percentage between gonad mass and carcass mass. The GSI is an indicator of gonad development (Zeyl 2012). We calculated the hepatosomatic index (HSI) or hepatosomatic ratio as the ratio expressed in percentage between liver mass and carcass mass. The HSI is an indicator of how glycogen storage and energy reserves are used during the breeding season (Leão et al. 2021). Glycogen is a glucose macromolecule that is the main source of energy in the body. It is stored in the liver, and thus the mass of the liver is proportional to the quantity of glycogen stored. A high HSI implies a large quantity of glycogen and therefore a large energy reserve (Leão et al. 2021).

Statistical analysis.—We used Levene's test on the body size data (SVL and mass) to confirm homoscedasticity of variances. We tested the body size data (SVL and mass) for normal distribution using Shapiro-Wilk test (α = 0.05), and after affirming that the Shapiro-Wilk test was consistent with normal distribution, we used independent *t*-tests to compare SVL and mass between males and females. We used a Chi-square test to evaluate the difference between the numbers of males and females sampled. We used Analysis of Variance (ANOVA) and Tukey *post-hoc* tests to evaluate differences among months in body mass and relative fecundity of *A. subsigillata* females in stage V. Before performing ANOVA, we confirmed that variables were normally distributed using a Shapiro-Wilk Test (α = 0.05). We used Levene's test to confirm homoscedasticity of variances. We checked that the sample cases were independent and that variances among the groups were approximately equal. We performed statistical analyses with SPSS Statistics Version 25 software (IBM, Chicago, Illinois, USA) with significance level set at α = 0.05. Values are expressed as mean ± standard deviation unless otherwise noted.

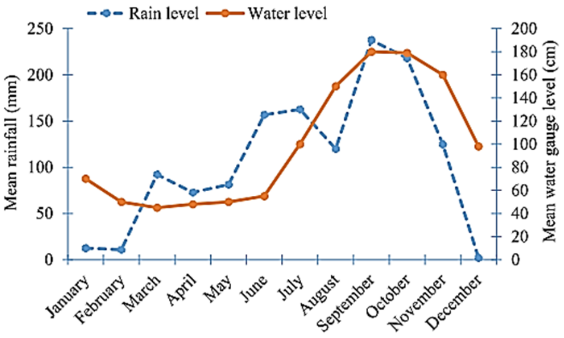

Figure 4. Monthly rainfall and gauge water level of the Ouémé River in the Commune of Dangbo, Ouémé Department, Republic of Benin, during the sampling period for West African Brown Frogs (*Aubria subsigillata*), June 2021 to May 2022. Gauge water level values refer to gauge values, not depth of the river.

Results

Environmental data.—During the study period (June 2021 to May 2022), monthly rainfall ranged 2–238 mm (Fig. 4). Rainfall was very low in December through February (2–11 mm), then increased markedly to a peak in September and October (218 and 238 mm, respectively) and declined steeply thereafter. The mean monthly gauge water level of the Ouémé River fluctuated between 55−180 cm (Fig. 4). The gauge water level peaked at the

Table 2. Total mass, relative fecundity (oocytes/g of body mass), and absolute fecundity (number of oocytes/female), of mature females (Stage V; Table 1) of West African Brown Frogs (*Aubria subsigillata*) sampled in the Commune of Dangbo, Ouémé Department, Republic of Benin from 1 June 2021 to 29 May 2022. Data are presented for June to November because mature females were found almost exclusively during these months. Sample size varied by month for relative fecundity and was three for all months for absolute fecundity. Values are mean ± standard deviation. Values with the same letters are not significantly different among the sampling months ($P > 0.05$).

Month in the breeding season	Number of females used for the relative fecundity determination	Mass of females used for the relative fecundity determination (g)	Relative fecundity (oocytes/g of body mass)	Absolute fecundity (oocytes/female)
June	7	43.15 ± 4.26 a	42.71± 2.4 a	1,622 ± 217
July	13	45.59 ± 5.02 b	39.33 ± 7.2 b	1,456 ± 142
August	16	41.17 ± 5.33 b	41.38 ± 2.1 a	1,463 ± 326
September	19	39.25 ± 5.15 a	39.67 ± 5.7 b	1,558 ± 201
October	19	36.00 ± 7.28 a	38.88 ± 3.7 b	1,556 ± 22
November	17	33.38 ± 6.63 c	36.93 ± 2.4 c	1,447 ± 218
June to November	91	39.75 ± 5.61	39.81 ± 3.9	1,517 ± 221

