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The direct and indirect effects of damming on the *Hippopotamus amphibius* population abundance and distribution at Bui National Park, Ghana

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Abstract

Landscape changes resulting from human activities have resulted in range restrictions and substantial reductions in population sizes of most animals. The construction of hydroelectric dams has the same effect on species, but the study of their impact on semi-aquatic megafauna species is limited. We examined the response of a *Hippopotamus amphibius* population to the inundation of their habitat after the construction of a hydroelectric dam in Bui National Park, Ghana. We conducted an abundance and distribution survey of *H. amphibius* and compared the population size from our results with a pre-dam construction survey to determine changes in the abundance and distribution of the species within the focal area. Furthermore, we conducted a landscape analysis to estimate land cover before and after the dam construction and determined if the changes in land cover were related to the changes in population of *H. amphibius*. Finally, we conducted selected interviews to understand additional threats to the species perceived by the local population, as indirect effects of the dam construction. Contrary to our original hypothesis on an increase in the abundance of *H. amphibius* in the medium term (within a decade) through population recovery after the disturbances caused by the construction of the dam, we found lower numbers of *H. amphibius* after the dam construction, compared to the pre-dam results. The results indicated a reduced abundance from 209 *H. amphibius* individuals in 2003 to 64 *H. amphibius* individuals in 2021. Some individuals may have migrated to areas outside the reserve during damming when their habitat was disturbed. The amount of land covered by water increased from 0.41% before damming to 19.01% after damming, which flooded the resting and grazing sites of the *H. amphibius*. We conclude that the abundance and distribution of *H. amphibius* significantly and negatively decreased after the construction of the dam at the Bui National Park. We tentatively relate this decrease to the species' semi aquatic ecology and sensitivity to changes in both the terrestrial and aquatic environment. The activities of human settlement encroachment such as poaching, as well as associated land cover changes, affected the stability of the *H. amphibius* population. However, as the species can survive in the medium to long term when effective management plans are implemented, we recommend *H. amphibius* to be given high conservation priorities by enhancing strict laws for habitat protection.

Keywords
Abundance, flooding, habitat destruction, hydroelectric dam land use, semi-aquatic mammals

Introduction

The spatial distribution and abundance of animals is an important factor to understand population changes, and a requirement to explain and predict interactions between species and habitat (Zhang et al. 2019; Xu et al. 2020). The abundance and distribution of animals is influenced by numerous habitat and climatic factors (De Boer et al. 2013), principally linked to fluctuations in food and water resources and anthropogenic-mediated disturbances (Lewison 2007). One such anthropogenic activitiy is hydroelectric dam construction. Hydroelectric dams higher than 15 m have been constructed on more than 50% of large rivers worldwide, affecting the eco-physiochemical features of rivers (McAllister et al. 2001), and resulting in population decline in numerous species (Peris and Morales 2004; Passamani and Cerboncini 2013; Benchimol and Peres 2015; Zhang and Xu 2018). Most hydroelectric dams are built on freshwater ways, which cover about 1% of the surface of the earth, but support 30% of vertebrate biodiversity (Flitcroft et al. 2019).

Reliance on hydroelectric sources incurs several negative effects to the environment (Beck et al. 2012), such as inundations resulting in the destruction of riparian ecosystems, biodiversity loss and obstruction of migratory pathways for aquatic species (Cunha and Ferreira 2012). The abundance and distribution of species are affected by these modifications, impacting their ecology and conservation (Lima et al. 2018; Brum et al. 2021). Specifically, the building of dams can result in local extinctions (Clavero and Hermoso 2011; Bohada-Murillo et al. 2021; Muniz et al. 2021). In general, large vertebrates are the most affected by damming because their ability to complete their life cycles relies on the extent of river connectivity (Hermoso et al. 2018; He et al. 2021). One species likely to be affected by flooding through dam construction is *Hippopotamus amphibius* because of its semi aquatic ecology and sensitivity to changes in both the terrestrial and aquatic environment. In addition, dams increase the risk of deaths as the species also faces poaching when migrating to suitable habitats (Kanga et al. 2011).

Changes in land-use because of human activities have resulted in range restriction in *H. amphibius*, leading to a substantial reduction in population size (Lewison and Pluhacek 2017). Global records indicate a population decline of about 30% in the past decade, and many countries have confirmed declining abundance, local extirpation and disconnected sub-populations requiring urgent attention (Lewison and Pluhacek 2017). For example, Algeria, Egypt, and Mauritania have reported local extinction of *H. amphibius* within their range (Horwitz and Tchernov 1990; Lewison and Oliver 2008). Specifically, in the Virunga National Park of Democratic Republic of Congo, populations of *H. amphibius* have declined by over 96% between 1970 and 2005 (Languy and de Merode 2006). To effectively manage and conserve wildlife populations, especially the threatened *H. amphibius*, information on the factors affecting population and distribution are required (Ertiban 2016).

The population of *H. amphibius* in Africa is around 155,000 individuals (HSG 2004). In West Africa, while a comparatively large population is present in Guinea and Senegal, only an estimated 2000 individuals live in Ivory Coast, Ghana, Togo, Benin and Burkina Faso in total. This population is under serious threat from direct and indirect human exploitation. As a result, *H. amphibius* is now listed as Vulnerable to extinction by the IUCN Red List of Threatened Species (HSG 2004). Understanding the response of *H. amphibius* to dam construction on rivers could contribute to the fundamental measures necessary to alleviate the ecological pressure and enhance conservation (Reitan and Thingstad 1999; Hunt et al. 2013; Dos Santos et al. 2022). Unlike some small mammals that have been well-researched (Thibault and Brown 2008; Passamani and Cerboncini 2013; Zhang and Xu 2018), studies on the effects of hydroelectric dam constructions on the megafauna are limited and a grey area in the literature (Nilsson and Dynesius 1994; Heinen and Singh 2001), especially in sub-Saharan Africa. This is particularly important for semi-aquatic species because of the severe changes in the terrestrial ecosystem resulting from flooding and the increase in water volume affecting the habitat. Information on the response of *H. amphibius* to damming is still inadequate (Meyer et al. 2005) and numerous studies ignore before and after impact assessments of dam construction (Brum et al. 2021; Rodrigues dos Santos et al. 2021) due to data unavailability, lack of funding and political expediency (Norris et al. 2018). Hence, our study focusses on assessing how the *H. amphibius* population of the Black Volta River was affected by dam construction. We determined the current population size of *H. amphibius* in Bui National Park, Ghana, and whether the population size changed after the construction of a hydroelectric dam using public historical data. To do so, we compared the abundance and distribution recorded in a previous study in 2003 eight years prior to the inundation of the area (Wildlife Division 2003), in a study after the dam construction (Agyei 2020), and this current study in 2021, ten years after the inundation of the area. As the population of *H. amphibius* can promptly increase in the presence of abundant or stable resources (Martin 2005), we hypothesized an increase in the abundance of *H. amphibius* in the medium term (within a decade) through a population recovery after the disturbances caused by flooding.

