

Occurrence areas of the common hippopotamus outside the Pendjari Biosphere Reserve, northern Benin: implication for sustainable conservation

G.R.M. Adoukè^{1*}, G.N. Kpéra², C.A.M.S. Djagoun¹, B.D. Kassa¹, G.A. Mensah²

¹ *Laboratory of Applied Ecology, Faculty of Agronomic Sciences, University of Abomey-Calavi, 01 BP 526 Cotonou, Benin*

² *National Institute of Agricultural Research of Benin (INRAB), 01 BP 884, Cotonou, Benin*

*Corresponding Author: gadounke@gmail.com

Abstract

This study was conducted to assess the distribution and occurrence areas of the common hippopotamus (*Hippopotamus amphibius*) outside the Pendjari Biosphere Reserve (PBR). Data were collected from 2018 to 2019 through the prospection of 139 grids of 2 km x 2 km. Tracks of hippo occurrence outside the protected area were surveyed and presence data in each of four habitats around the Pendjari River were analysed. Hippos are randomly distributed in the vicinity of the Pendjari River outside the protected area. Their distribution is significantly and negatively correlated with the distance from the Pendjari River ($\beta = -0.0003$; $p = 0.05$) and positively correlated with cereal crops numbers ($\beta = 1.004$; $p = 0.008$) around the Pendjari River. From the 227 hippo tracks recorded, 71.37 % were in cropland, 14% in gallery forest, 7.93% in grassland, and 6.6% at the riverbank. Because hippos occur in croplands, conservation programs and habitat management should focus on educating the local community and promoting positive conservation attitudes towards *H. amphibius* outside the Pendjari Biosphere Reserve.

Keywords: *Hippopotamus amphibius*, spatial distribution, occurrence area, threatened species

Introduction

The spatial distribution of an organism is mainly influenced by the appropriateness of the environment (Aarts et al., 2008) for its survival, growth, and reproduction. The knowledge of ecological requirement, habitat use and, preferences of the concerned organisms tend therefore to play key roles in wildlife conservation and management (Aramde, Girma & Tsegaye, 2011; Ekwai, Hussain & Tahir, 2012). Plants follow definite types of distribution, such as continuous distribution, discontinuous or disjunctive distribution, and very restricted distribution in small areas (Odum, 1971). As far as animals are concerned, their distributions vary widely with their tolerance to environmental conditions. Some can survive in a variety of habitats, whereas others perish when removed from their natural surroundings (Aramde, Girma & Tsegaye, 2011). The Common hippo is an amphibious creature that relies on a range of water sources – rivers, lakes, and wetlands, although seasonally the animal can survive in muddy wallows (Lewison & Pluháček, 2017). It spends the day in the water

and emerges at night to feed. Hippos typically leave wallows or pools soon after sunset and spend the night hours grazing on short-grass swards for up to several kilometers from water (Eltringham, 1999). The ecological requirements for hippo, therefore, include a supply of permanent or seasonal water, and adequate open grazing grassland spanning a few kilometers around the aquatic habitat. However, when these natural requirements are disturbed by human activities, the animals are forced to exist outside of their normal range and live outside protected areas. This condition particularly affects the distribution patterns of large mammals as they wander in search of preferred habitats which are found in patchy habitats of protected areas (Aramde, Girma & Tsegaye, 2011). Thus, some of the rare and endangered mammalian species have shifted their original ranges in some countries. In Benin, for example, hippos inhabit wetlands that often extend outside protected areas into agricultural landscapes dominated by high human population densities and continuous land-use changes. Outside the parks, hippos are found in small groups of 10-20 individuals

inside and around the Mono, Oueme, Sota, Niger, Pendjari, and Mekrou Rivers, where habitat destruction and poaching take their toll (Assogbadjo et al., 2011). However, there is a lack of information on their preferable habitat occurrence outside the protected area and their migratory corridors within the habitat. Because habitat loss and conflicts with humans represent the most threat to the species (Lewison & Oliver, 2008; Lewison & Pluháček, 2017), it is urgent to determine the habitat occurrence of the species in the agricultural landscape for adequate conservation action.

Indeed, knowledge of the habitat preference and spatial distribution of large herbivorous mammals is the basic tool for their effective management (Dekker, Van Rooyen & Bothma, 1996). Considering the threats on the hippos, knowledge of habitat requirement and distribution along the environmental gradient is essential not only for the species' survival

but also for the sustainable management and conservation of protected areas. The purpose of this study was to assess (i) the spatial distribution of the common hippo along the Pendjari River outside the Pendjari Biosphere Reserve (PBR) in northern Benin; (ii) factors predicting hippo spatial distribution along Pendjari River around the PBR; (iii) occurrence areas of hippos outside the PBR.

