Structure of buffaloes Syncerus caffer (Sparrman, 1779) (Mammalia Bovidae) of the Comoe National Park (North-East Ivory Coast)

Atta Assemien Cyrille-Joseph^{1,*}, Kadjo Blaise¹, Soulemane Ouattara¹ & Kouadio Yao Roger²

¹Laboratory of Natural Environment and Biodiversity Conservation, UFR Biosciences, Félix Houphouët-Boigny University, 22 BP 582 Abidjan 22, Côte d'Ivoire

²Ivorian Office of Parks and Reserves, Côte d'Ivoire, 06 BP 426 Abidjan 06

Corresponding author, email: cyrillejosephatta@gmail.com

ABSTRACT

This study was conducted from January to August 2018 in Comoe National Park (CNP), Ivory Coast. This park is home to a great biological diversity in general and an important fauna of large mammals in particular. It is one of the priority areas of the West African protected areas network. Today, many wildlife species are threatened by intensive poaching. Despite the importance of this scourge, the information available on buffaloes in CNP is still very patchy. In order to determine some parameters of the conservation status of buffalo populations, this study was conducted in the central zone and southern zone of CNP. The camera-trap method (12 camera-traps) made it possible to determine the different age classes and sex ratios of the buffalo populations. Family units were observed 11 times on all two (2) sites corresponding to 34.38 % of the events (32). The average size of family units is 23.18 individuals (standard deviation = 25.52; N = 11) with maximum of 77 individuals. Eleven (11) different groups (herds) of 255 individuals were identified with an average size of 32 individuals per herd. In the center, four groups composed of 15 adults, 31 subadults, 37 juveniles and seven calves were identified. In the south, seven groups with 34 adults, 49 subadults, 79 juveniles and three calves were observed. Calves were more numerous in the herds observed in the center than those identified toward the periphery at the 5 % (P-value = 0.0254). This high presence of calves in the herds observed in the center would reflect the fact that the buffaloes retire to the central part of the park for calving. Based on the high proportion of individuals in the young age classes (juveniles 44.5 % and subadults 32.07 %) and the sex ratio 1.65 (one male for 1.65 females), the buffaloes population in the CNP was considered viable. However, the inbreeding rate and anthropogenic pressures have yet to be evaluated to complete these data.

KEY WORDS Buffalo; Structure; Population; Sex ratio; Comoe National Park.

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INTRODUCTION

Management of wildlife and wildlife habitats requires fairly accurate up-to-date knowledge of the population structure, including abundance social

life, age classes and sex, which are fundamental demographic variables for the analysis of wildlife characteristics (Sinsin et al., 2006). In addition, large mammals have been the subject of numerous studies and well-established conservation plans

(Kassé et al., 2006; Kadjo et al., 2014). However, due to habitat loss, the vast majority of these mammals are confined to protected areas. But between 1970 and 2005, the overall number of African large mammals in protected areas fell by about 60 % on a continental scale and collapsed by about 85 % in West Africa (Craigie et al., 2010). Located in the north-east of the country, the Comoe National Park (CNP), Ivory Coast, is home to a high biological diversity in general and an important large mammals fauna in particular. This park is one of the priority areas of the West African protected area network (N'Goran et al., 2010; Kouakou et al., 2014; Bouché, 2016). Today, many wildlife species in this park are still threatened by intensive poaching (Djafarou & José, 2013; Koueita et al., 2018). Among these species is the buffalo for which the available information is still very patchy. However, the buffalo has a proven ecological role on vegetation, especially on the regeneration of higher plants (De Vos & Bengis, 1994). It is a species of high tourist value because it is part of the Big five game (Caro & Riggio, 2014). CNP, which is relatively well conserved and enjoys various national and international protection status, provides a favourable framework for studying the biology and ecology and defining the conservation status of this large wild West Africa ungulate, the buffalo. This study could also be benefit other wildlife taxa in CNP. The aim of this study is to determine some parameters of the conservation status of the buffalo populations. It will specifically (i) determine the structure of buffalo populations and (ii) the sex ratio of the ob-