Method

Study species

Hippopotamus amphibius is a semi-aquatic species which selects areas with sufficient grass for grazing and water for thermoregulation (Noirard et al. 2008; Chansa et al. 2011). The species forages for 7–8 hours per day usually at night (Furstenburg 2012). It stays close to water edges when grazing resources are sufficient (Timbuka 2012; Stommel et al. 2016), and grazes mostly within a distance of 750 m away from water sources in Bui National Park (this study), 1.5 km from water in Serengeti National Park (Olivier and Laurie 1974), 7 km from water in the Ruwenzori National Park (Field 1970) and 5 km from water in the Kruger National Park (Pienaar et al. 1966). It is the third largest terrestrial mammal and belongs to the family Hippopotamidae (Olivier and Laurie 1974; Jablonski 2004). The breeding strategy of *H. amphibius* greatly fits the semi-arid regions of Africa (Smuts and Whyte 1981), and the animals are therefore capable of maintaining stable populations by adjusting sexual productivity and maturity when food and water resources become limited (Martin 2005).

Study area

The study area, Bui National Park, covers about 1821 km^2 is in north-western Ghana (between 8.167°N–8.75°N and 2.083°W–2.45°W, Fig. 1). The hydroelectric dam was constructed at the southern portion of the Black Volta River within the Bui National Park. The impoundment was done in 2011, and at full supply level it will inundate almost 21% of Bui National Park. The dam can hold 12,350 million m^3 of water, with an average depth of 29 m. The area experiences wet and dry seasons (Alhassan 2013). It is one of the richest biomes in Ghana, largely formed by Guinea savannah woodland with moist semi-deciduous forest patches, hosting numerous vertebrates including *H. amphibius* (Bennett et al. 2000; Appiah et al. 2017; Dery 2017).

Hippopotamus amphibius survey

We first carried out a reconnaissance survey to establish the presence of *H. amphibius* in the BNP along the periphery of the Black Volta River.

The study area was divided into five shorelines, each with a team conducting survey simultaneously twice a week for two weeks in July 2020 covering a total survey shoreline length of about 124 km (Appendix 1). The pre - survey results indicated that along the Black Volta River in the BNP, the *H. amphibius* generally reside in five sites, namely "Herimankuna", "4 O'clock", "Didipreko", "Agave patase/Gareba" and "Nyameraga upwards". The site "4 O'clock" was the only site found to harbor an unknown population of *H. amphibius*, as the other four ("Herimankuna", "4 O'clock", "Didipreko ", "Agave patase/Gareba" and "Nyameraga upwards") harbored *H. amphibius* in

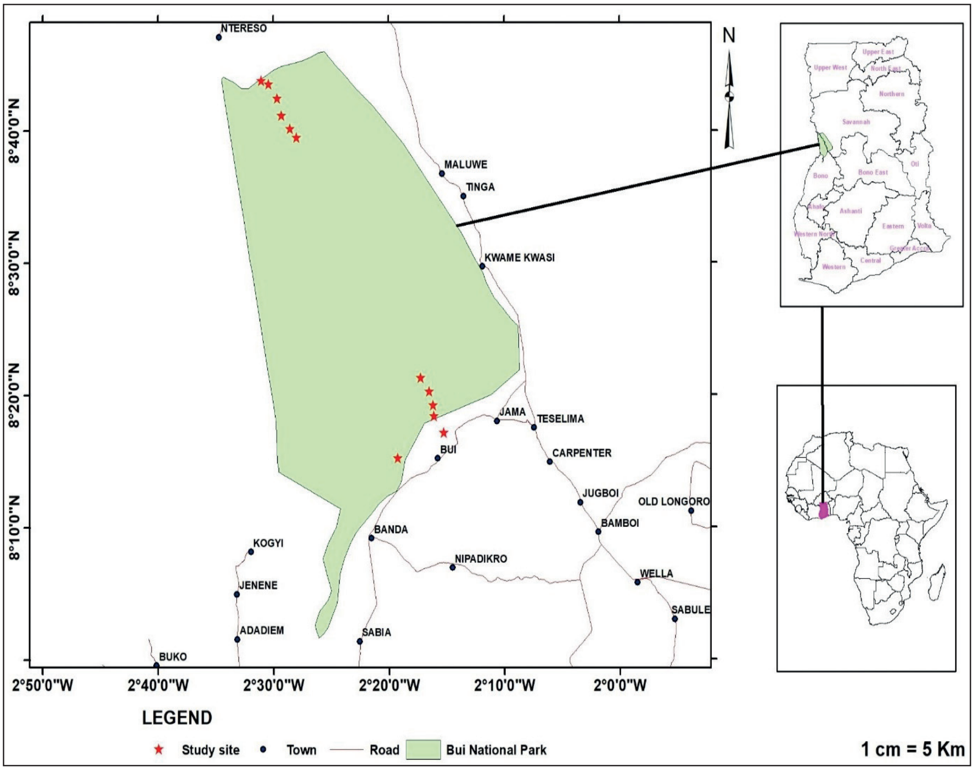

Figure 1. Map of Bui National Park, Ghana where population monitoring for *Hippopotamus amphibius* was conducted at three intervals between 2003 and 2021 (Wildlife Division 2003).

the pre-dam (2003) survey. We included "4 O'clock" to the 11 pre-dam survey sites, resulting in 12 sites for the current study. Then, we compared the 12 sites with the pre-dam (2003) sites to determine changes in abundance and distribution in *H. amphibius* population. It is possible that some individuals occur outside the reserve. The study was, however, focused on the reserve as individuals outside of the reserve are unlikely to be present in significant numbers. This current study focused only on the changes in abundance and distribution of *H. amphibius* population for the pre- and post- dam periods in the Bui National Park.

Ground counts survey techniques (land- and boat-based counts) provide comparatively accurate results to record changes in *H. amphibius* numbers and distribution. *Hippopotamus amphibius* census during this study were carried out at different periods of the year to determine the seasonal differences in population sizes (Olivier and Laurie 1974; Martin 2005; Kujirakwinja 2010; Zisadza et al. 2010; Timbuka 2012; Lhoest et al. 2015; Fritsch and Downs 2020). We followed the ground counts method as described by Kujirakwinja 2010 and Martin 2005 to estimate the number of *H. amphibius* in the Bui National Park from August 2020 to July 2021. We surveyed twelve refuge sites distributed along the Black Volta River within the Bui National Park

(Fig. 1). We selected the refuge sites based on a pre-dam *H. amphibius* survey in 2003 (Wildlife Division 2003) and the reconnaissance survey to allow for comparison, and also based on the knowledge of park rangers and local community members regarding the distribution of *H. amphibius* in the Bui National Park. During a pre-project survey, experienced park rangers and community members clarified that there is no population of *H. amphibius* outside the Bui National Park.

The study was therefore concentrated within the reserve and along the entire periphery of the river (Fig. 1). The area where the animals are present is based on knowledge of park rangers who survey the area regularly. We moved on the water using a canoe at about 5 km/h and counted *H. amphibius* along the water shore, maintaining a distance of at least 30 m away from the animals. When faced with an obstacle such as low water levels, sedimentation and emergent vegetation during canoe movement, animal counting was done by walking along the water bank at a minimum distance of 40 m (Martin 2005).