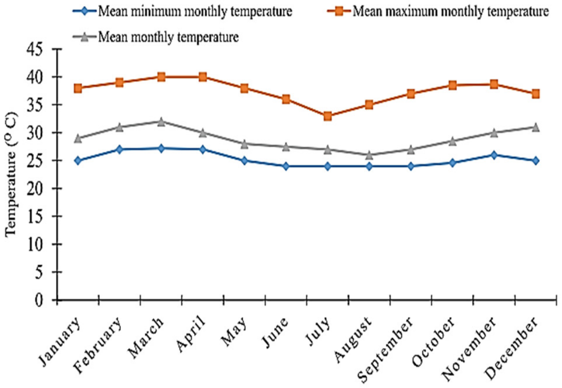

Figure 5. Mean monthly ambient temperatures in the Commune of Dangbo, Ouémé Department, Republic of Benin, during the sampling period for West African Brown Frogs (*Aubria subsigillata*), June 2021 to May 2022.

same time as rainfall (September-October, 179–180 cm), but the increase to this peak generally lagged rainfall. Specifically, gauge water levels were low from January to June (55–70 cm), but thereafter increased markedly until September (180 cm) and decreased steeply from October to January. Mean monthly ambient temperature generally increased from August (26° C) to March (32° C) and decreased thereafter (Fig. 5).

Body size and sex ratio.—We obtained a sample of 116 male (29.4 %) and 278 female (70.6 %) *A. subsigillata*. Females were significantly larger than males; body mass of females = 36.69 ± 6.85 g (range of values 24.96–47.39 g) and for males = 27.80 ± 5.41 g (range of values 17.42–32.72 g; $t = 12.44$, df = 292, $P < 0.001$), while SVL of females = 81.60 ± 4.29 mm (range of values 28.60–88.00 mm) and of males = 73.62 ± 5.06 mm (range of values 23.5–80 mm; $t = 15.93$, df = 292, $P < 0.001$). The sex ratio of the entire sample (1.0 M:2.40 F) differed significantly from a sex ratio of 1:1 ($X^2 = 44.86$, df = 1, $P < 0.001$). For 10 equal-interval SVL size classes, the sex ratio of collected frogs within size class showed a dramatic shift at 81 mm; the sex ratio of collected frogs was male-biased for SVL classes between 63 mm and 81 mm (five classes; sex ratio observed range, 1:0.17 to 1:0.83), whereas females dominated for SVL size classes ranging 82–99 mm (four classes; sex ratio observed range, 1:3.20 to 1:6.71). No males were in the largest size class, i.e., over 95.5 mm SVL.

Absolute and relative fecundity.—In mature females (Stage V), body mass averaged 39.75 g and differed significantly among the months considered (June-November; $F5{,}90 = 3.96$, $P = 0.002$; Table 2). The data suggest a generally declining pattern over time with the highest body mass recorded early in this period (July; mean = 45.59 g) while the lowest body mass occurred at the end of the period (November; mean = 33.38 g). Absolute fecundity was highest in females in June (mean = 1.622 oocytes) and lowest in November (1,447 oocytes; Table 2). Relative fecundity averaged 39.81 oocytes/g of body mass and differed significantly among the months considered ($F5{,}90 = 2.64$, $P = 0.028$; Table 2). As with body mass, relative fecundity followed a generally declining pattern over time with the highest value in June (mean = 42.71 ± 2.40 oocytes/g) and the lowest in November (mean = 36.93 ± 0.41 oocytes/g; Table 2).

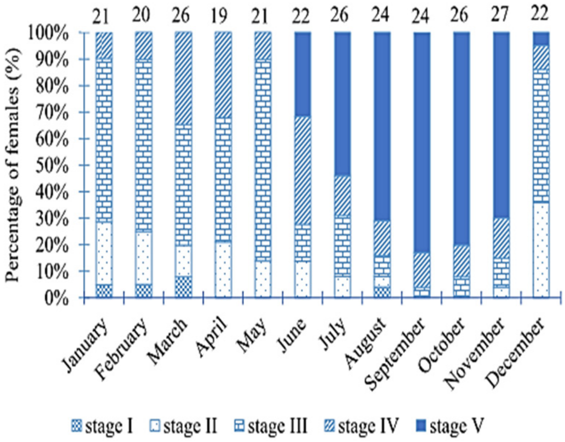

Figure 6. Monthly ovarian stage frequencies among female West African Brown Frogs (*Aubria subsigillata*) sampled in the Commune of Dangbo, Ouémé Department, Republic of Benin from 1 June 2021 to 29 May 2022