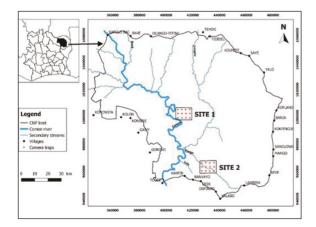


Figure 1. Map of the location and layout of camera traps in Comoe National Park, Ivory Coast.

served groups in order to get an idea of the viability of the buffaloes in this park.

MATERIAL AND METHODS

Study area

Comoe National Park (CNP) is located in the north-east of Ivory Coast, between latitudes 8°30 -9°37 north and longitudes 3°07 - 4°26 west and covers an area of 1,148,756 hectares (Fig. 1). It is crossed from north to south by the Comoe river in its western part. The climate of the CNP is the subhumid tropical type with two season: a long rainy season and a long dry season. The dry season is well marked and can last up to 8 months from October to May. The rainy season is from June to September. March is the hottest month with temperatures around 37 °C while January is the least hot with an average temperature of around 15 °C. Annual rainfall is between 900 mm and 1200 mm with an average of 1084 mm per year (Fisher et al., 2002). The mean annual temperature varies from 26 °C to 27 °C (OIPR, 2015).

In the CNP, there is a wide variety of microclimates in relation to the observations made for certain habitats. There are four main types of vegetation: gallery forests, forest islands, wooded savannah and shrubby savannah.

Savannah formations occupy more than 80 % of the total park area and are therefore characteristic of the landscape of CNP (Schweter, 2016).

Sampling

The images from the trap cameras were classified by date and camera (Kely et al., 2019). The videos containing the images of the buffalo were used to determine the population structure of these animals. Camera traps that detected at least one buffalo were defined as positive camera traps, while those that did not detect buffaloes were defined as negative camera traps (Doré et al., 2011). For the counting of buffaloes on the videos, these animals are classified by sex (male or female) and by age class (adult, subadult, juvenile and calf). Age classes were determined based on horn shape and development, general morphology, changes in colour and coat texture (Sinclair & Grimsdell, 1978; Ndhlovu & Balakrishnan, 1991; Aberham

et al., 2012). Four different age classes were therefore considered in this study (Table 1).

The methodology used in the study of the structure of buffalo populations in the CNP consisted of photographic trapping with the "Bushnell HD Trophy Cam Agressif Brown 119776" trap camera model. The camera traps were carried out in the central and southern zones of the CNP (Figure 1). These two zones were selected in areas with easy access and high concentrations of buffalo observed during the last aerial overflight in 2016 (Bouché, 2016). The two sites are 30 km apart.

Since the minimum home range of buffalo is estimated at 18 km² (Prins, 1996), a 3 km x 3 km grid covering an area of 144 km² was superimposed on the areas delimited for the study. Twelve (12) camera traps were placed, one inside each grid box. The choice of camera locations within the grids was dictated by buffalo presence clues (droppings, hoof prints, feeding track, etc.). The same cameras were used in each of the circumscribed areas (center and south) at different times. Data collection was carried out in two phases, from 3 January to 31 March 2018, in the central zone and from 2 June to 30 August 2018, in the southern zone. The camera traps that were removed after the first trapping phase were reused during the second phase. Each cameratrap was attached to a tree at a height of about 1 m