To avert double counting during the survey, we classified the 66 km river shore into segments and counting along the shore was carried out simultaneously (Kujirakwinja 2010). *Hippopotamus amphibius* are relatively easily visible from the morning until noon as they congregate in shallow water but move into the deep portion of the river after noon where it is difficult to notice them. We therefore conducted animal observation and counting between 6:00 am and 12:00 pm (Martin 2005; Kujirakwinja 2010). Each refuge site was assessed for two days (two weeks' interval) every month for 12 consecutive months from August 2020 to July 2021, making a total of 288 sampling events (12 refuge site × 2 days × 12 months = 288 sampling events). The refuge site included; Dam site, Tree house site, Asantekwa/Bope, Abunuabunu, Bachelor line, "4 O'clock" site, Dadinkoa, Herimankuna, Nyameraga downwards, Nyameraga upwards, Didipreko and Agave patase/Gareba site (Fig. 3). When we encountered a school of *H. amphibius*, we observed them every 7 minutes for 30 minutes, as the species can remain submerged in water for a period of 5–7 minutes before breathing (Stommel 2017). We used binoculars (ZD 10 × 43 Ricoh Imaging, France) to clearly identify and count the animals while we recorded the position of individuals with a hand-held Global Positioning System unit (Garmin GPSmap 60CSx, All Garmin Ltd., Olathe, KA, USA).

Local migration or cyclical pattern of *H. amphibius* at a particular site is common and it explains their movements during a particular period, including immigration and emigration (Furstenburg 2012). We calculated the rates of migration (expressed as percentage change) as:

$$\text{Rate (\%)} = \text{PtMA}_1 - \text{PvMA}_2 \,/\, \text{PvMA}_2 \times 100\%$$

where PtMA_1 is present month abundance and PvMA_2 is previous month abundance. A negative variation in percentage represents emigration and positive variation in percentage represents immigration.

Previous research

We evaluated the impact of the dam construction on *H. amphibius* population by comparing this current study to a pre-dam construction study (Wildlife Division 2003). The pre-dam study was carried out by the wildlife Division of the Forestry commission, Ghana, in conjunction with Conservation International in 2003 (Wildlife Division 2003). The pre-dam study supplied relevant initial findings about the area revealing abundance and distribution for *H. amphibius*. We followed the survey protocols used for the pre-dam study (Wildlife Division 2003) to ensure consistency. In addition, the current study (post-dam) was carried out in the same area as where the pre-dam study (Wildlife Division 2003) was conducted. This, therefore, makes it possible to compare the results of both surveys.

Pre-dam and post- dam land cover analysis

We performed a land cover analysis for the period 2000–2020 to understand how habitat types were linked to the impacts of the dam construction on abundance and distribution of *H. amphibius.* We acquired land cover matrixes from the Geographic Information System (GIS; https://glovis.usgs.gov/). For the pre-dam period (2000), during dam construction period (2010) and post-dam period (2020), we obtained cloud-free cover Landsat 7 Enhance Thematic Mapper Plus (ETM+) and Landsat 8 Operational Land Imager (OLI) images (Table 1) from the United States Geological Survey (USGS) Global Visualization Viewer (GLOVIS) website (https://glovis.usgs.gov/). We identified five land cover types: close forest, open forest, water, grassland, and built-up (Table 2). Due to the unavailability of data about water level changes for "before and after" dam construction, we used land covered by water as a proxy for water level.

Table 1. Acquisition of Landsat images used to generate land cover change.

Satellite	Sensor	Level of Processing	Tile Number	Number of Bands	Date
Landsat 7	Enhance Thematic Mapper Plus (ETM+)	L1T	195 054	9	02-02-2000
				9	12-11-2010
Landsat 8	Operational Land Imager (OLI)			11	01-02-2020

Table 2. Land cover Description.

Land cover	Description
Close forest	Dense woodland with trees canopy cover of more than 60%
Open forest	Open woodland with trees canopy cover between 15%–59%
Water	Rivers and Lake
Grassland	Shrubs, tree grass mosaic
Built-up	Building, cleared areas, mining sites, farms, bare land and rocky surfaces

Focus group interview

We collected brief information on the perceptions and knowledge regarding the impact of the dam construction on wildlife by interviewing participants who were regularly active on the Black Volta River in the Bui National Park. The focal group interview was aimed at finding out if the population of *H. amphibius* had changed following the construction of the dam and what could have accounted for the changes. We used open-ended questions and a conversational style interview (Bempah et al. 2019) to reduce any bias and to enhance the participation of the various groups. We randomly selected five individuals as participants from each of the three focus groups: fisherfolks, park rangers and canoe operators constituting 30 participants (15 participants from the southern section of Bui National Park and 15 from the Northern section). These groups were selected because they were familiar with the study area since before the dam construction until after the dam construction. These groups also have generally good knowledge about the presence of the *H. amphibius* in the study area. We asked each participant five questions (in local languages; Twi, Gonja and Ewe).

Records of illegal activities in the Bui National Park

As part of routine law enforcement and patrol activities, rangers of Bui National Park record a number of illegal activities occurring in the reserve to guide management. This data was accessed from the office of the Bui National Park to analyze the occurrence of illegal activities between 2012 and 2021, the period for which data is available. The illegal activities were classified into poaching (all poaching related activities such as poachers arrested, poachers observed, cartridges found and snares found), cattle herding, charcoal burning, tree felling and illegal mining. The percentage composition of the illegal activities was estimated by dividing the number of each illegal activity by the total number of all illegal activities multiplied by 100%. To test for any significant differences in the number of recorded illegal activities, we performed a Kruskal Wallis chi-square test.

Data analysis

We calculated the average numbers of *H. amphibius* per site for each month. We used a one-way ANOVA to test for significant differences in the number of *H. amphibius* between the pre-dam (2003) and post-dam periods (2021). The ANOVA test was appropriate because the normality test for the response variable (abundance) showed a normal distribution. We then tested for differences in *H. amphibius* abundance for; 1) the refuge sites where the study was done, 2) the various months during which data collection was done, 3) seasonal differences between the study sites and 4) rates of migration between the study sites using a Kruskal Wallis chi-square test. We used a Kruskal Wallis chi-square test, a non-parametric test, because the normality test for the response variable (abundance) showed a non-normal distribution and no data transformation restored normality. We performed a linear regression to determine the relationship between *H. amphibius* population and the years of study. We also performed a linear regression to determine the relationship between the population of *H. amphibius* and changes in landcover at Bui National Park for the pre-and post-dam construction periods. The study assumed $p < 0.05$ to be statistically significant. The statistical analysis was done using R (version 4.0.3) statistical tool (R Core Team 2020).

Results

Pre-dam and post-dam results and landcover changes

We determined that the population of *Hippopotamus amphibius* sharply declined in Bui 10 years after the inundation of the area during the dam construction (Fig. 2). The population was the highest in 2003 (pre-dam; 209 individuals) followed by a decline (55.2%) in 2019 (post-dam) and further declined by 31.91% in 2021 (post-dam; Table 3; Fig. 2). The population significantly declined by 69.38% between 2003 and 2021 (ANOVA; $F = 592.01$, df = 2, $p = 0.026$; Table 3), reaching a current density of 0.9 individuals/km of river. Using the prediction equation, we determined that the number of *H. amphibius* at Bui National Park could probably decline further to about 3.6 individuals in 2029, 18 years after the inundation caused by the dam construction.