Methodology

Study area

The research was carried out in Benin, at 23 villages located within 10 km on either side of the Pendjari River outside the PBR (Fig. 1). The PBR occurs in northwest Benin and consists of Pendjari National Park (2,660 km²), Pendjari Hunting Zone (HZ) (1,600 km²), and Konkombri Hunting Zone (250

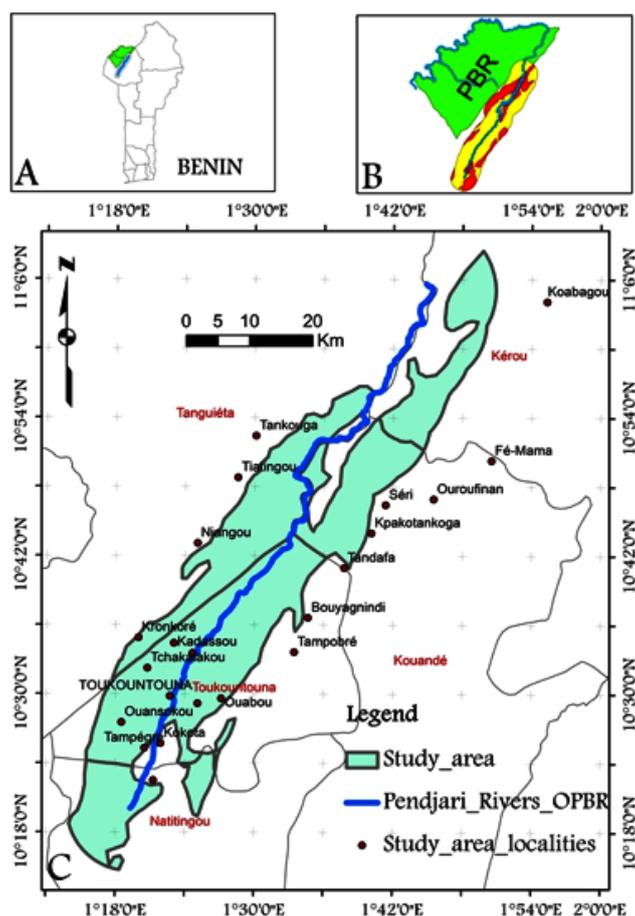


Figure 1: Map of study area showing the Benin country (A), the Pendjari River (blue), the Pendjari Biosphere Reserve (Green) with the 10,000 m buffer zone (Yellow) established, the Atacora chain (Red) around the Pendjari River (B), and the fieldwork (C)

km²) (Sogbohossou *et al.*, 2014). In the North and East, the Pendjari River forms a natural border of the Pendjari Biosphere Reserve (MAB-UNESCO, 1990;). The Pendjari River (10°22'-11°4'N and 1°20'-1°59'E) extends 100 kilometers outside the PBR (PCGPN, 2005) and is shared by five districts (Kérou, Kouandé, Natitingou, Tanguiéta and Toukountouna) of the Atacora Department. The vegetation along the Pendjari River is a mixture of different savannah types, mostly open shrub and tree savannah. Some dry and riparian forests were also observed along the Pendjari River (Assédé, Adomou & Sinsin, 2012). Located in the Soudanian zone, the study area experiences a dry season that extends from November to Mid-May and a wet season from Mid-May to October with a total annual rainfall of 900–1,100 mm (Mul *et al.*, 2015). The wet season provides an ideal condition for crop production and also for aquatic and semi-aquatic species which migrate from the PBR into the agricultural

landscape. Thus, several wildlife species that were supposed to live in the Reserve were found in human habitats outside the Pendjari Biosphere Reserve, including large and small antelopes, carnivores, primates, rodents, and hippos (*Hippopotamus amphibius*). Residents around the Pendjari River are primarily farmers who rely on subsistence rice, maize, millet, and other crops, but also derive supplementary income from hunting and fishing. Fish and bushmeat are the sources of protein in the diet of residents around the Pendjari River.