based on the average size of the buffalo (Nakashima, 2015; Hongo et al., 2016). The camera traps were set up in to video (hybrid) mode with recording sequences of one minute (60 s) each and separated by 30 seconds of intervals. The resolution of the photographs has been minimized (5 Mpx) to allow the memory cards to record more data. Information obtained from separate video sequence of less than 30 minutes are considered to information on the same buffalo herd (O'Brien et al., 2003; Nakashima, 2015; Hongo et al., 2016). Access to the navigation point of each camera trap was by navigation using GPS and compass. Once at the point indicated for the installation of a specific camera trap (theoretical position), we prospected within a radius of 200 m to choose the most appropriate position (Ancrenaz et al., 2012), in order to optimise buffalo detection (actual position). This actual position was chosen on the basic of the presence of a waterhole or buffalo signs (Ancrenaz et al., 2012; Mermod, 2012; Hedwig et al., 2018). The camera trap was installed to avoid direct exposure to the sun. It was oriented so as to avoid having seedlings or obstacles in the field of view. The camera traps were visited once a month during the trapping period to change batteries and SD memory cards.

After grouping the detections into events, we first counted the number of individuals for each

AGE GROUPS	PHYSICAL CHARACTERISTIC	REFERENCES
Calf (< 12 months)	They may or may not have visible horn buds, short, clearly visible horns, V-shaped upwardly protruding horns or straight horns growing outwardly and rearwardly. The coat of these animals is dark olive brown to black and appears smooth and soft, lighter to chocolate brown or yellow brown.	Funston, 1992; Pienaar, 1969
Juvenile (13 - 25 months)	This 13 to 24 months old age class of buffalo consist of individuals that are about twice as long as the horns. The horns are slightly curved outward, but are still widely separated at the tips. The coat is darker, rougher and brown.	Funston, 1992; Pienaar, 1969
Subadult (25 - 48 months)	These are buffaloes between 25 to 48 months old. They have sweeping horns on the inside. Male individuals have a huge frontal mass that covers the entire top of the skull above the eyes. The coat is uniformly smooth and dark chocolate brown in colour and turns black in females.	Sinclair, 1977; Pienaar, 1969
Adult (> 48 months)	Adult buffaloes are those over 48 months old. These animals considered adult have broad, back-sweeping horn tips. The colour of the coat becomes black.	Pienaar, 1969

Table 1. Characteristics of buffalo age classes.

event. This number is considered the size of the observed group (Bezerra et al., 2014; Hedwig et al., 2018; McCarthy et al., 2018). We then calculated the average size of buffalo groups in CNP, with or without the solitary individuals (Merz, 1986; White et al., 1993; Turkalo et al., 1996; Vanleeuwe et al., 1997; Maréchal et al., 1998; Querouil et al., 1999; Theuerkauf et al., 2000). Groups consisting of two or more individuals have been considered as "family units" (White et al., 1993; Maréchal et al., 1998).

The trapping effort is expressed in camera days and represents the number of days a camera is in operation multiplied by the corresponding number of cameras.

The catch rate corresponds to the number of independent photographs (useful catches) for the whole system reduced to a catch effort in terms of "nights-traps". A capture is useful when the information obtained from the video sequences is less than 30 minutes apart. The number of identified buffalo individuals is determined by counting individuals in each video sequence (useful capture). The correspondence between the images and the number of buffalo individuals was made through the dates of capture.

The sex ratio represents the ratio of the number of males and females overall and in each age group.

The chi² test was used to compared the abundance of buffalo by age class between the two zones. The student's t-test allowed to compare the composition of the buffalo populations observed in the center and south of the park. Finally, the non-parametric Kolmogorov-Smirnov test allowed to compare the distribution of buffaloes in the center and south of the park. The different tests were carried out with the software Xlstat 2016 version 18.02.01 and STATISTICA version 10.0.1011.7.

RESULTS

At the end of the two trapping phases, the data from 24 photographic traps were taken into account in our analysis. Twelve photographic traps in the central part and 12 photographic traps in southern part. All photographic traps functioned normally during both trapping phases. Of the 12 camera traps in the central part of the park, 7 were positive for the presence of buffalo (Fig. 2). In the south of the park, of the 12 photographic traps, 10 were positive for the presence of buffaloes (Fig. 2).

