



# Long-term changes in population size and the age structure and sex ratio of waterbuck in a Sudanian savannah of Burkina Faso

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## Abstract

The waterbuck (*Kobus ellipsiprymnus*), though widespread throughout Africa, is suspected to be declining overall. Data on population numbers and structure are lacking for many parts of its range, especially in West Africa, where the subspecies *defassa* is found. The aim of the present study was to evaluate the abundance, distribution and attributes of waterbuck populations from the Nazinga Forest Reserve, southern Burkina Faso. We investigated waterbuck population trends in the park using transect data collected in 1985–2019. For the more detailed analyses of population structure and distribution of the animals, we used census data gathered during 2019. Most animals were adults (46.6%), and the sex ratio was heavily skewed towards females (5:1). Most animals were concentrated along the larger rivers. There was no influence of poacher activity on waterbuck distribution. In the long term (1985–2019), the population dynamics of waterbuck can be roughly divided into two main periods: a phase of population increase from 1985 to 2005, and one of ongoing population collapse from 2007 to 2019. Although the declining population trend was obvious, coefficients of determination were low indicating that the years explained poorly the number of individuals and the number of sightings obtained. Waterbuck numbers in the Nazinga Forest Reserve are declining, but we found no single reason to explain this trend. It is likely that a combination of factors, including global warming (increased aridity) and illegal activities such as poaching, is responsible. Because there are probably multiple reasons for the observed waterbuck population decline in our study area, we suggest that a multifaceted approach should be adopted in order to enhance the conservation status of the local waterbuck populations.

## KEYWORDS

abundance, age structure, density, *Kobus ellipsiprymnus defassa*, sex ratio, West Africa

## Résumé

Bien que répandu dans toute l'Afrique, le cobe à croissant (*Kobus ellipsiprymnus*) semble être d'une manière générale en déclin. Les données sur les effectifs et la structure de la population font défaut pour de nombreuses parties de son aire de répartition, en particulier en Afrique de l'Ouest, où se trouve la sous-espèce *defassa*.

Le but de la présente étude était d'évaluer l'abondance, la répartition et les attributs des populations de cobes à croissant de la réserve forestière de Nazinga, au sud du Burkina Faso. Nous avons étudié les tendances de la population de cobes à croissant dans le parc à l'aide des données des transects recueillies en 1985 et 2019. Pour les analyses plus détaillées de la structure de la population et de la répartition des animaux, nous avons utilisé les données du recensement recueillies en 2019. La plupart des animaux étaient des adultes (46.6%) et le rapport des sexes observé a fait apparaître une forte proportion de femelles (5:1). La plupart des animaux étaient concentrés le long des grandes rivières. Aucune influence de l'activité des braconniers sur la répartition des cobes à croissant n'a été constatée. Sur le long terme (1985–2019), la dynamique de la population de cobes à croissant peut être approximativement divisée en deux périodes principales : une phase d'augmentation de la population de 1985 à 2005 et une phase de diminution continue de la population de 2007 à 2019. Bien que la tendance à la baisse de la population était évidente, les coefficients de détermination étaient faibles, indiquant que les années ne constituaient pas une explication suffisante du nombre d'individus et du nombre d'observations obtenues. Le nombre de cobes à croissant présents dans la réserve forestière de Nazinga est en baisse, mais nous n'avons trouvé aucune raison expliquant cette tendance. Il est probable qu'une combinaison de facteurs, notamment le réchauffement climatique (aridité accrue) et des activités illégales telles que le braconnage, en soit la cause. Comme il existe probablement de multiples raisons expliquant le déclin de la population de cobes à croissant observé dans notre zone d'étude, nous suggérons qu'une approche à multiples facettes soit adoptée afin d'améliorer l'état de conservation des populations locales de cobes à croissant.

## 1 | INTRODUCTION

The waterbuck (*Kobus ellipsiprymnus*) remains widespread across western, central, eastern and southern Africa and occupies a range of habitats such as grassy savannah plains and open woodland near permanent waterbodies (Nowak, 1991). Waterbuck are also an important game species (e.g. Berry, 1975; Cloete, Taljaard, & Grove, 2007), but they are often poached. According to the IUCN Red List (IUCN, 2020), the abundance of the species is suspected to be declining, but there is no evidence to confirm that the rate of decline meets the requirements of Near Threatened or Vulnerable status.

Although a number of studies on the ecology of the species have been published (e.g. Kassa, Libois, & Sinsin, 2008; Melton, 1978, 1983; Spinage, 1968, 1969; Tomlinson, 1978), reliable population estimates are scarce. This is especially true for waterbuck populations in the Sudanian savannahs of West Africa (subspecies *defassa*; Lorenzen, Simonsen, Kat, Arctander, & Siegismund, 2006), where the species is perceived to be declining (Chardonnet & Chardonnet, 2004). Although some preliminary surveys have been undertaken on the population status of the species in Zakouma, Chad (Mackie, 2004), Pendjari, Benin (Rouamba & Hien, 2004), Gashaka Gumti, Nigeria (Nicholas, 2004) and Gambia (Jallow, Touray, & Jallow, 2004), few quantitative studies are

currently available (i.e. in Benin: Djagoun, Codron, Sealy, Mensah, & Sinsin, 2013; Kassa et al., 2008), and little is known of the population dynamics of any West African waterbuck population.