Data collection

Common hippo distribution surveys

The common hippo distribution survey along Pendjari River was conducted through a sampling method based on grid-cells of a 2 km x 2 km sampling unit (Fig. 1). Using the GIS software, we generated a total number of 349 grids in a buffer zone of 10 km in different

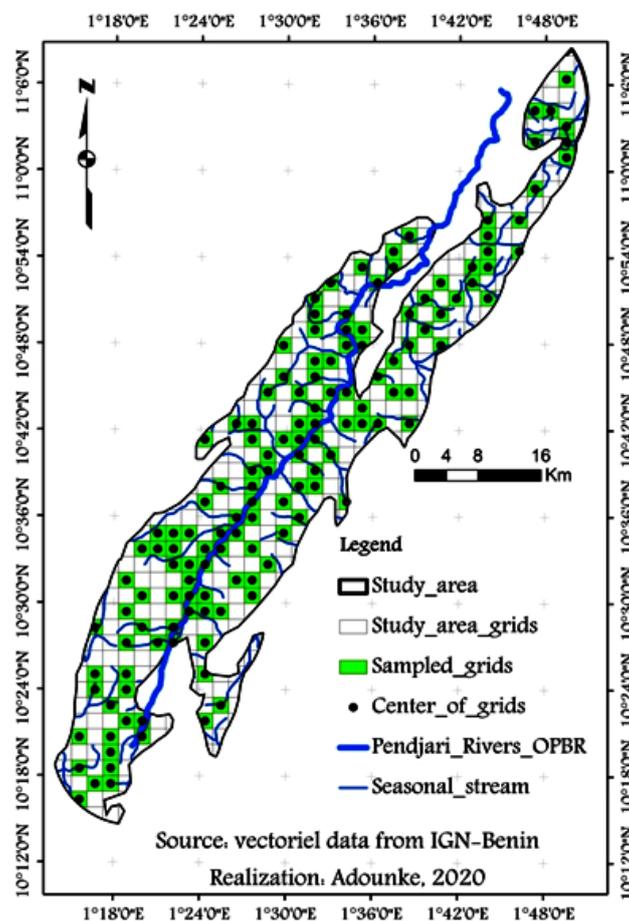


Figure 2: Map of the sampled grids around the Pendjari River

habitat types around the Pendjari River. The buffer zone was set at 10 km to include the area that is theoretically available (Krausman, 1999) to hippos based on the average distance (ranging from >1 km to 10 km) that hippos are reported to travel during their nocturnal search for grazing land (Harrison et al., 2007; Wengström, 2009; Chansa et al., 2011). Each grid cell was labeled using a unique identity (ID) whereas 40%, corresponding to 139 grids were selected randomly, and their respective GPS coordinates recorded (Djagoun et al., 2018). The 40% of randomly selected grids represented the grids located at a maximum of 5km from the Pendjari River where crop farms were located. Beyond the 5km, there were roads and houses. We assumed that hippo movement from one site to another outside the protected area is random and all sampling grids will be in the same detection probability (Royle & Nichols, 2003). Thus, with the "go to" function of a Garmin Geographic Positioning System (GPS), we found the selected sampling grids to investigate them for the presence or absence of hippo tracks e.g. footprints, mooing, trails, dung, feeding sites (Amoussou, Mensah & Sinsin, 2006). Investigations were done per band of 500m to ensure the complete grid prospecting. All hippo tracks observed were recorded with a GPS. Index locations were only recorded if there was at least less than 5 m accuracy of the GPS receiver. Besides, sites with non-selected grids in which hippo tracks were recently recorded according to the local communities were visited for additional data collection. For each track recorded, the vegetation type that characterized the area was also recorded. This helped to determine hippo occurrence areas and the frequency of observation outside the PBR. For subsequent analysis, coding "0" for absence and "1" for presence generated presence/absence data of hippo in each grid. The survey team was made up of two persons: the leader and a local guide and both were skilled very well in hippo track identification.

Identification of factors that influence hippo distribution around the Pendjari River

Knowledge of occurrence areas is essential not only for the species' survival but also for the sustainable management and conservation

of protected areas. Thus, for each grid of 2 km x 2 km prospected around the Pendjari River, all the different cereal crops, as well as their numbers in each grid present were recorded at the middle using GPS. We recorded only cereals crops because they represented the main food crops and the local communities within the study area complain about hippo attacks on cereals. Also, the nearest distance from the middle of each grid to the Pendjari River, the Pendjari Biosphere Reserve, and the surrounding localities were calculated with GIS software in order to determine their influence on hippo presence/absence in the study area.

Data analyzing methods

The ArcGIS 10.1 software was used to project the hippo track points recorded in the map of the study area to have an overview of the spatial distribution of the species along the Pendjari River outside the Pendjari Biosphere Reserve. The empirical function k (Venables & Ripley, 2002) was used to determine the hippo distribution shape (gregarious, regular, and random) outside the Pendjari Biosphere Reserve. When the theoretical distribution curve generated by the function k is above the confidential interval [$K_{hi}(r)$; $K_{lo}(r)$], the distribution is gregarious while the distribution is named as random when it's between the intervals. However, when the theoretical distribution is below the confidential interval, the distribution is regular (Rabeil, 2003).