In the center of the park, 14 buffaloes captures were obtained, 12 videos were useful for the identification of individuals, which allowed the detection of 90 individuals. In addition, the trapping effort was 332 camera days (Table 2). In the southern part of the park, 21 buffaloes captures were obtained, 20 videos were useful for the identification of individuals, which allowed the detection of 165 individuals. In addition, the trapping effort was 345 camera days (Table 2).

Family units (group size greater than or equal to two) were observed 11 times at both (2) sites, corresponding to 34.38 % of the events (32). Considering the number of individuals observed (255), we deduce that 96.08 % of individuals live in a family unit, while 3.92 % of individuals live alone (N = 255). For family units, the observed modal size is two (2) individuals, with three (3) events, representing 27.27% (N = 11) of the events. The average size of family units is 23.18 individuals (standard deviation = 25, 52; N = 11) with a maximum of 77 individuals.

Eleven (11) different groups (herds) of 255 individuals were identified with an average number of 32 individuals per herd. In the center, four groups composed of 15 adults representing 29.7 % (N = 90) of the population, 31 subadults representing 47.88 % (N = 90) of the population, 37 juveniles representing 20.6 % (N = 90) of the population and seven calves representing 1.82 % (N = 90) of the population were identified. While in the south, seven groups with 34 adults representing 34.44 % (N = 165) of the population, 49 subadults representing 41.11 % (N = 165) of the population, 79 juveniles representing 16, 67 % (N = 165) of the population and three calves representing 7.78 % (N = 165) of the population were observed. All solitary individuals observed were adults. Considering family units only, we have 3.27 % (N = 245) calves, 45.71 % (N = 245) juveniles, 31.84 % (N = 245) subadults and 19.18 % (N = 245) adults. Only four family units (36.36%; N = 11) are made up of adults only, all of which are groups of two individuals. The remaining family units (63.64 %; N = 11) are mixed, consisting of calves, juveniles, subadults and adults. The non-parametric Kolmogorov-Smirnov test showed that the distribution of buffalo by age group in the center and south is the same (P = 0.627) (Fig. 3).

In the central part of the park, proportion analysis showed that, according to t-test, there are more juveniles (P = 0.0001) and subadults (P = 0.0001)



Figure 2. Buffaloes observed in the CNP in the central zone (left) and in the southern zone (right).

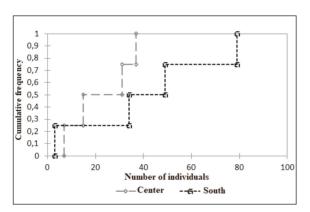


Figure 3. Distribution of buffalo by age group in the center and southern CNP.

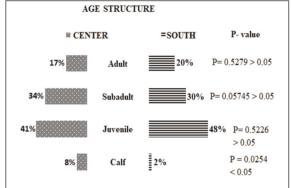


Figure 4. Composition of buffalo populations by age class in central and southern CNP.

than calves. However, no significant difference was observed between adults and calves (t-test, P = 0.108). Comparison of the proportions of juveniles and subadults showed that there was no significant difference between the proportions observed in these two age groups (t-test, P = 0.441). On the other hand, more juveniles than subadults were observed in the central part (t-test, P = 0.000). Finally, the number of subadults is significantly different from that of adults (t-test, P = 0.009).

In the southern zone of the park, a significant difference was observed between the number of calves and the other age classes, particularly juveniles (P = 0.0001), subadults (P = 0.0001) and adults (P = 0.0001) (Fig. 4). Proportions analysis showed that there are more juveniles than subaduls (t-test, P = 0.001) and adults (t-test, P = 0.0001). No significant difference was observed between the number of subadults and adults (t-test, P = 0.074). There

was also significant difference in the class composition of infants by zones.