The distribution of *H. amphibius* changed after the dam construction, and most of the population in the southern section of the Bui National Park disappeared after the dam construction, leaving only one sustainable population at 4 O'clock (Fig. 3). Damming increased the percentage of water from 0.41% in 2010 (during-dam construction) to 19.01% in 2020 (post-dam, Fig. 4) which flooded a significant portion of the riparian ecosystem. Among the various land cover, we found a significantly negative relationship between population of *H. amphibius* and changes in water between the pre-dam construction and post-dam construction periods (linear regression, Coeff. = -0.004,

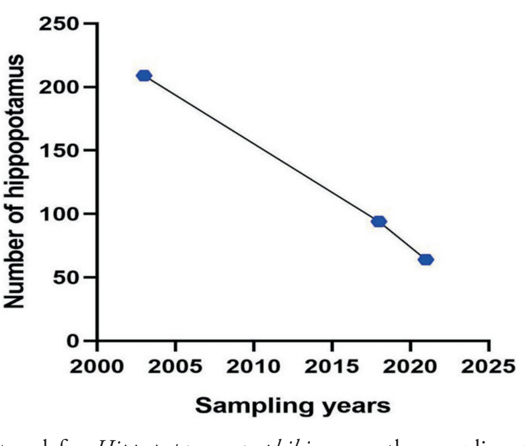

Figure 2. Population trend for *Hippopotamus amphibius* over the sampling period in Bui National Park, Ghana.

R^2 = 0.99, p = 0.002). However, we found no significant relationship among close forest (linear regression, Coeff. = 0.011, R^2 = 0.99, p = 0.06), open forest (linear regression, Coeff. = 0.002, R^2 = 0.98, p = 0.07), grassland (linear regression, Coeff. = -0.004, R^2 = 0.95, p = 0.14) and built-up area (linear regression, Coeff. = -0.078, R^2 = 0.26, p = 0.65), and *H. amphibius* population within pre- and post-dam construction periods.

Table 3. Number and variation in the number of *Hippopotamus amphibius* individuals counted in the Bui National Park for the years 2003, 2018 and 2021.

Reference	Year of study	Number	% of change from 2003
Wildlife Division (2003)	2003	209	–
Agyei (2020)	2018	94	-55.02
This study	2021	64	-31.91
Between 2003 and 2021			-69.38

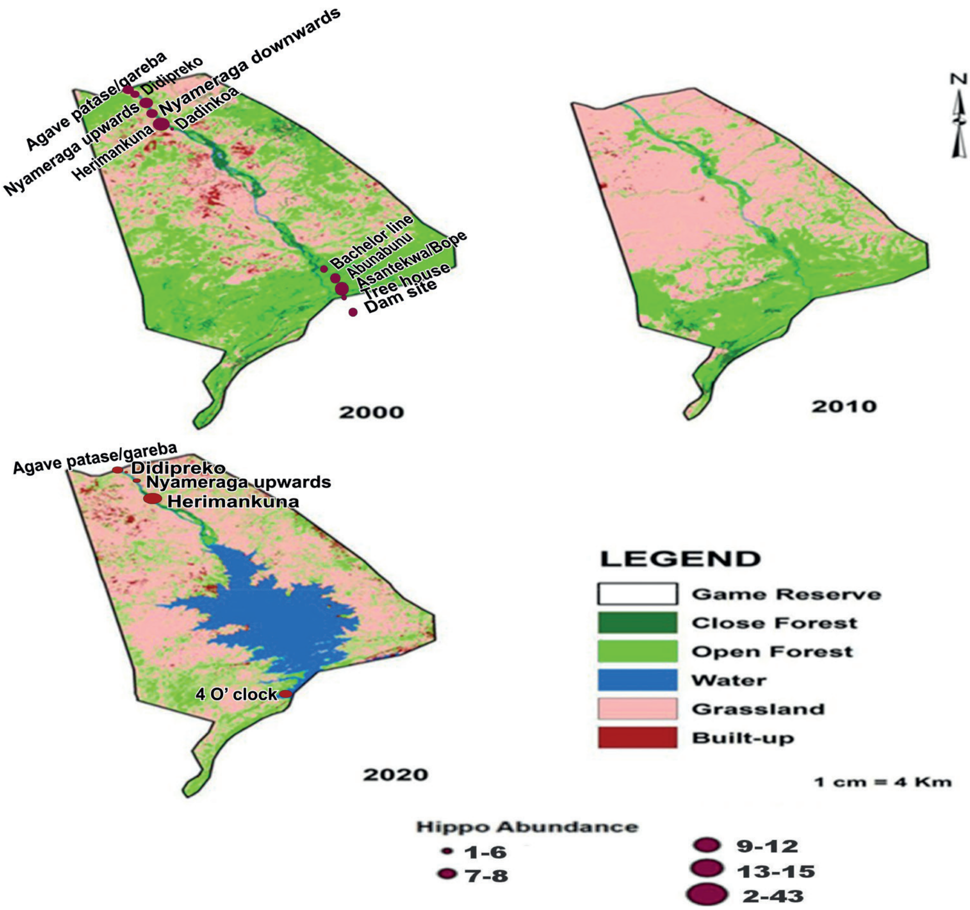

Figure 3. Spatial distribution of *Hippopotamus amphibius* and land cover in the Bui National Park before the dam construction (2003, Pre-dam), during (2010) and after the-dam construction (2020, post-dam).