Gathered data were analyzed using the statistical program R v. 4.1.0. To understand the factors best predicting common hippo distribution around the Pendjari River outside the protected area, a Generalized Linear Model (GLM) based on binomial regression was fitted to hippo presence/absence data with the crop number present in each grid, and the distance from each grid center to the Pendjari River. Previously, the backward stepwise procedure for model simplification revealed that the best model (Lowest AIC = 68.91) retained only "crop number (C.N)" and "Distance to the Pendjari River (D.pr)" variables. Thus, "Distance to PBR" and "Distance to localities" variables were removed from the model. The χ^2 test was used to assess the fitness of the GLM to data

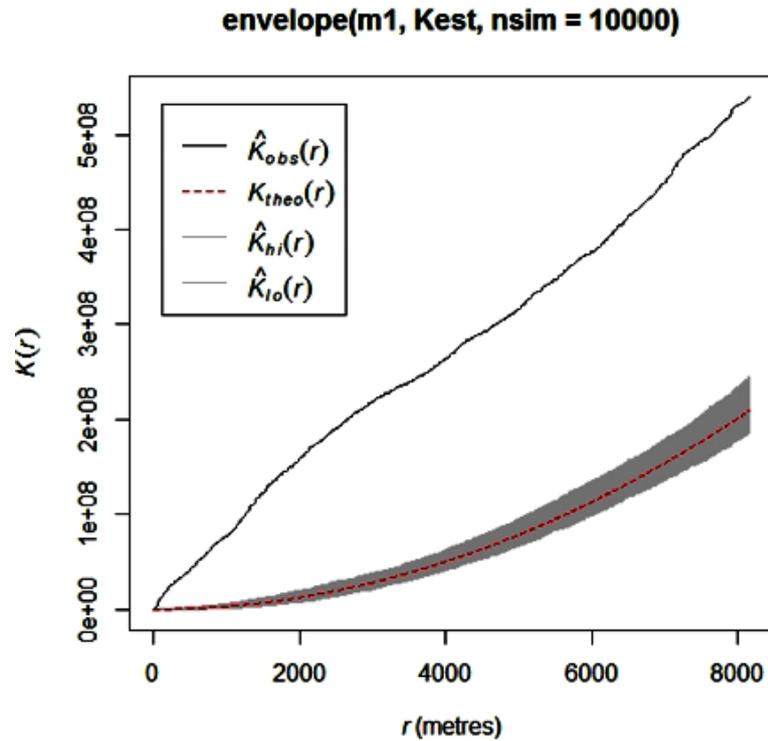


Figure 3: Common hippo distribution shape outside the Pendjari Biosphere Reserve in Northern Benin



Figure 4: *H. amphibius* tracks recorded outside the Pendjari Biosphere Reserve in Northern Benin
(A: Footprint; B: Dung; C: Trails; D: Feeding site)

and the pseudo-coefficient determinant, R^2 (Nagelkerke, 1991) calculated to evaluate the model's explanatory power. Using R packages, we obtained robust standard errors and calculated the p-values accordingly (Cameron

& Trivedi, 2009). Together with the p-values, we also calculated the 95% confidence interval using the parameter estimates and their robust standard errors. The model's odds ratios were calculated using "mfx" R package.

TABLE 1

Parameter estimates and odds ratios of the binomial regression model for the influence of two independent variables on the *H. amphibius* distribution outside the PBR. Full model, $\chi^2 = 46.7$, $df = 2$, $P(> X^2) < 0.001$

	OddsRatio	Robust SE	95%IC	p-value
Intercept	- 0.214	0.166	[-0.046; -0.981]	0.016*
D.river	- 0.999	0.0002	[-0.999; 1.000]	0.05
C.N	2.731	1.375	[1.017; 7.327]	0.008**

Signif. codes : 0 '****' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

The Kruskal-Wallis test–ANOVA alternative– was used to evaluate the significant difference of hippo tracks recorded according to the four habitat types (Riverbank, Grassland, Gallery Forest, and Cropland).

Results

Spatial distribution of common hippo along the Pendjari River outside the Pendjari Biosphere Reserve

From the 139 grids surveyed, hippo tracks were recorded in 43, totalizing 227 hippo tracks along the Pendjari River. Thus, figure 3 shows that hippo tracks are largely and randomly distributed along the Pendjari River outside the PBR. The most recorded hippo tracks were footprints (87.22%), trails (6.60%), feeding sites (5.28%), and dung (0.9%) (Figure 4), mainly up to 4 km from the Pendjari River at both sides. However, hippo tracks decreased

farther away from the PBR. For example, 134 hippo tracks were recorded at an average of 24 km away from the Reserve; 53 at 44 km away from the Reserve, and 23 at 55 km away from the Reserve.