Males and females, with average numbers of 22 and 41.75 individuals, account 35 % and 65 % respectively, resulting in an average sex ratio of 1 male to 1.65 females (Table 3). The proportion of females having young is 35.71 %. Based on the high proportion of individuals in the young age classes (juveniles 44.5 % and subadults 32.07 %) and the sex ratio 1.65 (1 male for 1.65 females), the buffalo population in CNP was considered viable.

DISCUSSION

Many of the videos viewed did not show buffalo visits or other events that could have triggered the camera. These artefactual detections considered false positives accounted for 30 % of the recordings. The

major problem with these recordings is that they consume a lot of memory and battery life. In addition, they waste a considerable amount of time when processing the data. The videos viewed without recordings were caused by wind and vegetation movement in the detection field of the device. Hence, it is important clearing the vegetation in the aircraft's field in anticipation of the gusts of wind that will occur. Other causes of false positives may be suspected, such as an animal leaving the camera's field of detection before it is triggered, or an animal entering the camera's field of detection without entering the field of view. There has often been the problem of identifying individuals with certainty. Indeed, in some cases the animal could not be identified because it was not completely in the field of view of the camera. In other cases, the quality of the image, often black and white, did not make it possible to accurately determine the identity of the individual when he presented many similarities with other individuals (case of hartebeest with buffalo calves). The lack of identification also led to a loss of data.

The analysis of the social structure of buffalo in the CNP based photographic images made it possible to identify eleven (11) different groups (herds) of 255 individuals with an average of 32 individuals per herd. In the center, four groups composed of 15 adults, 31 subadults, 37 juveniles and seven calves were identified. In the south, seven groups with 34 adults, 49 subadults, 79 juveniles and three calves were observed. It is however remarkable that the most represented age classes were juveniles and subadults, which reflect a good dynamics of the buffalo population. This result is different from that of Megaze et al. (2012) where the age structure was dominated by adults who accounted for 72.6 % of the total population. Our results do not corroborate those of Natta et

ai. (2011) where the bullato population of the classi
fied forest of Agoua located in central Benin appears
to be ageing (90 % adults and subadult) against only
10 % of juveniles. The poor observation of calves is
linked to the low mobility of these animals during
their young age (0 to 5 months), the small size of
these animals in relation to the height of the cameras
(1 m from the cameras), the very small age range
compared to the others (1 year instead of 2 years or
more for the others) and the low number of adults (of
reproductive age). Despite this difficulty of observa-
tion, the proportions of observations made in the two
zones remain valid. The low observation of adults,
which is a resource species, may be related to poach-
ing. On the other hand, the high number of juveniles
and subadults could be explained by the fact that these
animals are even less sought after by poachers and
are more fearful and therefore more vigilant. These
animals will thus take the necessary precautions to
move away from a human predator before the latter
sees them. Juveniles and subadults, most of which are
weaned, must feed and are therefore forced to travel
in search of food, which would also reflect their high
number. Calves were more numerous in the herds ob-
served in the center than those identified towards the
periphery. This high presence of calves in the herds
observed in the center would reflect the fact that buf-
falo retire to the central part of the park for calving.
Furthmermore, we obtain an average group size ex-
cluding solitary individuals of 23.18 individuals,
which is much higher than the value of 15.98
recorded by Megaze et al. (2012).

al. (2014) where the buffalo population of the classi-

The male to female sex ratio is one male for 1. 65 female. This result is different from that of Marzanne (2007) where the male / female sex ratio of buffaloes in the eastern Kalahari region of South Africa is two males to one female.

Sites	Trapping effort (camera days)	Number of buffalo catches	Useful captures	Number of buffalo individuals identified
Center	332 units	14	12	90
South	345 units	21	20	165
Average	338.5 units	17.5	16	127.5
Standard deviation	± 9.19	± 4.95	± 5.66	± 53.03

Table 2. Number of photographic catches and individuals of buffalo by area.