In Burkina Faso, where the waterbuck is found primarily in protected areas in the south of the country, some estimate data for the species (alongside other ungulates) are available for the gallery forests of the Comoé-Léraba region (Hema, Ouattara, Karama, et al., 2017) and the Nazinga region (Hema et al., 2018). In this study, we report abundance, density, group size, sex and age structure of waterbuck populations in the Nazinga Forest Reserve (FC/RGN). More specifically, we answer to the following key questions:

1. Is the population structure of Burkina Faso waterbuck consistent with that studied elsewhere in Africa in terms of sex ratio and age structure?
2. Are the yearly density estimates of Burkina Faso waterbuck comparable with those observed in East Africa or, as expected on the basis of the widespread threatened status of West African ungulates, are they lower than in other regions of the continent?
3. Is there any long-term consistent yearly trend (increasing, decreasing, stable) of waterbuck population in Burkina Faso?

Our results will serve to highlight the conservation needs of the species in West Africa, in the light of the extreme challenges that ungulates are currently facing in the West African savannahs due to extensive habitat loss and poaching (e.g. see Bouché et al., 2016).

## 2 | METHODS

### 2.1 | Study area

The field study was carried out in the FC/RGN, a protected area, 97,436 ha in area, in south-central Burkina Faso (West Africa) (Figure 1). The vegetation of the study area is Sudanian-type woody savannah vegetation dominated by *Detarium microcarpum*, *Burkea africana*, *Azelia africana*, *Isoberlinia doka*, *Pteleopsis suberosa*, *Acacia dudgeoni*, *Gardenia* spp., *Vitellaria paradoxa*, *Terminalia* spp. and *Combretum* spp. The dominant perennial herbaceous plants are *Andropogon ascinodis* and *Schizachyrium sanguineum*. The woody species of the alluvial valleys are *Anogeissus leiocarpus*, *Daniellia oliveri* and *Mitragyna inermis*, associated with *Andropogon gayanus* and *Vetiveria nigritana* as perennial herbaceous dominant of this type of environment (Dekker, 1985; Yameogo, 1999). Along the waterbodies,

relatively closed, 'wet' habitats made up of gallery forests can be seen; this formation is dominated by large woody species such as *Anogeissus leiocarpus*, *Khaya senegalensis*, *Diospiros mespiliformis* and *Piliostigma thonningii*, and for the herbaceous layer by grasses such as *A. gayanus* and *Pennisetum angustum*. Annual rainfall in the region of FC/RGN is about 1,500 mm.

In the study area, there still exist large populations of ungulates (*Tragelaphus scriptus*, *Sylvicapra grimmia*, *Alcelaphus buselaphus*, *Hippotragus equinus*, *Phacochoerus africanus*; cf. Hema et al., 2018) and *Loxodonta africana*, with *Crocuta crocuta* being the largest predator (Hema et al., 2019). Illegal poaching is present, especially in the boundary strips of the park (Hema, Ouattara, Parfait, et al., 2017), as well as other illegal activities (see Table S1).

### 2.2 | Data collection

Large mammal censuses in FC/RGN have been undertaken in the park since 1981 along 30 equidistant 1.4-km transects (Figure 1), during the months of February to early April. In 2019, we performed all transects during 19–25 March. Data collection protocols were first set up in 1981 (as occasional and somewhat unstandardised

