

Line-transect data may not produce reliable estimates of interannual sex-ratio and age structure variation in West African savannah ungulates

Emmanuel M. Hema¹⁻³, Yaya Ouattara⁴, Maomarco Abdoul Ismael Tou⁴, Giovanni Amori^{5*}, Mamadou Karama⁴ and Luca Luiselli^{3,6,7}

¹Université Dédougou, UFR/Sciences Appliquées et Technologiques, Dédougou, Burkina Faso; ²Laboratoire de Biologie et Ecologie Animales, Université Ouaga 1 Prof. Joseph Ki Zerbo, Ouagadougou Burkina Faso; ³Institute for Development, Ecology, Conservation and Cooperation, Rome, Italy; ⁴Secrétariat Exécutif, AGEREF/CL, Banfora, Burkina Faso; ⁵Research Institute on Terrestrial Ecosystems, CNR, Rome, Italy; ⁶Department of Applied and Environmental Biology, Rivers State University of Science and Technology, Port Harcourt, Nigeria; ⁷Département de Zoologie, Faculté des Sciences, Université de Lomé, Togo

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Abstract: Adult sex ratios and age structures are important wildlife population parameters, but they have been poorly investigated in ungulate species in West African savannahs. We used line transects to investigate these parameters in 11 ungulates from a protected area in south-western Burkina Faso during the period 2010-2018. We created an empirical model of “detectability” for each species based on its main ecological characteristics (habitat and group size) and body size, and then compared the observed interannual inconsistency in sex ratios and age structures with the a priori detectability score. Six out of 11 species showed low interannual inconsistency in sex ratio and age structure. In 82% of the study species, however, the predicted detectability score matched the observed score, with two exceptions being *Tragelaphus scriptus* and *Syncerus caffer*.

Key words: Ungulates; population structure; Comoé-Léraba; line transect; predictive “detectability” model.

Introduction

Expert-based approaches have been increasingly used in applied ecology studies, with a focus on management actions, especially in sites with difficult logistics and when the target species are poorly known or difficult to survey in the field (e.g., Amici and Battisti 2009; Battisti and Luiselli 2011; Battisti et al. 2014).

Studies on adult sex ratio and age structure (i.e., the proportion of juveniles versus adults) are very important in order to define population parameters of animals (e.g., Caughley 1977), including wild ungulates (e.g., Karanth and Sunquist 1992; Berger and

*Corresponding author. E-mail: giovanni.amori@cnr.it

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Gompper 1999; Clutton-Brock and Coulson 2002; Festa-Bianchet et al. 2003; De Cesare et al. 2012). These studies are also important to help define management and conservation approaches for ungulates (e.g., Ginsberg and Milner-Gulland 1994; Gaillard et al. 2008). It is therefore not surprising that ecologists have long studied demographic parameters in ungulates in East and Southern Africa, where these mammals are often observed in abundant, easy-to-observe, populations (e.g., Dasmann and Mossman 1962a, 1962b; Bourliere 1965; Spinage 1972; Hillman 1986; Mason 1990; Owen-Smith and Mason 2005). In contrast, Central and West African ungulates have been poorly studied with regard to sex ratio and age structure (Turkalo and Klaus-Hügi 1999), especially because their populations are small sized, heavily fragmented and uneasy to be observed.

One of the most intensely used sampling techniques for determining aspects of population demography of African ungulates is the line-transect survey (e.g., Plumptre 2000; Ogutu et al. 2006; Sutherland 2006; Viquerat et al. 2012). However, although several line-transect studies are available, it is not fully understood whether line-transect sampling can provide reliable data on adult sex ratios and juvenile-to-adult ratios for the various species of ungulates, or whether the species-specific ecological characteristics of the various species may affect the reliability of the collected data, such as through biases in the relative detectability of the various target species.