Age group	Sex Sex ratio			
Age group	Male	Female	Sex ratio	
Calf (< 12 months)	6	4	0.66	
Juvenile [13 - 25 months [39	77	1.98	
Subadult [25 - 48 months]	22	58	2.64	
Adult (> 48 months)	21	28	1.33	
Average	22	41.75	1.65	
Standard deviation	± 13.49	± 32.25	± 0.85	

Table 3. Sex ratio of buffalo catches in the central and southern CNP.

CONCLUSIONS

The present study constitutes a first scientific database on the population structure of buffalo in Comoe National Park. It made it possible to describe the different age classes of the buffalo populations observed in the south and center of the park. The average size of family units is 23.18 individuals with a maximum number of 77 individuals. Eleven different groups of 255 individuals were identified with an average herd size of 32 individuals. The different groups observed in the central and southern zones are composed of calves, juveniles, subadults and adults. The age structure is dominated by juveniles, followed by subadults, adults and then calves. The male / female sex ratio is one male for 1.65 female. The buffalo population in the center and south of the park is considered viable. It is capable of sustaining itself in the long term. Therefore, subsequent conservation actions must be carried out in relation to the riparian populations in order to maintain this population. However, the inbreeding rate and anthropogenic pressures have yet to be evaluated to complete these data.

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REFERENCES

- Aberham M., Gurja B. & Mundanthra B., 2012. Population structure and ecology of the African buffalo (*Syncerus caffer* Sparrman, 1779) in Chebera Churchura National Park, Ethiopia. African Journal of Ecology, 51: 393–401. https://doi.org/10.1111/aje. 12049
- Ancrenaz M., Andrew J.H., Ross J., Sollmann R. &Wilting A., 2012. Handbook for wildlife monitoring using camera-traps. BBEC II Secretariat publication, Kota Kinabalu, Malaisie, 57 pp.
- Bezerra B.M., Bastos M., Souto A., Keasey M.P., Eason P.,

- Schiel N. & Jones G., 2014. Camera trap observations of nonhabituated critically endangered wild blonde capuchins, *Sapajus flavius* (formerly *Cebus flavius*). International Journal of Primatology, 35: 865–907.
- Bouché P., 2016. Comptage aérien de la faune du Parc National de la Comoé et des deux zones de biodiversité. Rapport de mission, 64 pp.
- Caro T. & Riggio J., 2014. Conservation and behavior of Africa's 'Big Five'. Current Zoology, 60: 486–499. https://doi.org/10.1093/czoolo/60.4.486
- Craigie I.D., Baillie J.E.M., Balmford A., Carbone C., Collen B., Green R.E. & Hutton J.M., 2010. Large mammal population declines in Africa's protected areas. Biological Conservation, 143: 2221–2228. https://doi.org/10.1016/j.biocon.2010.06.007
- De Vos V. & Bengis R.G., 1994. The disease status of African buffalo in South Africa. In: Van Hoven, W., Ebedes, H. & Conroy (Eds.), Wildlife Ranching, A Celebration of Diversity, A. Pretoria: University of Pretoria.
- Djafarou T. & José K., 2013. Mission de suivi réactif au Parc national de la Comoé Côte d'Ivoire. Rapport de mission, 37 pp.
- Doré F., Grillet P., Thririon J-M. Besnard A. & Cheylan M., 2011. Premiers résultats d'un suivi à long terme sur une population de lézard ocellé *Timon lepidus* sur l'île d'Oléron. Revue d'Ecologie (Terre Vie), 66: 205–214.
- Fischer F., Gross M. & Linsenmair K.E., 2002. Updated list of the larger mammals of the Comoé National Park, Ivory Coast. Mammalia, 66: 83–92.
- Fuston P.J., 1992. Movements, habitat selection and population structure of buffalo (*Syncerus caffer caffer* Sparrman) in the Sabi Sand Reserve. M Sc dissertation, University of Pretoria.
- Hedwig D., Kienast I., Bonnet M., Curran B.K., Courage A., Boesch C., Kuhl H.S. & King T., 2018. A camera trap assessment of the forest mammal community within the transitional savannah-forest mosaic of the Batéké Plateau National Park, Gabon. African Journal of Ecology, 56: 777–790. https://doi.org/10.1111/aje.12497
- Hongo S., Nakashima Y., Akomo-Okoue E.T. & Mindonga-Nguelet F.L., 2016. Female reproductive seasonality and male influxes in wild mandrills (*Mandrillus sphinx*). International journal of primatology, 37 pp.
- Kadjo, B., Azani D., Tsague L. et Gomse A., 2014. Etat des lieux des populations d'Hippopotames et autres grands mammifères du Parc National de la Marahoué (Côte d'Ivoire). Agronomie Africaine, 26: 89–101.
- Kassé B.K., Kadjo B., Yaokokoré-Beibro H.K. & Foua-Bi, 2006. Inventaire, distribution et mesure de conservation des grands mammifères de la forêt classée de Badenou (Nord de la Côte d'Ivoire). Revue Ivoirienne des Sciences et Technologie, 7: 173–188