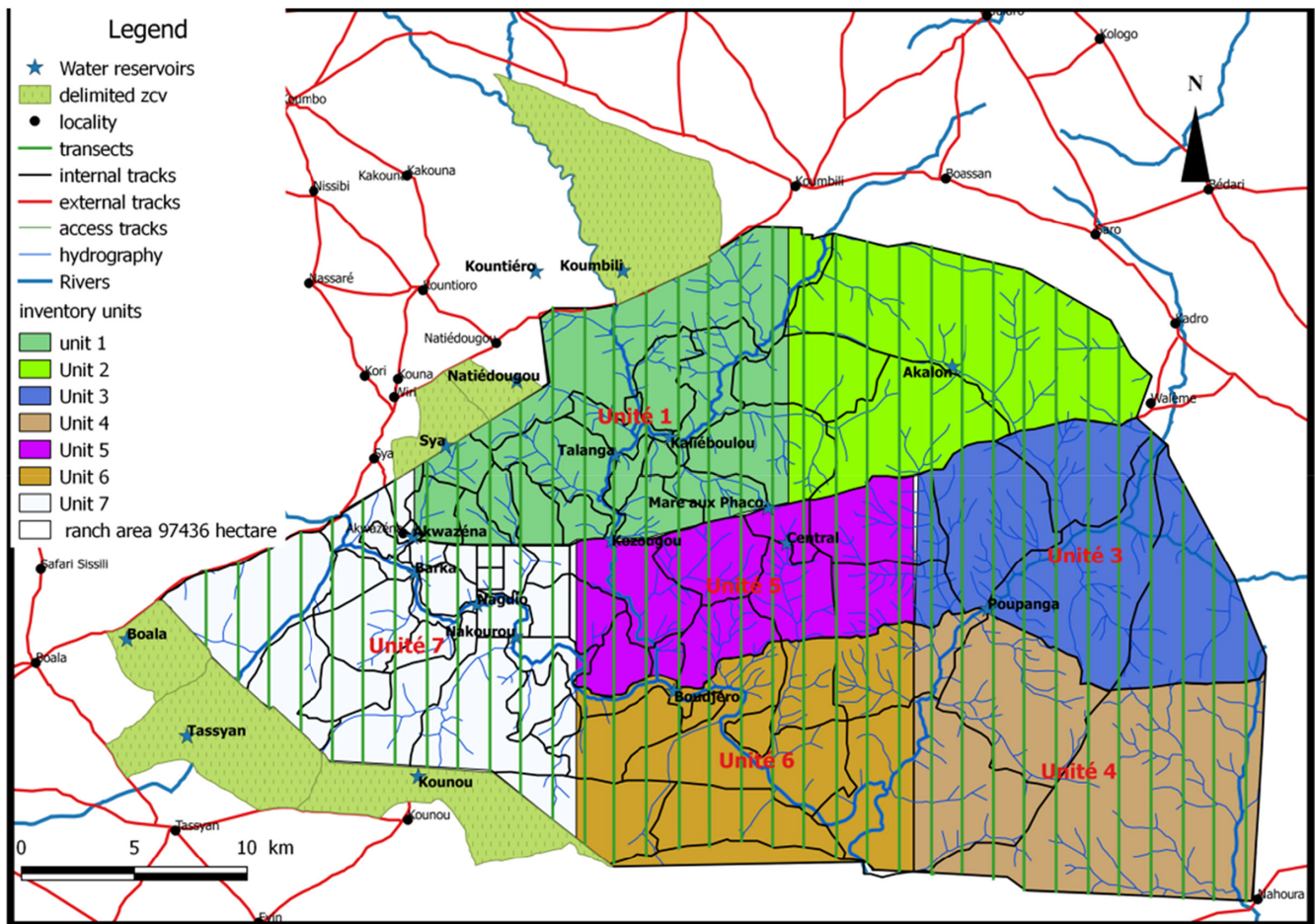


FIGURE 1 Map of the study area, showing the seven zones in which, the protected area was divided [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

surveys) and revised by O'donoghue (1985) after which standardised line transects were to be walked each year to obtain comparable estimates of the local abundance of animals. Sexes of adults were distinguished based on the presence/absence of horns (present in males). We defined juveniles as those individuals that were less than 8 months old, and subadults as those between 8 months and 1.5 years old for females and between 8 months and 2 years old for males. We used relative size and the appearance of the horns in males to determine the relative age of the observed animals.

All transects were oriented in a south–north direction throughout the entire park. The entrance and exit to each transect were signposted using a numbered metal disc fixed on a tree at eye level. During each annual census, the same 79 transects (691.811 km) in the seven FC/RGN zones were covered during the dry season. The methodology employed was always identical: after a training session, transects were walked by 12 teams of three people each; each team consisting of a team leader and two observers (i.e. a villager and a tracker). We applied unlimited bandwidth linear transects (Buckland, Anderson, Burnham, & Laake, 1993; Buckland et al., 2001; Burnham, Anderson, & Laake, 1980).

During each annual census, teams walked along the centre of a transect, equipped with binoculars, GPS, compasses, rangefinders, maps, and cards on which to note the species, number of individual animals observed, their sex and age, as well as radial distance, viewing angle, activity and signs of illegal human activities (bullets, tree cutting, human tracks, motorbike tracks, tree-branch thinning and pastoralism tracks). Animal observations were georeferenced using a Garmin 64S GPS, and compasses were used to measure angle with rangefinders to determine radial distances. All surveys started at 6 a.m., immediately after which visibility conditions allowed the surveyors to clearly see the animals, even at a distance.

### 2.3 | Data analysis

In this study, we investigated waterbuck population trends in FC/RGN using transect data for the period 1985–2019. Data for 1985–2007 have already been published (Hema et al., 2018), and previous census results (1981–1985) were not used because a different field method was employed during this period (O'donoghue, 1985). For the more detailed analyses of population structure (age and sex ratio) and distribution of the animals in the park, we used census data gathered in 2019 as the same type of data was not collected in the previous years.

QGIS 2.18.10 was used to map sighting records and for determining waterbuck concentration zones. QGIS was also employed to measure distances between the different waterbuck groups, and distances of waterbuck groups from the nearest waterbody, from paths/tracks and from signs of illegal human activity. We used the standardised Morisita dispersion index ( $I_p$ ) (Zar, 1999) to measure spatial dispersion.  $I_p$  ranges from  $-1.0$  to  $+1.0$ . The random dispersion modes (Poisson distribution) give an  $I_p$  equal to zero, while uniform distribution modes have an  $I_p$  less than zero. Grouped distribution modes have an  $I_p$  greater than zero.