Ovarian structure, ovarian stage frequencies and size at first maturity.—Oocyte diameter measured on 1,447 oocytes taken from the ovary of a mature female at stage V showed that the ovary of this female had oocytes of varying sizes and in different proportions. We determined frequency of oocytes for four size classes based on diameter. We were unable to count and measure oocytes in size class I due to their pasty aspect (i.e., impossible to separate eggs because they were almost liquid; Table 1). Among the size classes that were measurable, size class II (212–452 µm) contained 3.13% of the oocytes, class III (453–693 µm) contained 12.23%, class IV (694–934 µm) contained 31.73%, and class V (935–1,175 µm) contained 52.91% of the oocytes.

There was a general pattern of ovarian stage increasing among females from younger to older stages over the period of January through November

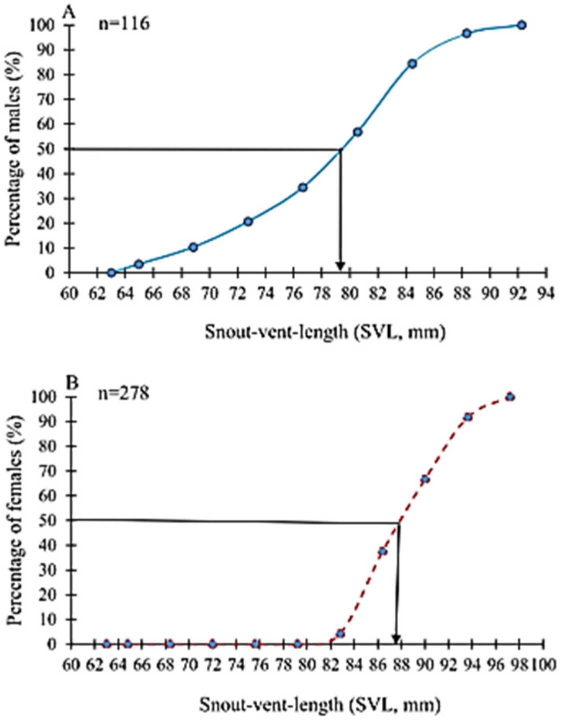

Figure 7. Size-maturity curves used to estimate size at sexual maturity in (A) male and (B) female West African Brown Frogs (*Aubria subsigillata*) sampled in the Commune of Dangbo, Ouémé Department, Republic of Benin, from 1 June 2021 to 29 May 2022. Each point represents a size-class grouping where the value on the X-axis is the median snout-vent length (SVL) for the group and the value on the Y-axis is the proportion of individuals in the class that are mature (i.e., males with gonads > 0.04 g; females with stage V oocytes). The arrow on the X-axis indicates the SVL at which 50% of males or females are projected to be mature.

(Fig. 6). Females with ovarian stage I oocytes were most abundant from January to March with a maximum frequency 8% in March. Females in ovarian stage II were most abundant in December (36% of females) and decreased thereafter. Females in ovarian stage III dominated from December to May, with a maximum frequency of 76% in May, females at stage IV dominated in June (41%), and females at stage V (mature females) dominated July-November, with a maximum frequency in September (83%).

The size at first maturity was greater in females (87.8 mm) than in males (79.4 mm; Fig. 7). Based on the fitted curves, all males (100% on Y-axis) were mature at 92.5 mm, while all females were mature at 97.2 mm. The smallest female reached sexual maturity at 82.8 mm, while the smallest male matured at 65.0 mm (Fig. 7).