Factors predicting H. amphibius spatial distribution outside the PBR

Table 1 shows the result of the Generalized Linear Model predicting hippo spatial distribution along Pendjari River outside the PBR. The model shows that hippo tracks are more often recorded nearest to the Pendjari River ($\beta = -0.0003$; $p = 0.05$). An increase in the distance from the Pendjari Rivers for 1 km, corresponds to hippopotamus tracks observation decreasing by 1 unity. Most (71.37%) of the hippo tracks were recorded in the surrounding of the Pendjari River. Also, hippos were mostly recorded where cereal crops were abundant ($\beta = 1.004$; $p = 0.008$). An increase in cereal crops abundance around

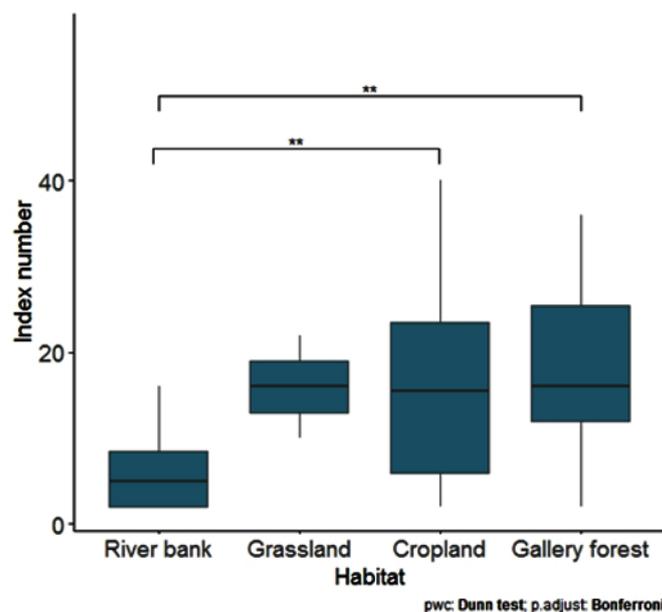


Figure 5: *H. amphibius* tracks recorded in different habitat types around the Pendjari River

the Pendjari River for 1 unit, corresponds to hippopotamus tracks increasing by 2.73. The number of crops in the prospected grid varied from 0 to 11 and hippo tracks increased accordingly with the number of crops increasing.

Frequency of observation of H. amphibius according to the habitat outside the Pendjari Biosphere Reserve

The average frequency of *H. amphibius* track observations differs significantly in four habitats types ($\chi^2(3)=12.65, p=0.0055$) around the Pendjari River, namely the riverbank, the cropland, the grassland, and the gallery forest. The pair-wise comparison of the variable shows a significant difference between hippo tracks recorded in cropland and riverbank ($p=0.00855$) and between tracks recorded in gallery forest and riverbank (0.00405). No significant difference was observed between hippo tracks recorded at cropland and gallery forest; cropland and grassland; gallery forest and grassland, grassland and riverbank (Figure 5). The cropland habitat consisted of rice, millet, maize, and Bambara farms. The higher frequency of hippo tracks (71.37%) was observed on cropland and the lower frequency on the riverbank (6.6%) and the grassland (7.93%) (Figure 5). The gallery forest habitat represents the second most common habitat where 14.10% of *H. amphibius* were recorded. Furthermore, hippo tracks were recorded in the habitats located beyond 4 km.

Discussion

H. amphibius tracks were found around the Pendjari River outside the Pendjari Biosphere Reserve. Our results are consistent with those of Assogbadjo *et al.* (2011) who identified threatened groups of hippos along the Pendjari River outside the protected area. With a high occurrence of 83.3%, the study revealed footprints as an excellent way to determine the presence of hippo as reported by another study (Alli & Viriri, 2013). This is because the footprints are usually smudged