On the basis of the number of contacts and the number of waterbuck individuals, we calculated the proportion of sex and age classes in the population for 2019, as well as the density (measured as the Kilometric Index of Abundance, KIA, and as the Kilometric Index of Contacts, KIC) (Maillard, Calenge, Jacobs, Gaillard, & Merlot, 2001). In KIC, we considered all independent sighting events; so, for instance, if we observed five individuals in a group and one solitary individual apart, the count was 6 for KIA but just 2 for KIC.

$KIA = (\text{number of individuals} / \text{numbers of kilometres covered})$ .

$KIC = (\text{number of observations} / \text{numbers of kilometres covered})$ .

In these formulas, the number of kilometres covered represents the sum of the total distance of the transects.

We calculated the total number of encountered individuals among transects from 1985 to 2019, but with some years in which these numbers were not available due to the lack of field surveys. We estimated waterbuck density with the distance sampling method (Buckland et al., 1993; Thomas et al., 2010), using the DISTANCE software, version 7.2. This method makes it possible to estimate the population density by calculating the probabilities of detection of animals as a function of their distance to the transect. The general formula for estimating the density of waterbuck groups is as follows (Burnham et al., 1980):

$$\hat{D} = \frac{n\hat{f}(0)}{2L}$$

where  $\hat{D}$  is the density estimator;  $n$  is the sample size (number of observations) of observations;  $L$  is the total length of the transects; and  $\hat{f}(0)$  is the estimator of the effective half-width of the band which is the detection probability function estimated by the software through robust mathematical models related to the probability density function.

The following estimators that are considered as the most robust (Buckland et al., 1993) were analysed: the cosine and polynomial-tuned uniform function, the cosine and Hermite polynomial-adjusted seminormal function, and the cosine and simple polynomial-adjusted chance rate function. The choice of the model was made according to the following criteria:

1. the value of the effective strip width was close to the calculated mean perpendicular distance and the value obtained with the threshold method;
2. the expected group size (calculated by DISTANCE software) was closest to the mean group size (calculated on Excel);
3. the Akaike information criterion (AIC) value was the lowest one, and the visual observation of the curve of the detection function was good;
4. chi-square value was not significant.

Two types of densities were estimated: the density of groups (DS) estimates the number of contacts with animal groups per unit area (in our case per  $\text{km}^2$ ); the density of individuals ( $D$ ) estimates the number of single animals per unit area (also per  $\text{km}^2$ ).

To evaluate age structure of the waterbuck population, we distinguished three age classes: adults, subadults and juveniles.

We used observed-versus-expected chi-square test to check whether adult sex ratio was even or not, and Pearson's chi-square to test for differences in the frequency of waterbuck sightings among zones of the protected area. Correlations between (Box-Cox-transformed) number of observed individuals and (a) (Box-Cox-transformed) distances to illegal activities, (b) (Box-Cox-transformed) distances to the nearest path/track used by people and (c) (Box-Cox-transformed) distances to the nearest water point were carried out by Pearson's correlation coefficient. Correlation between estimated yearly KIA and the (arcsine) percentage of females in the sample size was performed using a Pearson's product-moment correlation coefficient.

Box-Cox transformation (Box & Cox, 1964) was used to normalise variables whose data were not Gaussian (i.e. number of waterbuck individuals and distance separating the waterbuck groups to the illegal activities and to the nearest water points). The statistical software SPSS Statistics 21 and Past 3.0 were used to perform all analyses.

### 3 | RESULTS

#### 3.1 | Population structure by sex and by age (year 2019)

A total of 25 visual contacts of waterbucks were recorded during our 2019 census, with a total number of 103 observed individuals.

**TABLE 1** Synthesis of the density and population size estimates obtained by DISTANCE methodology on the bushbucks at the study area in southern Burkina Faso

Parameter	Estimate
DISTANCE model	Hazard rate/Cosine
$f(0)$	0.0118
Var [ $f(0)$ ]	0.02
Width of the W band (m)	85.011
Density ( $D$ ) of waterbucks per km <sup>2</sup>	0.515
Variance of ( $D$ )	1.164
95% upper confidence limit	1.359
95% lower confidence limit	0.195
% coefficient of variation	51.60
Estimate of waterbuck population size	502
95% upper confidence limit	1,325
95% lower confidence limit	190
$\chi^2$	5.184
$p$	0.269
$df$	4
Number of individuals per group (range)	1–18
Density of groups per km <sup>2</sup>	0.212
Mean number of individuals per group	4.12

Of the 25 visual contacts, in 13 cases the animals were fleeing or on alert, while in the rest of cases they were either resting or walking or grazing. Adults represented 46.6% of the observed population ( $n = 103$ ), subadults were 6.8%, juveniles were 17.5%, and undetermined individuals were 29.1%. Sex ratio was heavily skewed towards females (5:1; observed-vs.-expected  $\chi^2 = 24$ ,  $df = 1$ ,  $p < 0.0001$ ). The size of the great majority of the groups ranged 2–6 (Figure S1).