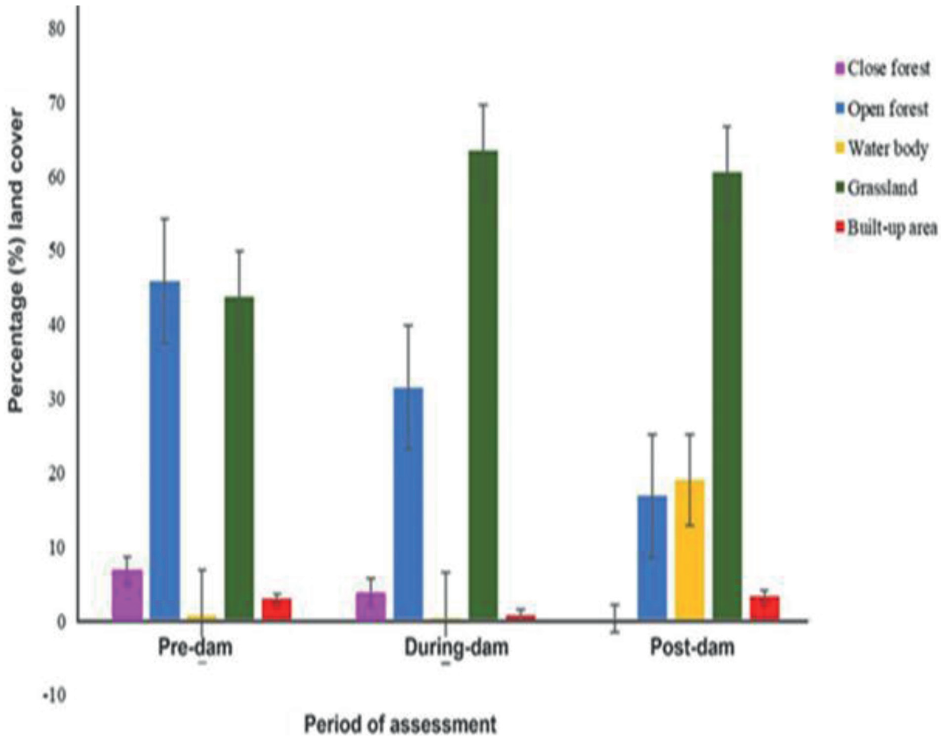

Figure 4. Percentage of area covered by each land cover type; pre-dam construction (2000), during dam construction (2010) and post dam construction (2020) periods.

Spatial-temporal variation in abundance of *Hippopotamus amphibius*

During the current study (post-dam), the maximum abundance of *H. amphibius* was recorded at "Herimankuna", followed by "4 O'clock", while "Didipreko" had the lowest number (Fig. 5). The abundance of *H. amphibius* was significantly different among the study sites (Chi-square test; $\chi^2 = 4.575$; $p < 0.001$), with the northern section of the Bui National Park supporting more than half of the current population. We also found a significant difference in seasonal abundance of *H. amphibius* at the study sites (Chi-square test; $\chi^2 = 25.921$; $p < 0.001$) with greater numbers recorded during the dry season, with the exception of "4 O'clock" where the abundance did not significantly vary (Fig. 5). The abundance of *H. amphibius* recorded in the various months during which we collected data varied significantly (Chi-square test; $\chi^2 = 25.564$; p < 0.001). We recorded higher numbers of *H. amphibius* between December and March, and lower numbers recorded between April and November.

Migration rates

Rates of immigration and emigration of *H. amphibius* did not vary between sites (Chi-square test; $\chi^2 = 0.369$; $p = 0.984$). We found a significant seasonal difference in migration of *H. amphibius* (Chi-square test; $\chi^2 = 7.914$; $p = 0.005$), and the rate of emigration was the highest in the month of June (-168.08%) while the highest immigration rate was recorded in December (512.12%, Table 4). Among the refuge sites, "Agave patase/Gareba" recorded the highest migration rate with 108.45%, followed by "Nyameraga upwards" with 84.17%, "Herimankuna" (52.84%), "4 O'clock" (9.69%) and "Didipreko" (-23.34%, Table 4).

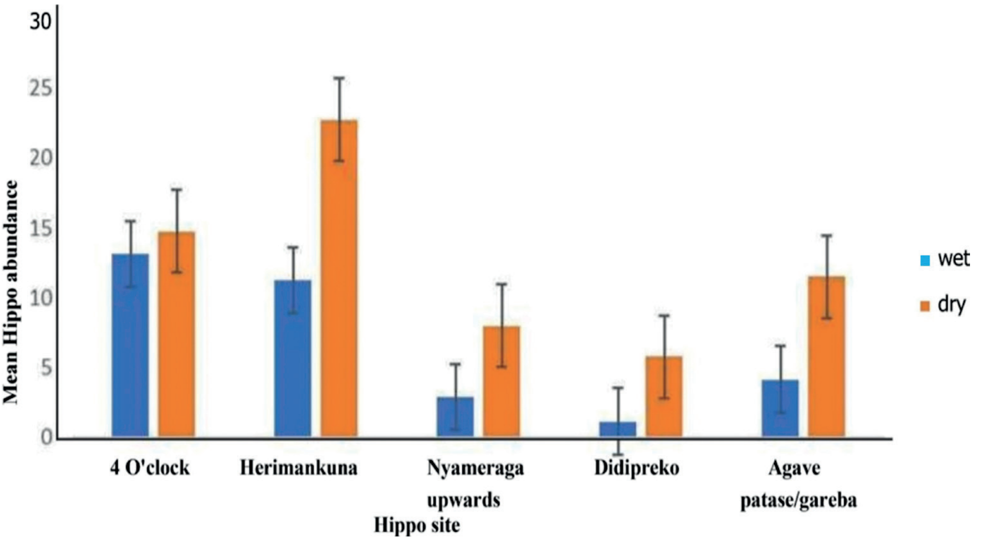

Figure 5. Seasonal differences in *Hippopotamus amphibius* abundance (August 2020–July 2021) at the refuge sites, Bui National Park.

Table 4. Monthly differences in migration rates (%) of *Hippopotamus amphibius* at the various refuge sites in Bui National Park.

Month	Sites				
	4 O'clock	Herimankuna	Nyameraga upwards	Didipreko	Agave patase/Gareba
August	0.00	0.00	0.00	0.00	0.00
September	-6.66	0.00	50.00	-100.00	-33.33
October	-14.26	33.33	-33.33	0.00	50.00
November	-8.33	-8.33	50.00	100.00	100.00
December	36.36	109.09	166.67	100.00	100.00
January	-6.66	0.00	0.00	0.00	-8.33
February	7.14	-4.35	0.00	0.00	9.09
March	0.00	4.54	0.00	-16.67	-8.33
April	-6.66	-39.13	-37.5	-40	-36.36
May	-7.14	-7.14	-20.00	-66.67	-14.29
June	-0.77	7.69	-25.00	-100.00	-50.00
July	16.67	-42.86	-66.67	100.00	0.00

Interviews

During the interview, the respondents emphasized that the human pressures in the Bui National Park increased during and after the dam construction. The answers detailed the increase in economic activities including illegal gold mining, increased fishing activities, cattle herding, charcoal production and settlement/farming in the area. The answers provided data for eight major gold digging sites, especially in the northern section of the reserve, with settlements, cattle herding and farming along the bank of the river (Figs 6, 7). Most of the sites that previously harbored *H. amphibius* became routes for illegal miners, and the species was not detected during our surveys. About 83.3% of the respondents indicated a perceived decline in *H. amphibius* population while about 10% stated the population was stable (Table 5). No respondent answered that the population increased. Fifty percent of respondents attributed these changes in *H. amphibius* population to poaching activities, with an additional 16.7% suggesting combined poaching and inundation as a cause. Also 10% of the respondents answered that only inundations were responsible for the changes (Table 5). Results from the interview suggested that more *H. amphibius* poaching occurred after the dam construction compared to the pre-dam periods (ANOVA: $F = 4.804$, df = 49.62, $p = 0.033$). Respondents answered that the majority of people involved in poaching *H. amphibius* are professional illegal hunters (40.9%) and other groups had a minor effect: gold miners (20.5%) and fisherfolks (18.2%). Cattle herdsmen (4.5%), and 15.9% of the respondents in general claimed not to know the category of people involved in poaching of *H. amphibius*.

