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Combining offtake and participatory data to assess the sustainability of a hunting system in northern Congo

Short running title: Hunting sustainability in northern Congo

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ABSTRACT

Research suggests that bushmeat is hunted at unsustainable rates throughout much of the Congo basin, although accurately measuring hunting sustainability is challenging. Offtake data can contribute towards sustainability assessments, and when incorporated with information on hunters’ strategies, can be used to monitor changes in hunting dynamics. We used a combination of 1) a long-term, quantitative yet low-resolution hunting offtake dataset, 2) qualitative data acquired through participatory methods, and 3) a high-resolution offtake survey, to examine the changes in a hunting system undergoing change due to new roads and associated socioeconomic developments in northern Republic of the Congo. Our results indicated that while the conclusions drawn from the different datasets were broadly the same (indicating wildlife depletion, particularly in one hunting zone), the results of the analysis of the participatory and the high-resolution offtake dataset provided an explanation for trends in the long-term low-resolution offtake dataset, including the degree to which long-term trends are due to changes in hunting strategy, or in underlying wildlife populations. We discuss how participatory hunter surveys can be used to distinguish between changes in prey populations and changes in hunting strategy in long-term low-resolution hunting offtake datasets, therefore improving the effectiveness of long-term offtake datasets to assess sustainability of hunting.

INTRODUCTION

Wildlife is thought to be hunted unsustainably across much of Central Africa, and, indeed, much of the tropics (Abernethy et al 2016; Bennett et al 2007; Fa et al. 2002; Nasi et al 2008; Ripple et al. 2016; Wilkie et al 2011). However, accurate monitoring of hunting sustainability can be challenging due to the dynamic nature of hunting systems (Ingram et al. 2021*;* Salo et al. 2014; Weinbaum et al. 2013). Furthermore, assessing the sustainability of hunting systems undergoing dramatic socio-economic and environmental change (Ingram 2020), for example new roads and the establishment of commercial forestry such as is the case in northern Republic of the Congo (Abernethy et al. 2013; Auzel & Wilkie 2000; Eves & Ruggiero 2000; Kleinschroth and Healey 2017; Kleinschroth et al. 2019), can be particularly challenging.

Quantitative measures are needed to assess the ecological sustainability of hunting (Sirén 2015). Hunting sustainability assessments often rely on models based on comparing hunter offtake in a given area and time-period with the maximum wildlife population production (e.g., population growth models; Robinson & Redford 1991). However, this approach to understanding hunting sustainability can be limited. These models contain inherent uncertainty because of poor biological knowledge of wildlife species and the different sampling methods used to calculate wildlife offtake (Ingram et al. 2021). Sustainability is also time and context specific, requiring tailored assessments that account for spatial and temporal variation in hunter offtakes (Clayton & Radcliffe 1996). However, some models are commonly used to assess sustainability during a short period of time, presenting a snapshot of what is a dynamic and changing hunting system (Ling & Milner-Gulland 2006). Lastly, data required for some models can require significant resources to collect (although citizen scientists or hunters have also collected such data; e.g., El Bizri et al. 2019), and can be technically challenging, requiring high levels of expertise (Coad et al. 2019; Weinbaum et al. 2013). Whilst such models can be invaluable to conservation scientists working in an area, they may be of limited benefit to community-based hunting management, which may require a more adaptive and less technically challenging approach.

An alternative approach to measuring sustainability, is to infer sustainability by using indices/proxies (Robinson and Redford, 1994). For example, monitoring changes in harvesting rates over time, using the overall number of animals and/or biomass harvested in a given area and time period, has been used to provide insights into whether a hunting system is moving towards or away from sustainability (Fa et al. 2005; Gill et al. 2012; Coad et al. 2013; Ingram et al. 2015). This requires a combination of longitudinal wildlife harvest data and detailed information about hunter behaviours (which could be collected by the hunters themselves). Other offtake-based proxies for sustainability include measuring changes in the species composition or mean body mass of prey profiles in order to detect possible wildlife population depletion trends (Rowcliffe et al. 2003; Crookes et al. 2005; Ingram et al. 2015; Marrocoli et al. 2019). This recognises that prey profiles from heavily hunted zones will contain fewer larger-bodied mammals, as hunters switch from more vulnerable, often larger mammal species, to smaller often more resilient species, when the former become depleted (Cowlishaw et al. 2005; Dirzo et al. 2014). Alternatively, Catch Per Unit Effort (CPUE) can be used as a proxy for resource abundance (Rist et al. 2010), whereby declining CPUE over a period of several years, or differences in CPUE between hunting zones, are indicative of wildlife depletion and differing wildlife abundances respectively.