From 2010 to 2018, we used line transects to study 11 ungulate species in a protected area in south-western Burkina Faso (West Africa). Our aim was to test the viability of using line transects to estimate the interannual inconsistency of sex ratios and age structures. We created a simple a priori model predicting the “performance” of the line-transect surveys. We used species-specific characteristics of body size, habitat use, and group size to estimate a “detectability” score for each of the 11 ungulate species. A species having a high “detectability” score would likely have the most consistent sex ratios and age structures across years. Thus, we divided the 11 species into three groups based on degree of detectability: high, medium, and low. Then, we compared the predicted model with empirical field data to assess the viability of line-transect surveys for assembling reliable data on sex ratios and age structures of West African savannah ungulates.

Materials and methods

Study area

This study was carried out during the dry season (February–May) over an 8-year period (2010–2018) in the Forest Classée et Réserve Partiel de Faune / Comoé-Leraba (FCRPF / CL), a 1,245 km² protected area in south-western Burkina Faso (region of Cascades, province of Comoé, departments of Mangodara and Niangoloko) (Figure 1). The reserve is about 100 km south of Banfora, capital city of the Cascades region. The southern limit is about 150 km along the international boundary with Côte d’Ivoire (Thiombiano and Kampmann 2010).

The climate is similar to that of southern Sudan with a rainy season of six months (May to October) and a dry season for the rest of the time (Guinko 1984). The study area is a transition zone between the dry tropical climates of the Sahelian north and the humid ones of southern Guinea. During the dry season, the prevailing winds are Harmattan, and during the rainy season, a humid warm monsoon wind blows from the southwest. Average rainfall ranges 200–950 mm (Thiombiano and Kampmann 2010). The Comoé and the Léraba rivers are the two most important rivers in the area. They are perennial and cross the zone from north to south by the Comoé and from the west to the east by the Léraba. The plains are traversed by important rivers, which cause flooding during the rainy season in some places.

The vegetation is characterized by semi-deciduous forest galleries and open forests, with the dominant species being *Daniellia oliveri*, *Isoberlinia doka*, *Pterocarpus erinaceus*, *Khaya senegalensis*, *Detarium microcarpum*, *Burkea africana*, and *Vitellaria paradoxa* (Thiombiano and Kampmann 2010).

Protocol

We applied a line-transect methodology in this study (see Hema *et al.* 2017a for details). We systematically placed transects (61 lines) at an average equidistance of 1.7 km and with a north-south and east-west orientation depending on the major drainage line of the major rivers in the census zone. Starting time was 6 a.m., 13 teams of three people each walked simultaneously along transects in straight lines, using GPS Garmin 64s. Every team consisted of an experienced warden (team leader) and two observers (one from the riverine villages and one field tracker). The same persons carried out the transects year-by-year.

Teams used binoculars to record data on the observed species, abundance, sex, age, and group size. Adult individuals that could not be sexed were also noted and recorded as undetermined (these individuals were not considered in the present paper). Depending on the species, sex was determined based on multiple criteria including general body size, shape of face or head, presence or absence of horns, observation of genital organs, and behaviour (i.e., association of calves and individual females, or association with other adults (solitary bulls in some species, groups of females, or groups of males). Details of sex determination criteria for each species are given in online supplementary materials (Table S1).