and partially visible for a megaherbivore weighing over 1000 kg (Owen-Smith, 1992) such as hippos (*Hippopotamus amphibius* Linnaeus 1758) and elephants (*Loxodonta africana* Blumenbach 1797). Another study revealed trails as a more important track ahead of footprints for the endangered pygmy hippo (*Choeropsis liberiensis*) (Garteh, 2013). However, the footprints may be a better option as it is also a good identification tool for hippos (Amoussou, Mensah & Sinsin, 2006). Another way to determine hippo presence is through feeding sites. Hippos follow regularly the same way from water to their feeding site leading to a permanent track (Eltringham, 1999; Kedl, 2015). However, the hippo's dung does not give an account really of hippo presence outside the Pendjari Biosphere Reserve. Only two dungs were recorded around the Pendjari River in the five districts surveyed. Garteh (2013) also record a low proportion of dung around the Gola Rainforest National Park. According to Subalusky *et al.* (2014), the common hippo defaecates mainly in the river and this may account for the low presence of dung in the study area. We recorded more hippo tracks near the Pendjari Biosphere Reserve and low tracks farther away showing that the majority of activities of hippos occur near the PBR. Owen-Smith (1992) reported that hippo feeding in the rainy season is doing less than 1 km from a water source and indeed, hippos can travel until 6-7 km searching for feeding resources in the dry season. However, after an average of 5 km from the Pendjari River are found the urban/rural infrastructure as road and human shelter. These factors represent a limit for hippo travel. The Atacora chain represents also a limit for hippo nocturnal travel outside the Pendjari Biosphere Reserve (Adoukè, 2018). The presence and abundance of crops around the Pendjari River seem to play an important role in the hippo distribution and abundance. A total of 227 hippo tracks were recorded in the surrounding habitats of Pendjari River and *H. amphibius* more often occurred on cropland than other habitats. However, hippos are known to prefer open habitats as grassland

or open forest (Eltringham, 1999) and according to Timbuka (2012), water and grass components of habitats are responsible for hippo abundance, immigration, and emigration (Timbuka, 2012), while Kanga et al. (2012) reported that in the absence of suitable natural grass, the hippo selects cropland. Amoussou, Mensah & Sinsin (2006) have shown that hippos diet around the Mono Biosphere Reserve (southern Benin) included 20.9% of cropland product. A recent study in Nigeria found that hippos were abundant near farms, which are prevalent around the Kiri reservoir, and its habitations (Baker et al., 2020). All these lend credence to our observation that *H. amphibius* were more often present at cropland and particularly, where the farms were abundant around the Pendjari River, suggesting that they fed on crops mostly. The least recorded habitats of *H. amphibius* were 1). the grassland, contrary to previous reports outlined above, and 2). riverbank habitat; also contrary to reports that hippos rest more often at a riverbank for warming (Noirard et al., 2008). According to Prinsloo (2016), hippos allocated significantly more time to rest than all other activities including moving and socializing. However, higher levels of human activities such as fishing, hunting associated with human settlements have the potential to generate significant disturbance to hippo resting (Onyeanus, 2004). A variety of effects including displacement from biologically important habitats, competition for resources, alteration of activity budgets, and behaviours associated with increased human disturbance have been documented for numerous species (Averbeck et al., 2009). Thus the low frequency of tracks of hippo recorded at the Pendjari riverbank may be indicative of the direct effects of human disturbances. The low frequency of tracks of hippo in grassland may also be due to competition with domestic livestock for access to grazing areas and this is consistent with Wengström (2009). Roaming herders graze their cattle on communal lands around Pendjari River, hippos are therefore potentially at risk of being excluded from these grazing sites, either through negative interactions (e.g. competition, avoidance) with cattle or the conversion of hippo grazing

areas into unsuitable fields by cattle grazing and trampling (Wengström, 2009). In this way, humans may indirectly affect the vegetation type, quality, and quantity available to hippos for grazing. Therefore, proper management is urgently needed to reduce the negative human impacts on hippo habitat for the survival of the species along the Pendjari River. Further research needs to be conducted with regards to riparian land cover dynamic over the last 10 years to evaluate the grassland habitat destruction dynamic and engage a conservation action of hippopotamus habitats in the future.

Conclusion

Human settlements and their socio-economic activities such as farming, hunting, and fishing around the Pendjari River near the hippo habitats outside the protected area cannot be overlooked if we are to ensure successful hippo conservation. Therefore, educating the local community and promoting positive attitudes towards *H. amphibius* outside the Pendjari Biosphere Reserve should be a key agenda for management planning.

Acknowledgments

We thank IDEA WILD Grant (www.ideawild.org) for providing us with research equipment. We are also grateful to Prof KASSA Barthélémy, of the Laboratory of Applied Ecology /University of Abomey-Calavi (Benin) who provided us with financial support for field work. Special thanks to the community members of the 23 villages located within 10 km on either side of the Pendjari River (outside the Pendjari Biosphere Reserve) in the Kérou, Kouandé, Natitingou, Tanguiéta and Toukountouna Districts), who collaborated with us and provided the data and insights necessary for this study.

Conflicts of interest

The authors claim no conflicts of interest concerning the results presented in this paper.