Among the illegal activities recorded in the reserve, poaching related activities was the highest (70%), followed by illegal mining (11%) and cattle herding (9%, Fig. 8). A significant difference was found in the number of illegal activities recorded in the Bui National Park ($\chi^2 = 13.73$; $p = 0.008$).

Figure 6. Farmers clearing trees along the rivers to begin cultivation at Bui National Park.

Figure 7. Illegal gold mining activities within the Bui National Park.

Table 5. General trend of *H. amphibius* population and perceived causal factors at the Bui National Park suggested by respondents in a focus group interview.

Trend of *H. amphibius* population	Number of respondents	Percentage (%)	Perceived cause of changes in trend	Number of respondents	Percentage (%)
Declining	25	83.3	poaching	15	50
Stable	3	10	Poaching/ inundation	5	16.7
Do not know	2	6.7	inundation	3	10
			Do not know	5	16.7
			Retaliatory killing	2	6.6

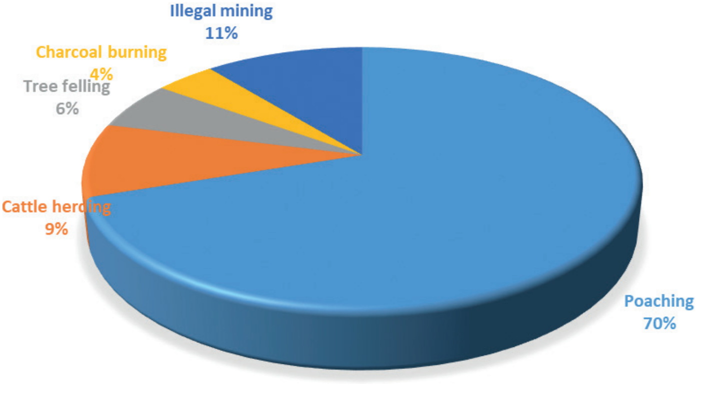

Figure 8. Percentage composition of illegal activities recorded in the Bui National Park between 2012 and 2021.

Discussion

Explaining the effects of hydroelectric dam construction on biological diversity and the response of species is essential for the management and conservation of species and their habitat (Palmeirim et al. 2018). The results of our study reveal that: 1) Construction of the dam caused an increase in illegal human activities in the reserve. Subsequently, illegal settlers in the reserve became directly involved in poaching activities. 2) Flooding impacted the habitat of *Hippopotamus amphibius*, resulting in displacement of the semi-aquatic species. These two threats, both resulting from the construction of the dam, account for changes in *H. amphibius* population at Bui National Park. Our expectation that there would be an increased abundance of *H. amphibius* after the dam construction was wrong. The abundance of *H. amphibius* decreased and continued to do so in the Bui National Park after damming, declining by more than 69% between 2003 (pre-dam, 8 years before the inundation) and 2021 (post-dam, 10 years after the inundation), and 31.9% within post-dam periods (2018, 7 years after the inundation and 2021). If the same trend is maintained, we predict the species will be functionally extinct at Bui National Park by 2030. We tentatively attribute the decline in *H. amphibius* numbers and changes in distribution to human pressures and habitat destruction arising from the dam project. This was suggested by Appiah et al. (2017) who emphasized an increased utilization of resources at Bui National Park by settlers within and outside the reserve after the dam construction. Similarly, several studies have confirmed significant declines in species population after dam construction on tropical rivers globally (Nilsson and Dynesius 1994; Peris and Morales 2004; Welbergen et al. 2008; Alho 2011; Passamani and Cerboncini 2013; Benchimol and Peres 2015; Zhang and Xu 2018). This study, however, acknowledges weaknesses due to the limitation in the number of data points; although other studies have applied similar point data set successfully (Alhassan 2013; Smokorowski and Randall 2017; Dos Santos et al. 2022).

The land cover analysis revealed significant changes in the Bui National Park (BNP) over the study period, covering 2000–2020. The decrease in forest cover (close and open), flooding of riparian grassland and an increase in "built up" areas were obvious during and after the dam construction at BNP. Between the period of 2008–2010, permits were given to contractors to fell trees in the flood zones along the southern section of the Black Volta River before the inundation. However, ineffective monitoring of contractors and other illegal settlers led to indiscriminate felling of trees in the national park. Tree felling continued after the completion of the dam, leading to a significant decrease in forest cover. In addition, the deployment of heavy machines during this process altered the grassland cover. The study revealed a decline in grassland cover between 2010 and 2020, during and after the dam construction. The observed increase in land use during and after the damming is attributed to the establishment of illegal settlers involved in illegal mining, uncontrolled cattle grazing, and charcoal production. This likely resulted in the decline of grassland and an increase in built up area during this period. The results of our study are confirmed by other studies reporting a decline in grassland after damming (Wiejaczka et al. 2017; Chalise et al. 2019; Xu and Chi 2019). Uncontrolled movement of several herds of cattle inside the BNP also potentially led to trampling of grasses and excessive grazing at water banks. As a result, this affects forage availability along with vegetation and soil modification (Panthi et al. 2017; Obahoundje et al. 2018; Sharma et al. 2019). In some cases, cattle herdsmen attempt to cause regeneration of fresh pasture by consciously setting fire to the vegetation. This often results in uncontrolled destruction of vegetation (Sharma et al. 2019) and the combined effects resulting in destruction of available grazing resources.

The results of the interviews showed that participants expected the population of *H. amphibius* to have declined following the construction of the dam. The participants mentioned the flooding of the area where the animals graze as well as the increased volume of water of the resting sites of the *H. amphibius* as the key elements. The results of our land cover analysis demonstrated the veracity of this expectation as it showed an increase in water cover from 0.41% before damming to 19.01% after damming, as exemplified by similar result (Alhassan 2013). About 21% of the BNP will be flooded following the construction of the dam when the reservoir reaches its full capacity (Environmental Resources Management 2007; Tornyie 2015). This decline in population indicated a significant negative relationship between changes in water and *H. amphibius* abundance before and after the dam construction. Among the land cover matrix, as water increased, the abundance of *H. amphibius* decreased, thus impacting the population of *H. amphibius* at the Bui National Park. A study by Prinsloo et al. (2020) also suggested that water level influenced the distribution of the *H. amphibius* population. The destruction of the habitat following the construction of the hydroelectric dam had a significant negative impact. The flooding led to an increase in water volume of the river, converting them into reservoirs and submerging grasses. The increase in the water level probably caused displacement of the animals, thereby resulting in a significant decline of *H. amphibius* population. The flood altered the water levels preferred by *H. amphibius* for thermoregulation and affected the abundance of food resources. Flooding affected the riparian grasses which served as food for the *H. amphibius*. This reduced the available food resources for *H. amphibius*, which prefers short grasses along water banks (Bempah et al. 2022). Hence, the decline in *H. amphibius* could have resulted from the lack of food availability as it is the major factor that regulates population density of *H. amphibius* (Chomba 2013). Besides, large equipment used during the construction coupled with the nuisance resulting from the transportation of building materials interrupted the activity and reproductive behavior of *H. amphibius*.