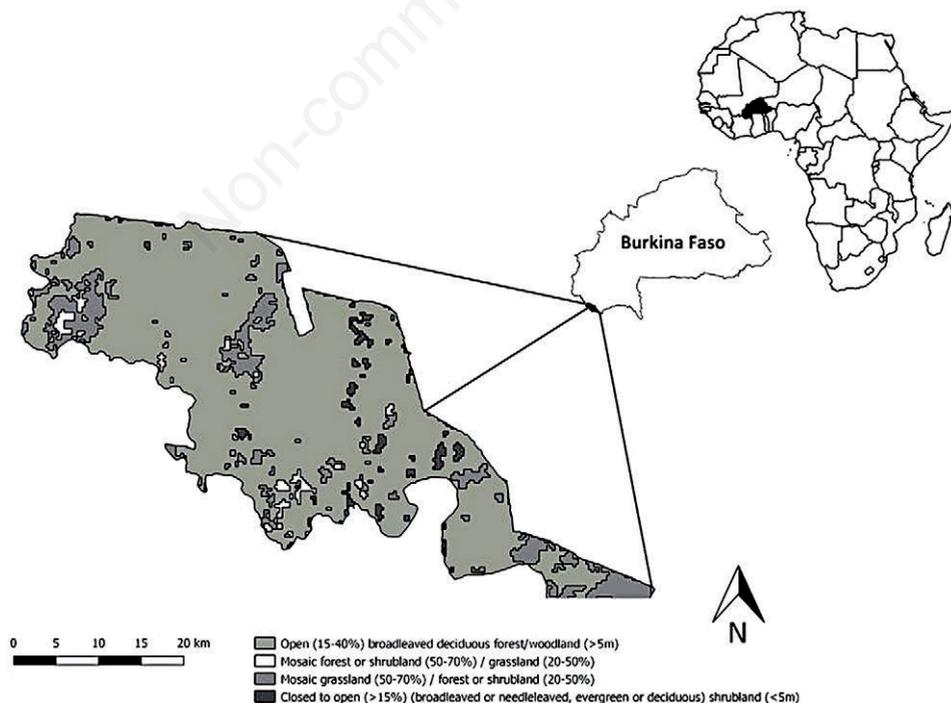


Figure 1. Map of Burkina Faso, showing the Comoé-Leraba National Park.

Because we could not determine the exact age of individual animals from direct observations, we classified individuals as either juveniles or adults based on morphological characteristics, including the general appearance of the individual, such as body shape and size, as well as the eruption of the tusk (for *Phacochoerus africanus*) or horns (for horned ungulates). The juvenile category consisted of (i) calves, characterized by their pinked colours and the capacity to walk under the belly of their respective mothers, and (ii) sub-adults, individuals that were clearly not calves and showed no signs of adulthood. The adult category included fully matured individuals with such characteristics as appropriate height, body size, presence of horns, tusk, etc.

The predictive modeling and the statistical analyses

We predicted that for species with lower detectability scores, sex ratios and age structures would vary to a greater degree across years than for species with higher detectability because of a much stronger effect of chance. So, assuming an interspecific similar population abundance, we established three independent variables that may make an ungulate species more or less visible during line transects: body size, habitat preferences, and group size. Detectability increases in species (i) with larger body size, (ii) that use open versus densely vegetated habitats, and (iii) that live in large groups compared to small groups or as solitary individuals. Thus, for each ungulate species, we assigned a score (1 to 3) for each of these three variables, with 1 being assigned to low detectability characteristics (i.e., small body size, densely vegetated habitats, and solitary/small groups), up to 3 for high detectability characteristics (i.e., large body size, open habitats, and large groups). Scores were assigned to each species based on published research (Haltenorth and Diller 1985; Estes 1991). The “overall detectability score” (OOS) for each species was given by the sum of the three species-specific scores relative to the three analyzed variables (Table 1). We empirically determined whether each species had a high OOS (≥ 6.5), a medium OOS (4.1–6.4), or a low OOS (3–4). If a

Table 1. Summary of the “detectability” scores for the various species in relation to their size (1 = small, 2 = medium, 3 = big), habitat (1 = very dense vegetation, 2 = bushy-open, 3 = open), and group size (1 = solitary of small groups, 2 = mid-size groups, 3 = large groups). Predicted = the “detectability” score that can be predicted on the basis of the three above-mentioned variables; Observed = the observed interannual consistency of sex-ratio and age structure of observed individuals across the study period.