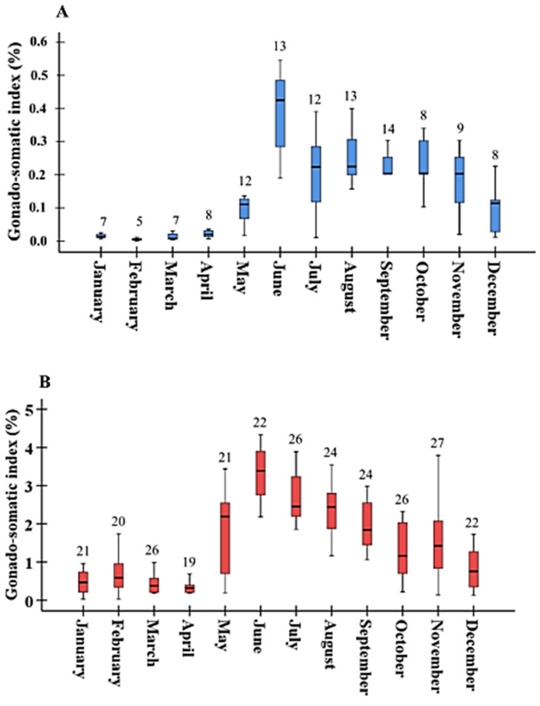

Figure 8. Monthly gonadosomatic index (gonad mass/carcass mass; GSI) in (A) 116 male and (B) 278 female West African Brown Frogs (*Aubria subsigillata*) sampled in the Commune of Dangbo, Ouémé Department, Republic of Benin, from 1 June 2021 to 29 May 2022. Boxplots represent median (horizontal line), 25 and 75 percentiles (boxes), and range (vertical lines). Sample sizes are shown above each bar.

Gonadosomatic index (GSI) and hepatosomatic index (HSI).—The GSI of males and females showed strikingly similar patterns of change over the annual period (Fig. 8). Both sexes showed low GSI values from January to April (males, 0.01–0.02%; females, 0.31–0.58%), with a dramatic increase thereafter to a peak in June (males, 0.42%; females, 3.38%), and a gradual decline thereafter until January. The HSI of both males and females (Fig. 9) roughly followed the annual pattern of GSI. For males, HSI was lowest in March (0.42%) and steadily increased to a peak in July (1.57%). Thereafter, HSI was at an intermediate level September-December, then peaked in January before returning to its lowest level in March. For females, HSI was lowest in November-December (0.25–0.26%), increased gradually to a peak in June (2.86%), then declined thereafter.

Trends among environmental data, GSI, and HSI.—Starting in February and continuing until June, rainfall increased moderately (10.8 mm to 156.7 mm), water levels increased from 50 to 55 mm (Fig. 4),

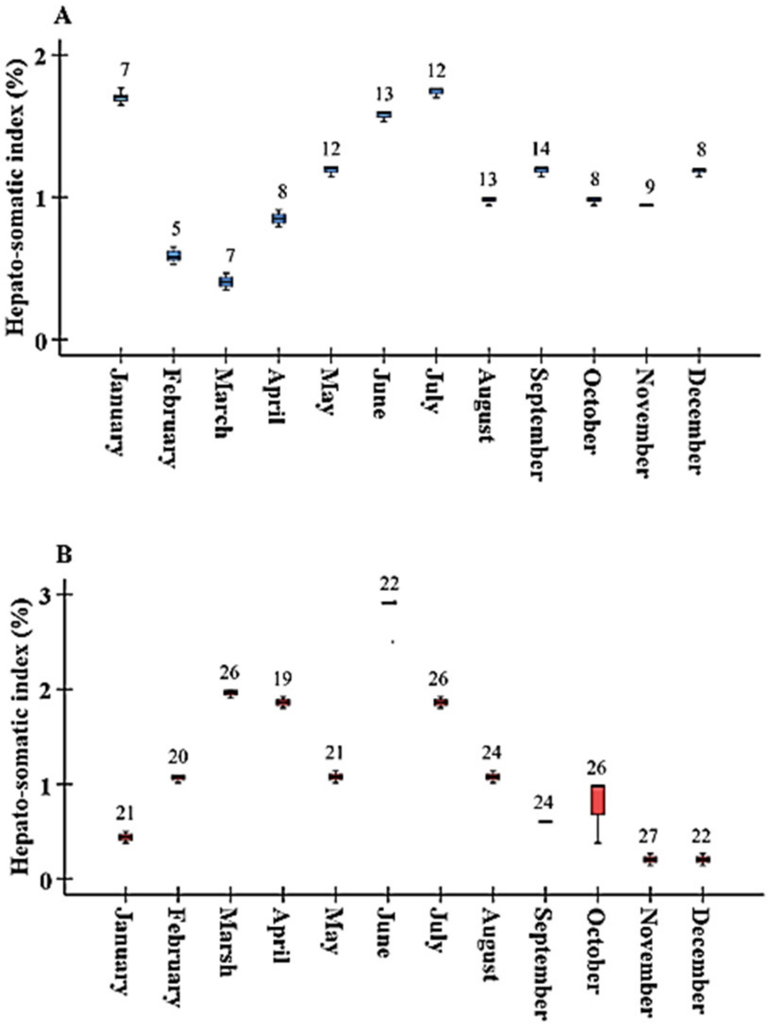

Figure 9. Monthly hepatosomatic index (liver mass/carcass mass; HSI) of (A) 116 male and (B) 278 female West African Brown Frogs (*Aubria subsigillata*) sampled in the Commune of Dangbo, Ouémé Department, Republic of Benin, from 1 June 2021 to 29 May 2022. Boxplots as in Figure 8. Sample sizes are shown above each bar.