Differences in *H. amphibius* abundance between the pre-dam and post-dam period revealed a decrease in the number of individuals, as suggested by the respondents of the interview. This decrease is likely to be driven by the displacement and assumed death of young individuals that were not able to escape from the flooding, as demonstrated in other studies in National Zoological Park Washington, USA and Australia (Welbergen et al. 2008; Fisher et al. 2010). While being semi-aquatic, the swimming performance of *H. amphibius* is debated. Evidence of poor swimming abilities has been provided

(Fisher et al. 2010), contrasting with several other studies considering *H. amphibius* as good swimmers (Leivestad et al. 1973; Sondaar 1977; Feldhamer et al. 2007), and seldom observed drowning in normal conditions (Peris and Morales 2004). Nonetheless, they become susceptible to drowning during catastrophic floods, such as those resulting from dam construction. The individuals most affected under such circumstances are the inexperienced calves, along with the females because of their relationship with their young ones (Welbergen et al. 2008). Translocation of individuals could result in the avoidance of risks, but the lack of technology and equipment to capture and move *H. amphibius* due to their size and aggressiveness was a drawback, despite the potential success of such exercise done in Kenya (Lekolool 2012).

The decline in abundance was associated with distribution changes as the population size of *H. amphibius* significantly dropped in the affected floodplains. Our results are in line with several studies relating to dam construction and significant negative decline in semi-aquatic species (Eskew et al. 2012; Brum et al. 2021; Zwahlen 2022). Due to their high sensitivity to flow regime variations and the possibility of fragmenting habitat, semi-aquatic populations such as *H. amphibius* face risks of displacement and significant decline (Lind et al. 1996; Liang et al. 2022). It is important to note that some individuals may have moved to suitable locations near the flooded area and survived there (Environmental Resources Management 2007). This might explain the current and only sustainable group of *H. amphibius* harbored by the "4 O'clock" area at the southern section of the Bui National Park where the habitat structure was similar to that of the areas before the flooding. However, the *H. amphibius* population in the southern section of the area where the dam was constructed, probably had been lost due to habitat fragmentation. Fragmentation, here, was due to lower water availability downstream following the dam construction, as determined to have resulted in extirpation by other studies. Reduced abundance and subsequent local extirpation of *H. amphibius* were the result of dam construction on the Katuma River, Katavi National Park and Lake Rukwa ecosystem in Tanzania (Meyer et al. 2005; Elisa et al. 2010; Timbuka 2012). For example, Benchimol and Peres (2015) showed that several arboreal and terrestrial vertebrates found at three forested sites in the Amazon where one of the largest South American hydroelectric reservoirs was built are threatened with extinction. In addition, Nilsson and Dynesius (1994), reported that mammals were severely affected by the permanent inundation of large areas because of river flow regulation globally.

Other effects on wildlife accompanying floods during damming were outbreaks of wildlife-related diseases. Outbreaks of diseases were predicted during hydromechanical projects (McAllister et al. 2001), and there are also records of anthrax and rinderpest killing *H. amphibius* (Marshall and Sayer 1976; Turnbull et al. 1991). However, Ford (1971), refuted the impact of disease on the *H. amphibius* population claiming the animals have natural immunity to the disease. Even though Tornyie (2015) reported an outbreak of Schistoso and Onchocerciasis during the Bui damming, there were no reports of *H. amphibius* death related to the diseases.

The results of our study show a higher number of *H. amphibius* recorded during the dry season than during the wet season. The variation in numbers can stem from the difference in count accuracy between seasons. Observations during the wet season show *H. amphibius* mostly submerge in pools, therefore reducing visibility and researchers' ability to detect and count them. Several studies have confirmed this observation challenge during *H. amphibius* census in wet seasons, suggesting higher counts during the dry season than the wet season when water levels are higher (Olivier and Laurie 1974; Martin 2005; Kujirakwinja 2010; Zisadza et al. 2010; Lhoest et al. 2015; Fritsch and Downs 2020). Counts in the dry season are suggested to produce a reliably valid estimate of the *H. amphibius* population (Timbuka 2012). This probably could account for the differences in abundance of *H. amphibius* between the wet and dry seasons during our study. Thus fluctuations in counts during census of wild animals are expected for seasonal differences (Stoner et al. 2006). Besides, it was possible that individuals of *H. amphibius* could have moved to suitable areas outside the national park during and after the construction of the dam when their habitat was disturbed, and seasonally migrated to the refuge sites during the dry season thereby accounting for the seasonal differences in the abundance of *H. amphibius* at BNP.

Our results from the interviews attributed illegal hunting of *H. amphibius* to the illegal settlers intruding into the Bui National Park during and after the dam construction. This is supported by the analysis of the data from the Bui National Park for which poaching related activities constituted about 70% of illegal activities recorded in the reserve (Fig. 9). A study by Ayivor et al (2020) corroborated our results by suggesting that poaching and mining are the greatest threats to the reserve. Consequently, the construction of the dam also indirectly resulted in the decrease in population size through poaching, an activity already linked to the decline of *H. amphibius* in other populations (Kujirakwinja 2010; Timbuka 2012; Klingel 2013; Redpath et al. 2015). This indirect relationship between population decline and dam construction relates to the increase in direct exploitation of resources by humans during dam construction (Lekolool 2012; Chen et al. 2015). Similarly, a study by Appiah et al. (2017), reported the invasion of the Bui National Park by settlers in the exploitation of natural resources during and after the dam construction. Other studies have also confirmed that the construction of dams causes the migration of people and human activities into such areas (Environmental Resources Management 2007; Beck et al. 2012; Woldemichael et al. 2012).

An observed builtup area in the reserve for the pre-dam period (2003, Fig. 3) was as a result of local communities residing in the reserve since the government of Ghana acquired and gazetted the area into a national park. However, during the dam construction period (2010), the local communities were resettled to lands outside the reserve. It was therefore expected that there would be a decline in the builtup areas within the reserve during the post-dam construction period. Contrarily, buildup increased with invasion of the reserve by fishing communities, illegal miners and other settlers. Specifically, the presence of illegal mining camps, especially in the northern section of the reserve with an estimated population of 7,000 people and related infrastructures (electricity generating plants, markets, and leisure establishment; pers. Obs.) were a matter of concern for the survival of the *H. amphibius* populations. Sites such as Agave patase/Gareba, Didipreko and Nyameraga (Fig. 3), which have become routes for illegal miners, have all lost a large proportion of their *H. amphibius* population, and poaching by miners is also likely to occur here (see Scholte and Iyah 2016 for additional examples). The ongoing settlement and exploitation of the Bui National Park, especially along the Black Volta River, by illegal settlers had an additional negative effect on the population of *H. amphibius* because of poaching and land use especially in the northern part of Bui National Park. Informal communication with people familiar with the area, including fisherfolks, canoe operators and park rangers, confirmed that poaching of *H. amphibius* increased in the Bui after the dam construction. Effective conservation efforts were undermined by the large number of illegal settlers after the inundation who overwhelmed law enforcement activities of the logistically less equipped park rangers. The deployment and operations of park rangers were met with fierce opposition from the settlers as the area turned into an economic zone (see MyjoyOnline.com 2012; Modern Ghana 2013).