	Size	Habitat	Group	Sum	Predicted	Observed
<i>Alcelaphus buselaphus</i> Pallas, 1766	3	3	3	9	High	High
<i>Syncerus caffer</i> Sparrman, 1779	3	2	3	8	High	Low
<i>Cephalophus rufilatus</i> Gray, 1846	1	1	1	3	Low	Low
<i>Sylvicapra grimmia</i> Linnaeus, 1758	1	1.5	1	3.5	Low	Low
<i>Kobus kob</i> (Erxleben, 1777)	2	1.5	2	5.5	Medium	Medium
<i>Kobus ellipsiprymnus</i> Ogilby, 1833	2	2	2	6	Medium	Medium
<i>Redunca redunca</i> Pallas, 1767	1	1	1	3	Low	Low
<i>Hippotragus equinus</i> É. Geoffroy Saint-Hilaire, 1803	3	3	3	9	High	High
<i>Tragelaphus scriptus</i> Pallas, 1766	2.5	1.5	1	5	Medium	Low
<i>Ourebia ourebi</i> Zimmermann, 1783	1	1.5	1	3.5	Low	Low
<i>Phacochoerus africanus</i> Gmelin, 1788	2	3	1.5	6.5	High	High

species had a high OOS, the interannual inconsistency of its sex ratio and age structure should in theory be lower than in a species with a low OOS. We determined the species-specific interannual inconsistency in these demographic parameters by applying some criteria that were unambiguously determined when reporting the year-by-year differences in sex ratio (expressed as % of males versus females) and size structure (expressed as % of juveniles versus adults). These criteria were:

- (a) high consistency in sex-ratio and age structure: 1) all sex and age groups are present in all years of study; 2) their percent contributions are relatively stable (< 25% variation) across the years of study;
- (b) medium consistency in sex-ratio and age structure: 1) all sex and age groups are present in most years of study, but not in one or two years; 2) their percent contributions show a 26-50% variation across the years of study;
- (c) low consistency in sex-ratio and age structure: 1) at least one sex or age group is not present in at least three years of study; 2) their percent contributions show a >50% variation across the years of study.

Observed score for interannual consistency of sex ratio and age structure in each species was correlated with the observed sample size using Spearman's rank correlation coefficient. In this analysis, the independent variable, interannual consistency score, was ranked from 1 to 3 (1 = low, 2 = medium, and 3 = high). Differences in sex-ratio frequencies, either within species or overall, were assessed by observed-versus-expected χ^2 test. All statistical tests were performed by PAST version 3.0 software, with alpha set at 5%.

Results

We recorded 1,143 individuals belonging to 11 species of both sexes and age structures of each species (unsexed individuals were not included in this count). The raw dataset concerning the study species is given in the supplementary materials (Table S2). Overall, the number of observed males and females did not differ significantly ($\chi^2=0.59$, $df=1$, $P=0.559$), and juveniles accounted for 33.3% of the total observed individuals.

Three species showed a high interannual consistency of the age and sex structures across years: *Alcelaphus busephalus*, *Hippotragus equinus* and *Phacochoerus africanus* (Table 1). In *A. busephalus*, females were more abundant than males in all years of study (but not significantly: $\chi^2=2.8$, $df=5$, $P=0.731$), and juveniles were always observed; however, in 2010, there was a considerably higher frequency of encounters with juveniles than in the following years (Figure 2). In *H. equinus*, there were similar patterns as the above-mentioned species, with the sex ratio being equal in each year of study ($\chi^2=8.3$, $df=5$, $P=0.136$) and with a considerably higher frequency of encounters with juveniles in the year 2010 than in the following years (Figure 2). In *P. africanus*, the sex ratio was also equal and stable across years ($\chi^2=8.16$, $df=5$, $P=0.151$), and the percentage of juveniles was stable in the population (Figure 2).

Two species (*Kobus kob* and *Kobus ellipsiprymnus*) showed a medium interannual inconsistency of the age and sex structures across years. In *K. kob*, sex ratio was even throughout the study period ($\chi^2=2.28$, $df=5$, $P=0.843$), and juveniles constantly accounted for less than 20% of the observed individuals each year. In 2018, no juvenile was observed during the line transect surveys (Figure 2). In *K. ellipsiprymnus*, the sex ratio was significantly skewed toward females ($\chi^2=11.05$, $df=5$, $P<0.05$), and juveniles, which were observed in each year of study, accounted for a substantial percentage of the recorded

individuals, with a peak in 2012 when juveniles comprised more than 80% of the observed individuals (Figure 2).