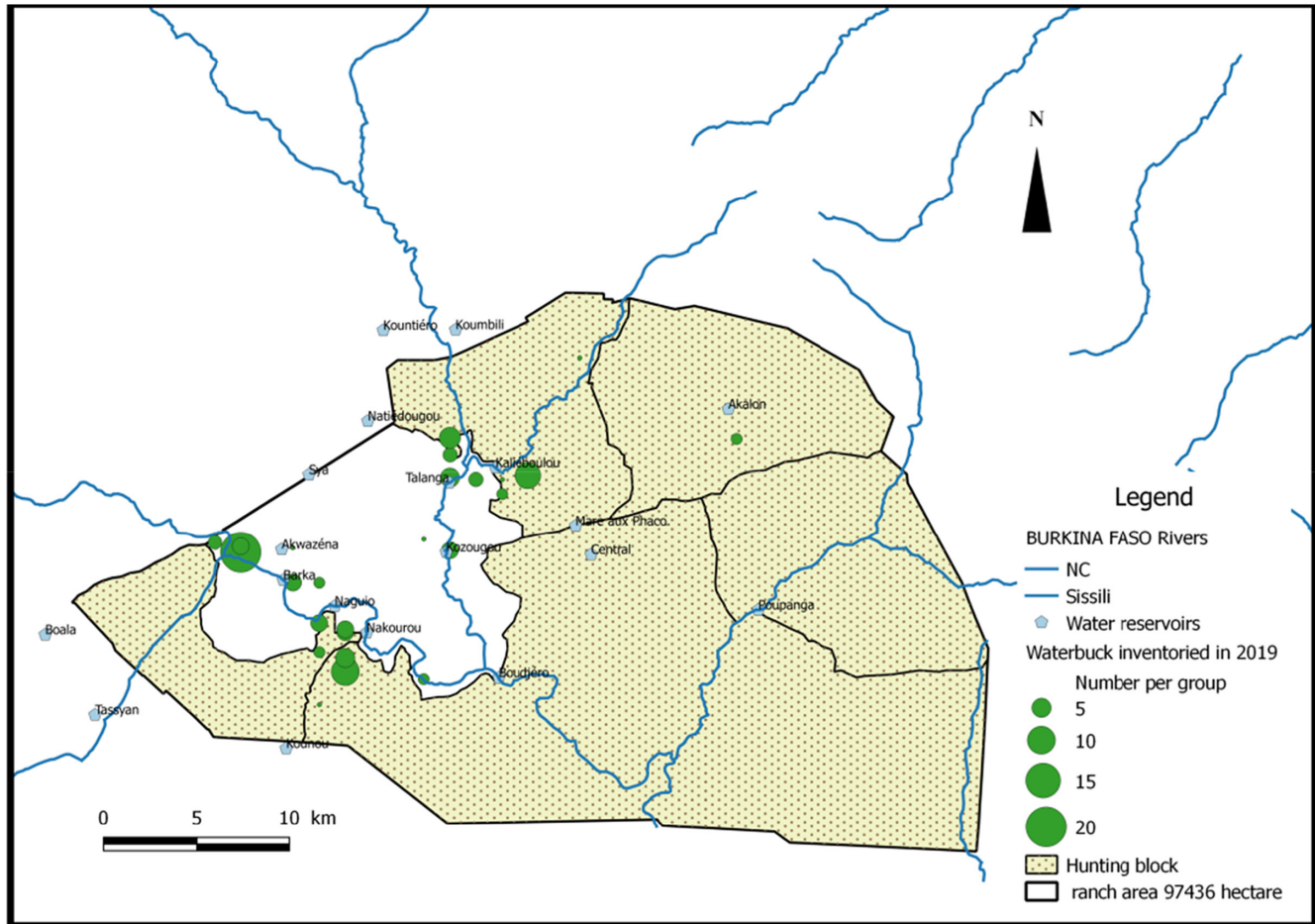
#### 3.2 | DISTANCE-generated estimates of population parameters (year 2019)

The probability of detecting waterbucks according to the hazard rate/cosine model (Figure S2) showed that there were a small number of observations between 0 and 30 m compared to observations made between 31 and 49 m. The summarised results on the estimates of parameters of the waterbuck population by the hazard rate/cosine model are given in Table 1. The population estimate showed wide confidence limits (Table 1), and there was large variation in the sizes of the various groups observed (up to 18 individuals; Figure S1). The fit between the observations and the visibility curve was also not good (Figure S2). The calculated population size in FC/RGN for 2019 was 502 animals (see Table 1 for the confidence intervals of the estimate).