References

- Aarts, G., MacKenzie, M., McConnell, B., Fedak, M. and Matthiopoulos, J.** (2008). Estimating space-use and habitat preference from wildlife telemetry data. *Ecography* **31**:140-160.
- Adoukè, M. G. R.** (2018). Common hippopotamus (*Hippopotamus amphibius*) distribution along Pendjari River and local communities' perceptions on human-wildlife conflicts in agricultural landscapes outside the Pendjari Biosphere Reserve in Northern Benin. Master of Science Dissertation, Laboratory of Applied Ecology, University of Abomey Calavi. 69 Pages.
- Alli, M. N. and Viriri S.** (2013). *Animal Identification Based on Footprint Recognition*. 978-1-4799-3067-8/13/\$31.00 ©2013 IEEE.
- Amoussou, G. K., Mensah, G. A. and Sinsin, B.** (2006). Données biologiques, éco-éthologiques et socio-économiques sur les groupes d'hippopotames (*Hippopotamus amphibius*) isolés dans les terroirs villageois en zones humides des départements du Mono et du Couffo au Sud-Bénin. *Bulletin de la Recherche Agronomique du Bénin* **53** : 22-35.
- Aramde, F., Girma, M. and Tsegaye, B.** (2011). Spatial distribution and habitat preferences of selected large mammalian species in the Nech SAR National Park (NSNP), Ethiopia. *Nature and Science* **9(3)**:80-90.
- Assédé, E. P. S., Adomou, A. C. and Sinsin, B.** (2012). Magnoliophyta, Biosphere Reserve of Pendjari, Atacora Province, Benin. *Check List* **8(4)**: 642-661.
- Assogbadjo, A. E., Amoussou, G., Sinsin, B. and Neuenschwander P.** (2011). Hippo. In P. Neuenschwander, B. Sinsin, and G. Goergen, G. 2011. Protection de la Nature en Afrique de l'Ouest: Une Liste Rouge pour le Bénin. Nature Conservation in West Africa: Red List for Benin. International Institute of Tropical Agriculture, Ibadan, Nigeria. 365 pages.
- Averbeck, C., Apio, A., Plath, M. and Wronski, T.** (2009). Environmental parameters and anthropogenic effects predicting the spatial distribution of wild ungulates in the Akagera savannah ecosystem. *African Journal of Ecology* **47**: 756–766.
- Baker, L. R., Che, J., Teneke, V. N., Kadala, E., Uba, M. S., Geoffrey, N. and Haskainu C.** (2020). Common hippo in Nigeria: New census data and literature review confirm the conservation importance of sites outside protected areas. *Aquatic Conservation Marine and Freshwater Ecosystems* **30(10)**:1996-2003.
- Cameron, A. C. and Trivedi, P. K.** (2009). *Microeconometrics Using Stata*. College Station, Texas, USA, Stata Press.
- Chansa, W, Senzota, R, Chabwela, H. and Nyirenda, V.** (2011). The influence of grass biomass production on hippo population density distribution along the Luangwa River in Zambia. *Journal of Ecology and the Natural Environment* **3(5)**: 186-194.
- Dekker, B., Van Rooyen, N. and Bothma, J.** (1996). Habitat partitioning by Ungulates on a Game Ranch in the Mopani Veld. *South African Journal of Wildlife Research* **26**: 117-122.
- Djagoun, C. A. M. S., Sogbohossou, E. A., Kassa, B., Ahouandjinou, C. B., Akpona, H. A. and Sinsin, B.** (2018). 'Effectiveness of Protected Areas in Conserving the Highly Hunted Mammal Species as Bushmeat in Southern Benin', *The Open Ecology Journal* **11(1)**: 14-24.
- Ekwal, I., Hussain, T. and Tahir, M.** (2012). Modeling of Habitat Suitability Index for Muntjak, *Muntiacus muntjak*, Using Remote Sensing, GIS and Multiple Logistic Regressions. *Journal of Settlements and Spatial Planning* **3(2)**: 93-102.
- Eltringham, S. K.** (1999). *The hippo: Natural History and Conservation*. Academic Press, London, UK.
- Garteh, J. C.** (2013). Studying the distribution and abundance of the endangered pygmy hippo (*Choeropsis liberiensis*) in and around the Gola Rainforest National Park in southeastern Sierra Leone. A Dissertation