the mean ambient temperature was 29.7° C (Fig. 5), and HSI increased substantially from 0.63 to 1.51% among males and from 1.22 to 2.86% among females (Fig. 9). The GSI of both sexes followed a similar trend from February to June, with male GSI increasing from 0.02 to 0.42% and female GSI increasing from 0.57% to 3.38% (Fig. 8). Observations of the ovarian structure in the same period showed that most females (65%) had oocytes in stage III in February then in June most females had oocytes in stages IV (41%) and V (32%), respectively (Fig. 6). From June to December, the mean ambient temperature was 28.25° C, rainfall decreased from 157/163 mm (June/July) to 125/2 mm (November/December), and the water level decreased from 100 mm (July) to 98 mm (December; Fig. 4). During this period, the HSI of both sexes decreased (Fig. 9). In males it decreased from 1.5/1.7% (June/July) to 1.0/1.2% (November/December), and in females it decreased from 2.9/2.0% (June/July) to 0.5/0.5% (November/December). In the same period the GSI decreased also in both sexes (Fig. 8). In males it decreased from 0.4/0.2% (June/July) to 0.15 (December), and in females it decreased from 3.4/2.5% (June/July) to 0.98% (December). The ovarian structure showed in the same period that females with oocytes in stage V were the most abundant (July = 54%, August = 71%, September = 83%, October = 81%, and November = 70%; Fig. 6).

Discussion

We studied the reproductive biology of *A. subsigillata* sampled from commercially harvested frogs between June 2021 and May 2022. We observed that the sex ratio of collected frogs was female biased, females were larger than males, and size at first maturity was greater in females than in males. We also observed an asynchronous development of oocytes in females. The GSI of males and females showed a strikingly similar pattern of dramatic increase between April and June and diminishing progressively thereafter. The HSI for females also peaked in June, whereas males peaked in July. The period of gonadal maturation occurred early in the period of increasing rainfall. Females with mature oocytes predominated from July through November,

The female frogs in our investigation displayed oocytes at various developmental stages, suggesting a prevalence of asynchronous oogenesis in *A. subsigillata.* This asynchronous oogenesis pattern is consistent with findings in numerous frog species inhabiting tropical regions (Rastogi 2011). In these species, the ovary exhibits multiple stages of follicular growth for a significant portion of the year. Consequently, recruitment of pre-vitellogenic follicles for vitellogenesis, as well as vitellogenesis itself, takes place continuously throughout the year. Species demonstrating this oocyte development pattern have been described as having extended reproductive periods. Notable examples among African species with asynchronous oocyte development include the *Xenopus laevis* (del Pino 1989), Xenopus tropicalis (Dumont 1972), and Hopplobatrachus occipitalis (Gustave et al. 2018).

In our study, the close correspondence for the seasonal pattern in GSI between males and females of *A. subsigillata* did not occur for males and females in *H. occipitalis* (a species of edible frog sharing the same habitats as *A. subsigillata* in Africa) in Ivory Coast. In Ivory Coast, while the GSI of females increased from April to May and then from August to September, that of males decreased (Tohé et al. 2016). Similarly, when the GSI of females decreased from June to August, that of males increased. By contrast, the GSI of males and females showed strikingly similar patterns of change from September to March; the GSI of both sexes increased from September to October and then decreased from November to March (Tohé et al. 2016). In *X. laevis* (another African aquatic frog), the GSI trends also differed between the sexes. While the GSI of females increased from May to October/November and then decreased from November/December to January before gradually increasing until April, that of males remained constant throughout the year (Everson 2006).

Regarding the comparison of temporal patterns of GSI and HSI observed in *A. subsigillata*, we noticed that the patterns in *A. subsigillata* differed from those of the frog *H. occipitalis* (Akhil Mali 2008). Indeed, while the HSI of male and female *A. subsigillata* roughly followed the annual pattern of GSI, in *H. occipitalis* HSI and GSI did not follow the same annual pattern. Specifically, in *H. occipitalis*, when HSI increased from April to September, GSI decreased. By contrast, both increased from October to November (Akhil Mali 2008).