#### 3.3 | Density and spatial patterns of occurrence (year 2019)

Waterbuck sightings in FC/RGN were concentrated along the principal rivers: 96% of the species' sightings were within 1.8 km of the water, mainly around the artificial perennial waterbodies built along some streams for elephants (Figure 2). Most observations occurred in the core conservation area (density of individuals was 0.39 per km<sup>2</sup>), but very few were in the hunting area (density = 0.05 individuals per km<sup>2</sup>). These two sectors differed significantly in terms of waterbuck density: Pearson's  $\chi^2 = 31$ ,  $df = 1$ ,  $p < 0.001$ . We obtained a KIC = 0.036 and a KIA = 0.149. The dispersion analysis also revealed that waterbuck groups were spatially aggregated (Morisita  $I_p = 0.568$ ;  $\chi^2 = 902.3$ ,  $df = 78$ ,  $p < 0.0001$ ).

Regarding illegal activities, a total of 146 signs could be counted along the transects during our 2019 surveys (Table S1). These activities were observed throughout FC/RGN but were statistically concentrated (dispersion index of Morisita:  $I_p = 0.521$ ) in its eastern side where waterbucks were not observed (Figure S3). The distance from the nearest sign of poacher activity did not influence the number of observed individuals ( $r = 0.04$ ,  $n = 25$ ,  $p = 0.842$ ), and the same was true for the distance from the nearest waterbody ( $r = -0.21$ ,  $n = 25$ ,  $p = 0.324$ ) as well as for the distance from the nearest path/track ( $r = 0.191$ ,  $n = 25$ ,  $p = 0.360$ ).



**FIGURE 2** Distribution of the waterbuck sightings in the study area, during the year 2019 [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com)]

### 3.4 | Yearly population trends: 1985–2019

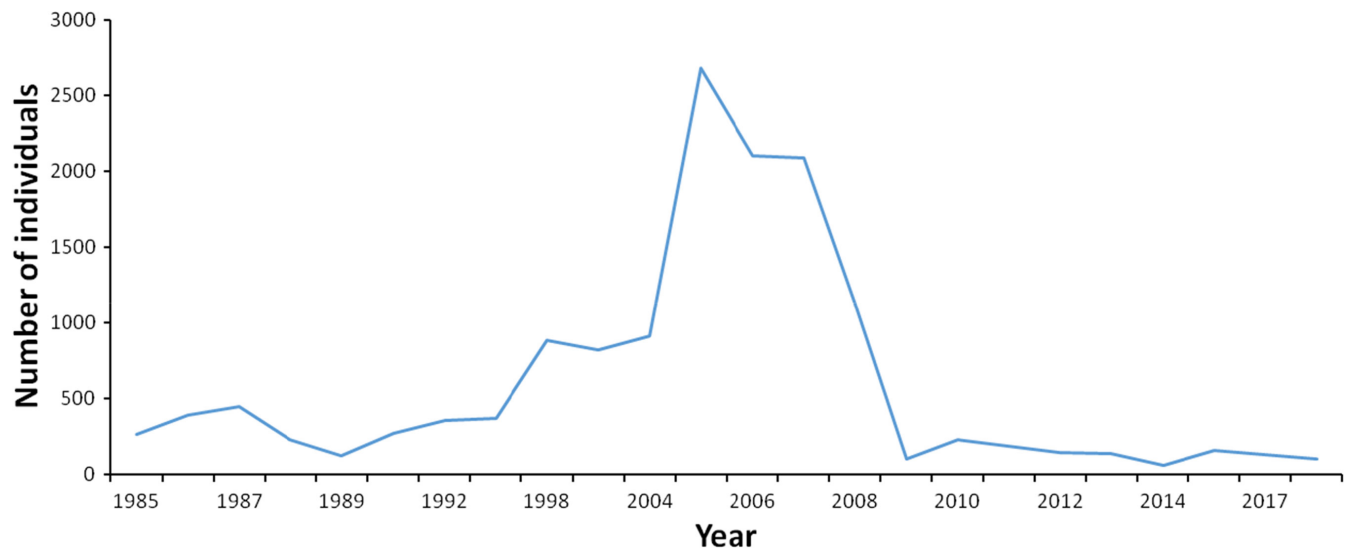
During the period 1985–2019, the population dynamics of the studied waterbuck population can be roughly divided into two main periods (Figure 3): (a) a population increase between 1985 and 2005 (Spearman's rank correlation coefficient:  $r_s = 0.692$ ,  $p < 0.05$ ) and (b) an ongoing population collapse from 2007 to 2019 ( $r_s = -0.715$ ,  $p < 0.01$ ). There was also an annual slightly, nonsignificant, negative trend ( $r_s = -0.520$ ,  $p = 0.123$ ) in the number of individual waterbucks observed during the period 2008 to 2019 (Figure 3). However, in this latter phase, the coefficients of determination ( $R^2$ ) were low (respectively, 0.1366 (number of individuals) and 0.1803 (contact numbers)), thus indicating that the years explained poorly the number of individuals and the number of contacts obtained. In general, both the number of contacts and the number of individuals showed a sharp decline from 2010 to 2014 followed by a slight increase from 2014 to 2016.

The interannual observed sex ratio was not affected by the density estimates: indeed, there was no correlation between estimated yearly KIA and the (arcsine) percentage of females in the sample size ( $r = 0.086$ ,  $p = 0.893$ ).