- in the Department of Biological Sciences submitted to the School of Environmental Sciences of Njala University in partial fulfillment of the requirement for the Award of Degree of Master of Science in Biodiversity Conservation. 66p.
- Harrison, M. E., Kalindekaffe, M. P. and Banda, B.** (2007). The ecology of the hippo in Liwonde National Park, Malawi: implications for management. *African Journal of Ecology* 46: 507- 514.
- Kanga, E. M., Ogutu, J. O., Piepho, H. P. and Olf, H.** (2012). Human-hippo conflicts in Kenya during 1997-2008: vulnerability of a megaherbivore to anthropogenic land use changes. *Journal of Land Use Science* 7: 395-406.
- Kedl, G.** (2015). Impacts des barrages sur les populations d'hippopotames et gestion du conflit avec l'homme : le cas du barrage de Kandadji sur le Fleuve Niger. Mémoire de maîtrise, Université de Sherbrooke. 81p.
- Krausman, P. R.** (1999). Some basic principles of habitat use. In: Launchbaugh, K.L., Sanders, K.D. and Mosley, J.L., Eds., *Grazing Behaviour of Livestock and Wildlife*, Idaho Forest, Wildlife and Range Exp. Sta. Bull. No. 70, University of Idaho, Moscow, ID, 85-90.
- Lewison, R. and Pluhaček, J.** (2017). *Hippopotamus amphibius*. The IUCN Red List of Threatened Species 2017: e.T10103A18567364. <http://dx.doi.org/10.2305/IUCN.UK.2017-2.RLTS.T10103A18567364.en>.
- Lewison, R. and Oliver, W. (IUCN SSC Hippo Specialist Subgroup)** (2008). *Hippopotamus amphibius*. The IUCN Red List of Threatened Species. Version 2014.2 <www.iucnredlist.org>.
- MAB-UNESCO** (1990). Pendjari (Bénin): Contribution aux études d'aménagement du Parc National et de sa zone périphérique. Rapport d'étude. ENGREF-FSA, Cotonou, Bénin. 47 p.
- Mul, M., Obuobie, E., Appoh, R., Kankam-Yeboah, K., Bokoe-Obeng, E., Amisigo, B., Logah, F.Y., Ghansah, B. and McCartney, M.** (2015). Water resources assessment of the Volta River basin. IWMI Working Paper 166. International Water Management Institute, Colombo.
- Nagelkerke, N.** (1991). A note on a general definition of the coefficient of determination. *Biometrika* 78 : 691-692.
- Noirard, C., Le Berre, M., Ramousse, R. and Lena, J. P.** (2008). Seasonal variation of thermoregulatory behaviour in the hippo (*Hippopotamus amphibius*). *Journal of Ethology* 26: 191-193.
- Odum, E. P.** (1971). *Fundamentals of Ecology*. Saunders College Publishing, Philadelphia.
- Onyeausi, A. E.** (2004). Some behavioural characteristics of common hippo (*H. amphibius* Linn. 1758) in Nigeria's Kainji Lake National Park. *International Journal of Agriculture and Rural Development* 5: 27-35.
- Owen-Smith, R. N.** (1992). *The Influence of Very Large Body Size on Ecology*. 2nd Edition, Cambridge, Cambridge University Press, 388 p.
- PCGPN** (2005). Plan d'aménagement et de gestion de la Réserve de Biosphère de la Pendjari 2004-2013. Version finale. CENAGREF/GTZ. 86 p.
- Prinsloo, S.** (2016). Aspects of the spatial and behavioural ecology of *Hippopotamus amphibius* in the Saint Lucia Estuary, KwaZulu-Natal, South Africa. 161p.
- Rabeil, T.** (2003). Distribution potentielle des grands mammifères dans le Parc du W au Niger. Ecologie, Environnement. Université Paris-Diderot-Paris VII. Français. tel-00006931.
- Royle, J. A. and Nichols, J. D.** (2003). Estimating abundance from repeated presence-absence data or point counts. *Ecology* 84: 777-90.
- Sogbohossou E.A., Bauer H., Loveridge A., Funston P.J., De Snoo G.R and Sinsin B.** (2014). Social structure of lions (*Panthera leo*) is affected by management in the Pendjari Biosphere Reserve, Benin. *PLoS ONE* 9(1): e84674.
- Subalusky, A. L., Dutton, L. C., Rosi-Marshall, E. J. and Post, D. M.** (2014).

The hippo conveyor belt: vectors of carbon and nutrients from terrestrial grasslands to aquatic systems in sub-Saharan Africa.

Freshwater Biology **60**: 512-525.

Timbuka, C. D., (2012). The Ecology and Behaviour of the Common hippo (*Hippopotamus amphibius*) L. in Katavi National Park, Tanzania: Responses to Varying Water Resources. Thèse de Doctorat, University of East Anglia, Norwich, Royaume-Uni, 316 p.

Venables, W. and Ripley, B. (2002). *Modern statistics with S*. Springer-Verlag, New York, fourth edition.

Wengström A. (2009). How Maasai settlements affect the grazing habits of the common hippo (*Hippopotamus amphibius*) in the Maasai Mara National Reserve, Kenya. Unpublished Student report 255, Swedish University of Agricultural Sciences. ISSN 1652-280X.