The reproductive cycle of an anuran is the series of successive transformations undergone by male and female gametes (oogenesis and spermatogenesis, cellular maturation, and vitellogenesis) to reach maturity, and the behaviors implemented by the spawners (courtship displays, amplexus, spermiation, and oviposition), with the aim of having offspring and the synchronization of these events in terms of seasonality or its absence (Rastogi 2011). In *A. subsigillata,* females showed an annual cycle of oocyte development with oviposition appearing to occur at one time of year. Females with a high proportion of stage V oocytes in their ovarian cavity (stage V females) increased in relative frequency from June to August/September and then decreased from September/October to December. Considering the dramatic decrease in the relative frequency of stage V females from September to December, it appears that oviposition occurred chiefly in October and November, though some females likely oviposited earlier. Thus, the frog *A. subsigillata* seems to oviposit in a single time period each year (June to November) with October and November as the main months of oviposition. This observation is similar to that of the reproductive biology of the South African Burrowing Frog (*Pyxicephalus adspersus*), which has a single breeding during one rainy season (from October to April) in South Africa (Balinsky and Balinsky 1954; Cook 1996; Yetman and Ferguson 2011). The Pixie Frog (*Pyxicephalus edulis*), another species of the Pyxicephalidae family, also has the same reproduction pattern as *A. subsigillata.* It breeds during December and January of a single rainy season in South Africa (Engelbrecht and Ali Halajian 2015).

The reproductive physiology of *A. subsigillata* appears to be synchronized with patterns of rainfall and water levels. We found that when rainfall increased moderately, starting in February and continuing until June, *A. subsigillata* mobilized a large quantity of glycogen reserves in the liver (i.e., HSI increased substantially). Likewise, this increase in rainfall seemed to trigger the gonads of females to reach maturity by promoting the transition of oocytes in oocyte stage III into the final phase of oocyte expansion (stage IV). The mobilization of glycogen reserves also seemed to intensify as the water level rose in June. Thus, females apparently reached a sufficient level of glycogen reserves in June and males in July. The rise in water level, which began in June and subsided in December, appeared to trigger mating and oviposition, which led to declines in the GSI as increasing proportions of both sexes reproduced. The reserves accumulated during the gonad maturation phase also declined in quantity during this same period. High water levels were sustained for a prolonged period (June/July to November/December) and, as a result, mating and oviposition were asynchronous and occurred throughout the latter half of the year. In addition to sustaining the necessary suitable habitat for oviposition and larval development, the increase in water level presumably served to provide spawners with the food necessary for reproductive activities (Hirschfeld and Rödel 2011; Crump 2015; Guo et al. 2019). This strong connection between rainfall and reproduction is common among anurans (Channing 2001; Pujol and Exbrayat 2001; Tohé 2016; Freitas et al. 2022).

Given the existing relationship between the reproductive physiology of *A. subsigillata* and water availability, any disruption to the rainy season would likely impact the population of *A. subsigillata*. In this regard, Beninese meteorological forecasts revealed that by 2050, rainfall is expected to decrease by 3% from March to May, accompanied by an extension of the dry season (Boko et al. 2012). By 2100 significant fluctuations in rainfall are anticipated in March (19% decrease) and April (10% decrease). Concerning water levels, the reduction in rainfall in March, April, and May by 2050 would be accompanied by an extension of rainfall duration between June and October/November, leading to an increased flood risk. Conversely, there would be a hydrological deficit due to a prolonged dry season (Boko et al. 2012). Scarce precipitation followed by pond drying would likely decrease embryo and juvenile survival, leading to reproductive failure and premature sexual maturation we purchased our study animals were instructed to capture frogs without preferences for sex or size. Females, however, are typically preferred due to their larger size, and it is possible that hunters inadvertently targeted females disproportionately to their representation in the population. Further field studies will be necessary to confirm the population sex ratio.

To ensure that this economically important species remains abundant in Benin Republic, we recommend developing a program to monitor populations where hunting occurs, and to implement size, season, and bag limits to ensure stable populations. The information we obtained in this study should help to inform the development of such regulations. Specifically, our findings concerning size at sexual maturity should be useful in setting size limits. Moreover, the seasonal patterns that we have reported help to clarify the breeding phenology for the species and should be considered in setting a harvest season and bag limits.

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