The decline in the number of *H. amphibius* temporally matched with the influx of illegal mining, nomadic herdsmen and fishing village settlements where poaching occurs. For example, at Virunga National Park in the Democratic Republic of the Congo, fishing settlers supported and participated in poaching of wild fauna including that of *H. amphibius* (Kujirakwinja 2010). Similarly, in the southern section of Bui National Park, there have been reports of retaliatory killings due to conflicts with humans leading to the death of *H. amphibius*. The combined effects of habitat destruction and poaching caused the population of *H. amphibius* in Bui National Park to be far lower when compared with the population of *H. amphibius* in other protected areas such as the Masai Mara National Reserve, the Virunga National Park and the Katavi National Park (Kujirakwinja 2010; Kanga et al. 2011; Timbuka 2012). Similarly, the density of *H. amphibius* in Bui National Park is lower than that of geographically close regions, such as 6.5 individuals km^{-1} in Faro National Park, Cameroon (Tsi et al. 2011) and 3.7 individuals km^{-1} in Bénoué National Park, Cameroon (Scholte and Iyah 2016). Our study results indicate a steep de-

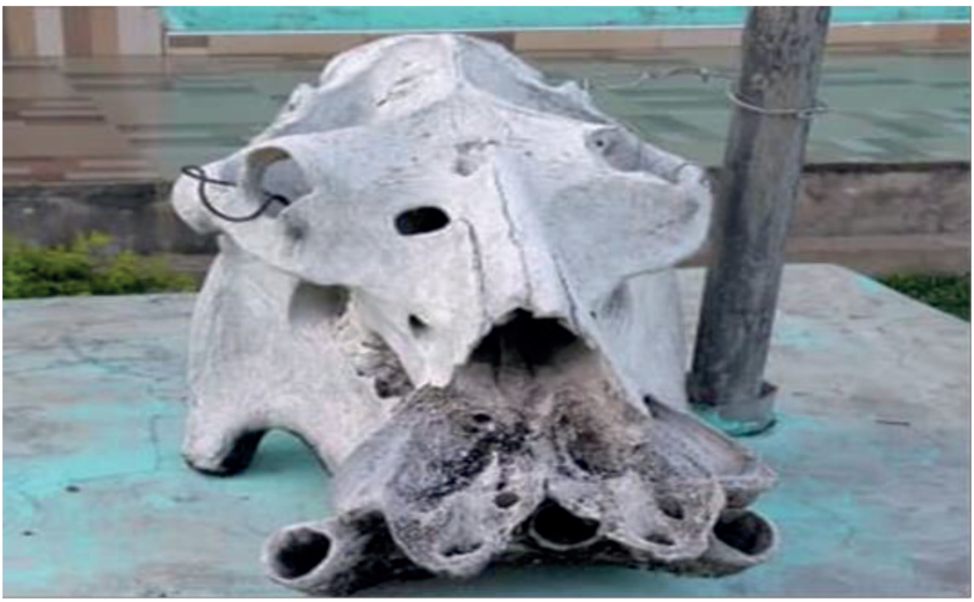

Figure 9. A seized skull of *Hippopotamus amphibius* at the Bui national Park.

cline of about 69% since 2003 at Bui National Park. The close proximity of settled illegal migrants along the Black Volta River in Bui National Park where law enforcement activities are limited, requires urgent protection of the remaining population of *H. amphibius*. Much attention must be given to the ranges of *H. amphibius* in Bui National Park as any further decrease in range would result in higher extinction risk when following the criteria of the IUCN Red List of Threatened Species (Ripple et al. 2017).

Conclusion

The results of our study demonstrate that the population of *Hippopotamus amphibius* has declined drastically with the construction of the dam because of direct effects such as the flooded area, and indirect effects such as poaching facilitated by the construction of the dam. Even though *H. amphibius* is considered a highly mobile species, it is highlighted from the land cover analysis that flooding affected the riparian grasses which served as food for the *H. amphibius* and as a major factor regulating the population density of *H. amphibius*. The co-resultant degradation of suitable grass and increased builtup areas caused additional stress on *H. amphibius*, further impacting the species. The *H. amphibius* population could possibly be displaced by the combined effects of flooding and anthropogenic activities of encroached settlements and associated land cover changes. Illegal mining activities and human settlers who become poachers are currently a major challenge towards conservation efforts and could cause further decline in the *H. amphibius* population. Effective law enforcement actions with commitment from all levels of government and stakeholders should be implemented to avoid further invasion of the protected area by illegal actors that affect species and their habitat. We also recommend establishing a consultative process to evacuate all illegal settlers in the Bui National Park, especially those along the Black Volta River.

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Appendix 1

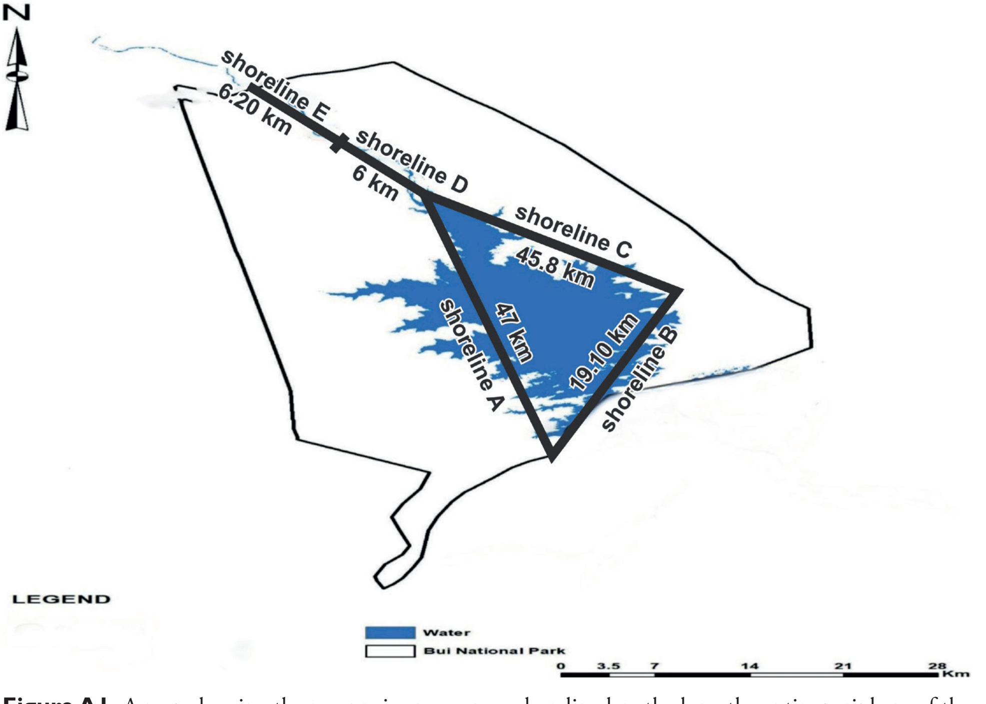

Figure A1. A map showing the reconnaissance survey shoreline length along the entire periphery of the Black Volta River at Bui National Park.