## 4 | DISCUSSION

### 4.1 | Population structure by sex and by age

In FC/RGN, waterbuck groups are typically mixed families of adult females and juveniles, with females being largely dominant over males (5 to 1). Such a skewed sex ratio was very different from that reported in the literature: for instance, in Uganda, the male:female sex ratio was 1:1.6 (Spinage, 1970), and in Ethiopia, it was 1:1.72 (Tsegaye, Bekele, & Balakrishnan, 2015). However, within a national park in Tanzania, the sex ratio was 3:1 in favour of females, and outside the same national park, it was 2:1 in favour of females (Caro, 1999). Thus, it seems that the adult sex ratio is very variable in the species, with poor predictability on the basis of habitat characteristics, exposure to exploitation or resources available, but almost invariably with a higher number of adult females compared to the adult males. In ungulates, males are killed disproportionately to their abundance compared to adult females with local predation directly affecting patterns of sex ratio variation among adults (Berger & Gompper, 1999). Since differences in survival of sexes may arise as a direct consequence of greater age-specific mortality among



**FIGURE 3** Yearly trend (period 1985–2018) in the number of individuals of waterbucks at the study area in southern Burkina Faso [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

males, with selection operating differently on males and females (Berger & Gompper, 1999), we suggest that the same should be possibly the case at our study area with predation risks (especially by hyaenas and crocodiles) being much higher in males than in females. There are no available data on whether waterbuck males are indeed more preyed upon compared to females in FC/RGN. It is also possible, however, that the strong sex ratio deviation could be due to a higher incidence of illegal hunting on males or to behavioural differences between females and adult males causing less detectability in the latter. Although there are insufficient data to test any of these hypotheses, it is clear that the long-term changes in age structure and sex ratio of the studied waterbuck populations played a minor role in the decline of numbers. Given this, the effects of hunting and changes in the animals' behaviour should be more adequately assessed with ad hoc studies.

Data on age structure of waterbuck populations in different parts of Africa are still limited. However, our data were comparable to other populations: in Ethiopia, for instance, adults accounted for 55.65%, subadults for 23.5% and juveniles for 21.06% (Tsegaye et al., 2015). However, if we exclude indeterminates (29%) from our study, the proportions of age classes are as follows: adults, 65%; subadults, 10%; and juveniles, 25%, scarcely comparable to that of Ethiopia (Tsegaye et al., 2015). The ratio of adults/juveniles averaged 2.66 in FC/RGN, which was very similar to that observed in (=2.52) South Africa's Kruger National Park (Owen-Smith & Mason, 2005). Thus, neither the sex ratio nor the age structure is comparable to that from other studies, and, in general, transect surveys can be suboptimal in determining the actual sex ratios and age structure of savannah ungulates (Hema et al., 2020). In ungulate populations, age structure is an important determinant of adult survival as the mean survival is associated with age of adults (Festa-Bianchet, Gaillard, & Côté, 2003). More studies are needed to understand annual variations in age structure and their implications for survival.

## 4.2 | Density and associated parameters

Our study revealed that (a) waterbuck density varied significantly among the different FC/RGN zones (ranging from 0.05 individuals per km<sup>2</sup> up to = 0.39 individuals per km<sup>2</sup>) and that (b) the various groups showed clumped spatial pattern of distribution. The various groups observed tended to be nonrandomly distributed within the FC/RGN area but showed 'spatial contagion' effect between each other. When we tried to identify the main factor explaining this 'aggregated pattern', we rejected any linear relationship with both anthropic negative factors (distance from paths/tracks and distance from sites with sign of illegal activities) and environmental positive factors (distance from waterbodies). However, our survey was undertaken during the dry season when water is clearly a limited resource, and since these ungulates are highly water-dependent species (e.g. Melton, 1978), there was obviously a greater chance that they are grouped around the permanent water points (Hien, Jenks, Klaver, & Wicks, 2007). This would explain the strong aggregative distributions of their groups around permanent water points without any linear relationship with the distance from the waterbody itself.

We estimated an average density of 0.25 individuals × km<sup>2</sup> and a mean group density of 0.21 × km<sup>2</sup>. Although the individual density observed at FC/RGN was much lower than the highest observed so far in Africa (at Lake Nakuru in Kenya, with over 10 individuals × km<sup>2</sup>; Kutilek, 1974), it was still higher than in most areas: indeed, the mean density is 0.05–0.15 × km<sup>2</sup> in areas where the species is reasonably common and 0.2–0.9 × km<sup>2</sup>, more frequently 0.4–1.5 × km<sup>2</sup> in remote areas that are presumably in good habitat status (Furstenburg, 2005). Thus, our data suggest that waterbuck population abundance is still high in FC/RGN despite the observed declining population trend. Waterbuck density at Lake Nakuru, as a comparison, was likely to have been artificially high to be stable, and we suggest that this extraordinary concentration of animals was perhaps unusual due to abnormally favourable ecological conditions