In the remaining six species, the interannual consistency of the age and sex structures across years was low. In *Tragelaphus scriptus*, the sex ratio was even across the years ($\chi^2=6.05$, $df=5$, $P=0.300$), but juveniles were seldom observed (Figure 2). In *Ourebia ourebi*, there was no stability across years, with juveniles being observed only in three years, and males varying from less than 40% to 100% of the observed individuals (in 2018, but with just $n=1$) (Figure 2). In *Syncerus caffer*, juveniles accounted for a great percentage of the recorded individuals in three years (2010, 2012, and 2018), but a very low percentage in 2011, also with no stability in sex ratio being identified (Figure 2). In *Cephalophus rufulatus* and *Redunca redunca*, we did not observe even a single juvenile throughout the study period, and the sex ratio varied from 100% males to a predominance of females, and a similarly high interannual inconsistency in sex ratio and proportion of juveniles in the sample was also recorded in *Sylvicapra grimmia* (Figure 2).

In nine of 11 species (82%), the predicted OOS matched the observed score (Table 1). The two exceptions were *T. scriptus* (with a predicted medium OOS and an observed low score for stability of sex ratio and age structure) and, especially, *S. caffer*, which was predicted to have a high OOS but resulted in a low observed score (Table 1). In these two species, the frequencies of the various group sizes at each sighting along the line transects were significantly different ($\chi^2=41.1$, $df=3$, $P<0.0001$), with all *T. scriptus* sightings being single individuals or

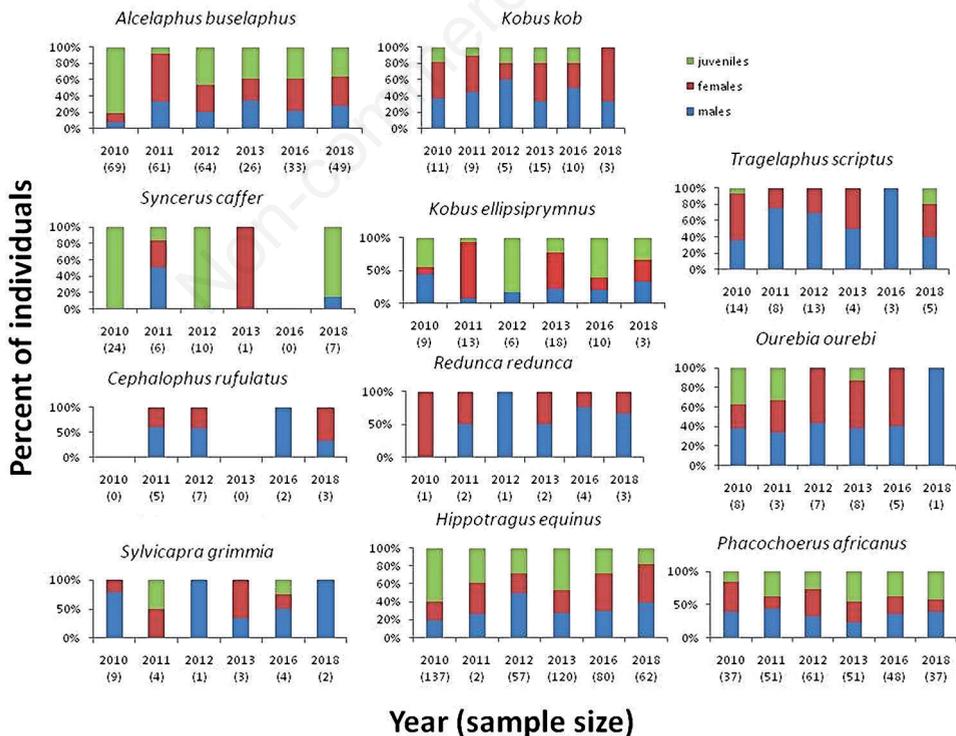


Figure 2. Percentages of males, females and juveniles, for each of the 11 ungulate species at the Comoé-Leraba National Park, by year.

very small groups, whereas those of *S. caffer* being either single individuals/small groups of relatively large groups, with no intermediate values at all (Figure 3).