- Kely M.R., Kouakou C.Y., Bene J.C.K., Koffi A.D., N'guessan K.A. & Tiedoue M.R., 2019. Spatial distribution and period of activity of the forest elephant (*Loxodonta africana cyclotis*) at Tai National Park, south western Côte d'Ivoire. Journal of Applied Biosciences, 133: 13542–13551.
- Kouakou Y.C., Maho N.R. Tiédoué R., Ouattara A., Vergnes V. & Normand E., 2014. Etat de conservation du Parc National de la Comoé et de sa zone périphérique: Rapport de l'inventaire faunique par survol du 17 au 24 Avril 2014. Rapport WCF, Abidjan.
- Koueita M.K.K., Diomandé M. & Brou A.N., 2018. La problématique de gestion du Parc National de la Comoé (PNC) en Côte d'Ivoire, entre la survie des populations riveraines et la conservation de la biodiversité. European Scientific Journal, 14: 1857–7881. https://doi.org/10.19044/esj.2018.v14n35p391
- Maréchal C., Maurois C. & Chamberlan C., 1998. Size and structure of forest elephants groups (*Loxodonta africana cyclotis* Matschie, 1900) in the Odzala National Park, Republic of Congo. Mammalia, 62: 297–300.
- Marzanne C., 2007. The ecology of the African buffalo in the eastern Kalahari region, South Africa. Thesis, University of Pretoria, South Africa. 190 pp.
- McCarthy M.S., Després-Einspanner M-L., Samuel L., Mundry R., Lemoine S., Preis A., Wittig R.M., Boesch C. & Kuhl H.S., 2018. An assessment oh the efficacy of camera traps for studying demographic composition and variation in chimpanzees (*Pan troglodytes*). American Journal of Primatology, 80: e22904. https://doi.org/10.1002/ajp.22904
- Megaze A., Belay G. & Balakrishnan M., 2012. Population structure and ecology of the African buffalo (*Syncerus caffer* Sparrman, 1779) in Chebera Churchura National Park, Ethiopia. African Journal of Ecology, 51: 393–401. https://doi.org/10.1111/aje. 12049
- Mermod S., 2012. Etude et comparaison de la diversité spécifique des moyens et grands mammifères des aires protégées à statut de protection différent: Rukwa Game Reserve et Mlele Beekeepin Zone, région de Katavi-Tazani. Thèse de Bachelor en gestion de la nature, Haute Ecole du Paysage d'Ingénierie et d'Architechture de Genève, Suisse, 68 pp.
- Merz G., 1986. Mouvement patterns and group size of the African forest elephant, *Loxodonta africana cyclotis* in the Tai National Park, Ivory Coast. African Journal of Ecology, 24: 133–136. https://doi.org/10.1111/j.1365-2028.1986.tb00353.x.
- Nakashima Y., 2015. Inventorying medium and largesized mammals in the African lowland rainforest using camera trapping. Tropics, 23: 151–164. https:// doi.org/10.3759/tropics.23.151