(high food resource availability in an exceptional year, migrations or something equivalent) that do not occur in the other above-mentioned areas. In fact, high densities of *K. ellipsiprymnus* populations have been observed during very favourable years. For example, in FC/RGN, in 2010 there was a density fourfold higher than in 2014 (Figure 3), so annual variability should be mentioned as an important factor when making comparisons between populations, and an important factor to be considered in further studies of the demography of this species. Since the data were not analysed with the same statistical methodology in the various areas of Africa studied so far, the density estimates reported in the various studies may not be totally comparable. DISTANCE methodology also requires about 60 contacts to obtain unbiased density estimates (Buckland et al., 1993, 2001), whereas our study achieved an insufficient number of contacts ( $n = 25$ ) for obtaining a robust estimate. Thus, the density values reported in this paper should be considered merely as preliminary. Similarly, previous estimates of waterbuck densities using DISTANCE methodology in West Africa were also biased by too small sample sizes: for instance, Brugière et al. (2005) in Guinea and also Cornelis (2002) in our same study area. Group density at FC/RGN was consistent with published studies (range  $0.27\text{--}0.96 \times \text{km}^2$ ; see Brugière et al., 2005).

On the basis of the KIA estimates (that is least prone to statistical biases than DISTANCE but obviously more empirical), our data ( $\text{KIA} = 0.149$ ) suggest a much higher abundance in the FC/RGN savannah than in the gallery forests of south-west Burkina Faso (Comoé-Léraba National Park:  $\text{KIA} = 0.022$ ; Hema, Ouattara, Karama, et al., 2017). In the latter, available habitat is differently shaped as it basically exists along the banks of the river Comoé (Hema, Ouattara, Karama, et al., 2017).

### 4.3 | Yearly population trends: 1985–2019

Our study revealed that in FC/RGN, waterbucks had a phase of population growth between 1985 and 2005 and then a significant decrease between 2007 and 2019. However, for the declining phase, the determination coefficient and sample size (10 years) are low and the strength of the negative tendency cannot be totally reliable. We consider that the low value of the coefficient of determination is due to the low slope in the straight line after 2008 so that a relatively small population decline cannot be explained as having such large variations between years. In other words, a leap up from a new year can make the negative trend disappear. Hema et al. (2018) analysed the fluctuations in population size of waterbucks in FC/RGN during 1985–2008 and found that these fluctuations were stronger than those for other sympatric ungulates. It should be taken into account that, concerning the period 2009–2019, the population estimates showed wide confidence limits because the number of contacts was relatively low and there was large variation in the sizes of the various groups observed, thus reducing the estimate performances of the DISTANCE method. The low number of contacts also produced the suboptimal fit between the observations and the visibility curve as estimated by DISTANCE.

Why then did the population trend become constantly negative after 2005 and with a clear collapse after 2007? Previous studies uncovered a significantly positive correlation between rainfall and population size of *K. ellipsiprymnus* (Bouché et al., 2016; Ogutu, Piepho, Dublin, Bhola, & Reid, 2008), and at FC/RGN, it was demonstrated that the probability of high population sizes of this species increased with an increase of precipitation in August (Hema et al., 2018). Therefore, it can be hypothesised that the increasing aridity due to global warming that is affecting the Sahel region may be an important cause of the decreasing trend of the waterbuck population at the study area. Other reasons, for instance the changes in the management schemes adopted by the authorities (responsible for considerable population fluctuations in the warthog *P. africanus*; see Hema, Douamba, et al., 2017), are least likely to be involved in this declining trend. These management strategies implemented by the FC/RGN managers involved the strengthening of the FC/RGN surveillance teams, the development of reservoirs and saltwater basins, and the permanent monitoring of the fire system. Indeed, waterbuck population fluctuations did not mirror the changes in management type observed in warthogs (Hema, Douamba, et al., 2017). Illegal exploitation by poachers may also be an additional reason for the declining trend of the local waterbuck population (Hema, Ouattara, Parfait, et al., 2017). Indeed, other two ungulate species are declining at FC/RGN (*Ourebia ourebi* and *Sylvicapra grimmia*), and their decline has been attributed to overhunting because these species were highly valued in the illegal bushmeat trade (Hema, Ouattara, Parfait, et al., 2017). In addition, in another protected area of southern Burkina Faso (Comoé-Léraba), Hema, Ouattara, Karama, et al. (2017) uncovered a negative correlation between hunting intensity and KIA estimates for waterbucks as well as for *Kobus kob*, *Ourebia ourebi* and *Cephalophus rufilatus*. Nonetheless, there was no direct evidence that poaching was a main reason for the continued decline of the species in our study area. Overall, it is likely that a combination of factors may explain the negative population trends of waterbucks in FC/RGN. Factors, including global warming (by increasing aridity) in combination with illegal activities such as poaching, may be responsible. We suggest that a multifaceted approach should be adopted in order to enhance the conservation status of the local waterbuck populations, with also an analytical approach using threat analysis (Salafsky & Margoluis, 1999).

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### CONFLICT OF INTEREST

The authors declare no conflicts of interest.

### DATA AVAILABILITY STATEMENT

The authors declare that their data will be provided in case of request by interested readers.

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