The observed score for stability of sex ratio and age structure was significantly influenced by the observed sample size throughout the whole period ($r_s=0.90$, $n=11$, $P<0.001$), thus showing that the most elusive species are those with the highest variation in their observed demographic parameters.

Discussion

Our study showed that sex ratios and age structures of West African ungulates varied greatly by species and by year, and that the instability of these demographic parameters across years can be effectively predicted by considering just three independent species-specific variables (body size, habitat type, and group size). In fact, we accurately predicted the level of inconsistency of these demographic parameters in nine of eleven species, with only one species (*S. caffer*) clearly contradicting our predictions. In the case of *S. caffer*, we think that the remarkable inconsistency in its group sizes at the study area, even within single years (compared to available literature showing that this species lives in large groups; Halternorth and Diller 1985; Estes 1991), had affected the precision of our prediction.

Our study gave remarkable indications for future studies in West African savannahs, when direct sightings along line transects are used for data collection. It is clear that not all the species in a given ungulate assemblage can be detected with the same probability, thus some species are more suitable for line-transect surveys directed at studying their demographic attributes (for instance *A. busephalus* and *H. equinus*) and other species that are very unsuitable for line transects (for instance, *R. redunca* and *C. rufulatus*). Thus, we recommend alternative methods to study population demography attributes for the species that showed high inconsistency in sex ratio and percent of juveniles during the present study. Camera traps may represent an important tool for studying these species in addition to just line transects. However, any method shows point of strength and point of weakness,

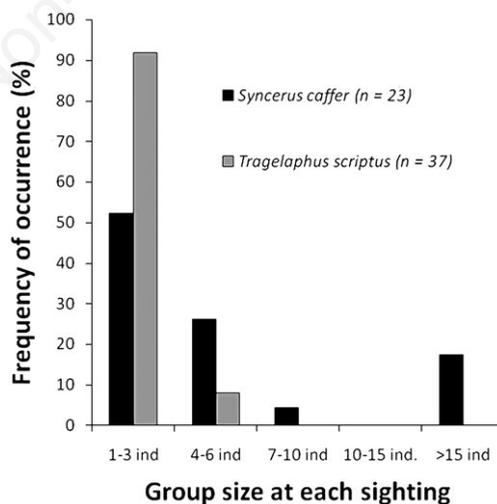


Figure 3. Observed group size at each sighting of *Syncerus caffer* and *Tragelaphus scriptus* (expressed as percent frequency of each group-size-interval in the total observed independent sighting events) during line transects at the study area.

and therefore also camera traps have their weaknesses: reduced sample numerosity is probably the main shortcoming of this latter method. Although it is obvious that total sample size has an effect on the consistency of the examined traits, it should be remarked that some species that were frequently observed during our study (for instance, *T. scriptus*, *S. caffer*, and *O. ourebi*) still had a low score of stability of sex ratio and age structure.

Importantly, our study shows that it is easy to predict the score of interannual consistency of sex ratio and age structure of a given species by simply determining a priori “detectability” score for each species by using the existing literature if available, or that relative to a closely related species if literature is not available. Using an “expert-based model approach” as the one presented in this paper, experimenters can understand whether direct sightings of animals along line-transect surveys are appropriate for determining demographic parameters of a species, thus minimizing the risk of getting biased results for the least suitable species by applying a methodology (line transect surveys) that is relatively expensive and time consuming (Hema et al. 2017b). Obviously, among the various demographic parameters, also the simple abundance (and density) along the transect could be affected in species having low detectability scores.

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Conflict of interest

None.

Contributions

LL and EMH produced the idea; EMH defined the protocol; EMH, YO, MAIT and MK collected the data; LL and GA analysed the data; GA, LL and EMH drafted the manuscript; all authors revised and approved the various drafts.

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