Offtake data are, however, notoriously hard to interpret as they represent the outcome of several processes (Crookes et al. 2005). Both prey profiles and CPUE are sensitive to changes in hunter behaviour (e.g., Bowler et al 2020; Coad et al. 2019; Dobson et al. 2019; Keane et al 2011; Mockrin et al. 2011, Rist et al. 2008). For example, an increase in CPUE can occur with concomitant declines in overall resource abundance as harvesters move to more profitable sites (Fonteneau et al. 1999), a phenomenon referred to as hyperstability (Hilborn & Walters 1992). The reliability of offtake data in detecting changes in underlaying prey populations depends on being able to control for changes in hunting strategies (which includes factors such as who hunts, where, when, and how). Working with hunters to understand their hunting strategy can allow an improved interpretation of local hunting dynamics (Jost Robinson et al. 2011).

Here, we test the degree to which participatory hunter surveys can be used to distinguish between changes in prey populations and changes in hunting strategy in a low-resolution offtake dataset, therefore improving the effectiveness of long-term offtake datasets to assess the sustainability of hunting. To examine this, we ask whether sustainability inferences based on offtake surveys, and hunter focused participatory surveys with explicit knowledge of hunter identity (here ethnicity) and behaviour (hereafter combined as 'hunting strategy'), resulted in different conclusions. We use data gathered from a site that underwent socio-economic transformations in northern Republic of the Congo due to new roads and the establishment of commercial forestry, where long-term offtake data were collected as part of a Protected Area management program. The overall hypothesis of this research is that long-term low-resolution offtake data combined with participatory hunter surveys can explain changes and sustainability of a hunting system undergoing socio-economic change. Specifically, we pose the following hypotheses: 1) New roads and associated socio-economic developments increase hunting levels (number of animals, biomass), but without accounting for hunting strategy we can only provide limited inferences about sustainability; 2) New roads and associated socio-economic developments affect prey profile as medium-large animals are hunted out around the village (halo effect) and small ungulates, primates, and other prey increase in the hunt profile, but without accounting for hunting strategy we can only provide limited inferences about sustainability; 3) Hunters can clearly articulate how they respond to changing abundance of wildlife and local socio-economic changes and these changes can be incorporated into the design of offtake surveys; and 4) Comprehensive assessment of hunting strategy in relation to hunt offtake (number of animals per hunt, biomass per hunt, prey profile per hunt, and CPUE per hunt), illustrates that hunting strategy significantly influences offtake.

METHODS

Study site

The study was conducted in the village of Makao-Linganga in the Likouala region of the Republic of the Congo (hereafter 'Congo'; Figure 1). Makao-Linganga is the second closest permanent human settlement to the Nouabalé-Ndoki National Park (NNNP, established in 1993; Maisels & Djoni-Djimbi [2001]), situated 45 kilometres from the park's eastern border. At the time of the study, NNNP was managed by the Congolese Ministry of Forest Economy and the Environment (MEFE) in collaboration with the Wildlife Conservation Society (WCS) – in 2014 it became a Public-Private Partnership (Hatchwell 2014).

The region has a low human population density (0.7-0.8 individuals/km^2; Madzou 2002), and in 2007, the population of Makao-Linganga comprised 565 people from two principal ethnic groups with inter-dependent livelihoods: farmer-fishers, mainly Kaka-Ikenga, and the Aka-Mbendjelé hunter-gatherers (Madzou & Yako 2000), hereafter referred to as the 'Kaka' and the 'Aka' respectively. Traditionally the Aka were semi-nomadic, spending between four and eight months a year in forest camps (Kitanishi 1995), although due to influences of commercial forestry and the conservation project, the Aka now increasingly spend far more time in the villages and gun hunt for the Kaka, as Aka rarely own guns or cartridges themselves.

Hunting regulations and monitoring of wildlife offtake

Given that NNNP is uninhabited, its integrity depends largely on effective management of its peripheral 'buffer' zone. In 1991, the NNNP management and the local population of the two villages closest to the NNNP border (Bomassa to the south-west and Makao-Linganga to the north-east (Figure 1) entered into an agreement that these communities would sustainably manage the natural resources of the buffer zone outside of NNNP, in turn receiving employment opportunities and infrastructural support from NNNP. As part of this agreement, hunting regulations, broadly following the Congolese hunting regulations fixed by Forestry Law 48/83, were drafted. These included: no night hunting, no hunting with nylon or wire snares, no hunting of fully or partially protected species without the appropriate license, and no transport or sale of bushmeat between sites (Ruggiero 1998). To evaluate hunting sustainability, the NNNP project established a base in Makao-Linganga village, whose rangers have monitored all bushmeat entering the village since 1997. Hunters are obliged to register their hunts with the project both prior to hunting and on their return, which they have complied with since 1997. However, it is possible that protected species are hunted and not registered, and that in-migrants to Makao-Linganga are less compliant with registration of hunts. The population of Makao-Linganga use four hunting zones, all of which vary in their historic and current hunting pressure (Figure 2; Table 1).