- Natta A.K., Nago S.G.A. & Keke P.J.C., 2014. Structure et traits ethnozoologiques du buffle de forêt (*Syncerus caffer nanus*) dans la forêt classée d'Agoua (Centre Benin). Annales de l'Université de Parakou, Série Sciences Naturelles at Agronomie, 4: 39–52.
- Ndhlovu D.E. & Balakrishnan M., 1991. Grands herbivores dans la zone de gestion du gibier de la haute Lupande, vallée de Luangwa, Zambie. African Journal of Ecology, 29: 93–104. https://doi.org/10.1111/j. 1365-2028.1991.tb00990.x
- N'goran K.P., Maho N.R., Kouakou Y.C., Dowd D. & Herbinger I., 2010. Etat des ressources naturelles du Parc National de la Comoé et de sa zone periphérique. Rapport de l'inventaire faunique par survol aérien, 32 pp.
- O'Brien T.G., Kinnaird M.F. & Wibisono H.T., 2003. Crouching tigers, hidden prey: Sumatran tiger and prey populations in a tropical forest landscape. Animal Conservation, 6: 131–139. https://doi.org/10.1017/S1367943003003172
- OIPR, 2015. Plan d'amenagement et de gestion du Parc National de la Comoé, 116 pp.
- Pienaar U.D.E.V., 1969. Observations on developmental biology, growth and some aspects of the population ecology of African buffalo (*Syncerus caffer caffer* Sparrman) in the Kruger National Park. Koedoe, 12: 29–52.
- Prins H.H.T., 1996. Ecology and Behaviour of the African Buffalo: Social Inequality and Decision Making. Wildlife Ecology and Behaviour Series Vol. 1. London: Chapman & Hall.
- Querouil S., Magliocca F. and Gautier-Hion A., 1999. Structure of population, grouping patterns and density of forest elephants in north-west Congo. African Journal of Ecology, 37: 161–167. https://doi.org/10.1111/aje.1999.37.2.161
- Schweser, 2016. Mission d'appui à l'interprétation des images satellites du Parc national de la Comoé et sa zone périphérique, rapport de mission, 28 pp.
- Sinclair A. R. E., 1977. The African Buffalo: A Study of Resource Limitation of Populations. In Chicago University Press, USA.
- Sinclair A.R.E. & Grimsdell J.J.R., 1978. Population Dynamics of Large Mammals. Handbook No. 5, African Wildlife Foundation, Nairobi.
- Sinsin B., Akpona H. A. & Ahokpe E., 2006. Dénombrement aérien de la faune dans la Réserve de Biosphère de la pendjari (CENAGREF) (Rapport provisoire) PCGPN/Projet Pendja-ri-GTZ GAF Consulting, 35 pp.
- Theuerkauf J., Ellenberg H. & Guiro Y., 2000. Group structure of forest elephants in the Bossematié Forest Reserve, Ivory Coast. African Journal of Ecology, 38: 262–264. https://doi.org/10.1046/j.1365-2028.2000. 00236.x

- Turkalo A., 1996. Studying forest elephants by direct observation in the Dzanga clearing: an update. Pachyderm, 22: 59–60.
- Vanleeuwe H., Gautier-Hion A. & Cajani S., 1997. Forest clearings and the conservation of elephant (*Lox-odonta africana cyclotis*) in North East Congo Re-
- public. Pachyderm, 24: 46-52.
- White L.J., Tutin C.E. & Fernandez M., 1993. Group composition and diet of forest elephant, *Loxodonta africana cyclotis* Matschie 1900, in the Lopé Reserve, Gabon. African Journal of Ecology, 31: 181–199.