Commercial forestry roads and developments

The NNNP is now surrounded by Congolese logging concessions to the north, east and south (Forestry Management Units, FMUs, Figure 1). The Western border of the Park is the international border between the Central African Republic and Congo, and most of that border is contiguous with the protected areas of the Dzanga and Ndoki National Park sectors, and the Dzanga Special Reserve (République du Cameroun; République centrafricaine; République du Congo, 2012). The establishment of logging concessions within Congo (as elsewhere), have resulted in the development of roads and in-migration into the region (Mavah 2006; Poulsen et al. 2007). In 2001 a new road built by logging concession holder *Societé THANRY-Congo* (STC), reached Makao-Linganga village, the first road ever to reach this previously very remote village. In 2003-4, 200-250 migrants arrived to work for STC. They first settled in the village, and then, in 2003, along with approximately 65 Aka from Makao-Linganga, they relocated to Sombo forestry site (the HQ of the STC, 6km north of Makao-Linganga). The population of Sombo was ~2500 in 2007 (Thanry-Congo 2012), including commercial bushmeat hunters, who arrived between 2001 and 2003. A second road built by forestry company *Congolaise Industrielle de Bois* (CIB) arrived in Makao-Linganga from the south in 2006, bridging the Motaba river and increasing access to the Loundoungou FMU (Figure 2).

Data collection

To understand whether sustainability assessments based on traditional offtake surveys, and hunter-focused participatory surveys to provide information on hunting strategies, resulted in different assessments as to the sustainability of the hunting offtake, we used data from sources outlined in the following three sections.

Long-term offtake records

We used a 10-year (1997-2006) dataset of bushmeat offtakes from the village of Makao-Linganga, collected by the NNNP conservation project staff. Data included prey species, hunting zone in which the kill occurred, sex of prey, date of kill, hunter's name, and gun-owner's name. Snare-trapping was very limited due to enforcement of conservation regulations in the village, although some trapping still occurred and the resulting animals were consumed in forest camps. Project staff recorded bushmeat directly from returning hunters on a daily basis, by walking around the village during the day and by visiting returning hunters' households. A total of 30 species were recorded during the 1997-2008 period, but three species (*Philantomba monticola*, *Cephalophus callipygus*, and *Potamochoerus porcus*) accounted for 69.5% of the total number of animals harvested, and 82.7% of the total biomass harvested. Although project staff knew when every hunter left the village, not all returning hunters reported their return, so staff supplemented the hunter register with word-of-mouth to select hunters' households to visit. Whilst this village-level monitoring approach could have recorded almost all offtake from hunters in the village between 1997-2000, when Makao-Linganga was still a relatively small community, it likely underestimated absolute offtake after the arrival of the road in 2001, when the village population grew relative to the number of NNNP rangers. Incoming migrants were also less inclined to volunteer hunting information. The number of hunters rose from 56 in 2000 to 111 in 2004, while data collection effort remained similar. As a result, the prey and biomass figures we present are likely to be an underestimate of the total number and biomass of animals hunted at the village level, after 2000. Given that 1) hunting offtakes were monitored at the village level, rather than monitoring a specific subset of hunters; and 2) the number of hunters increased over time and survey effort remained the same, the offtake data therefore comprises a greater number of hunters for the same effort, so total offtake from individual hunters becomes less complete. For these reasons, these data cannot be used to analyse changes in individual hunting offtakes overtime. In addition, due to the relative decrease in survey effort over time, we have exercised caution in the interpretation of these data to infer site-level long-term changes in hunting offtakes. However, given the effort to record bushmeat entering the village was substantial, we are confident that the taxonomic composition of the catch (prey profile), and the relative contributions of each hunting zone to the catch was accurate.

The long-term records are incomplete due to administrative (e.g., occasional staff shortages) and political factors; in total the dataset contains 88 of 120 possible months (6693 animals) between 1997 and 2006, although no hunting zone data were available for 1998 or 1999. Therefore, to fill gaps in the data, we extrapolated yearly totals from these data by calculating monthly averages from existing data within each year, and multiplying these averages for missing months within each year to account for differences in the number of hunters per year. Extrapolating assumes that monthly offtake is constant throughout the year, and that there are no seasonal peaks, which is rarely the case.

Participatory techniques

Participatory rural appraisal (PRA) techniques were employed at the start of the research period, June-July 2007, and again in June-July 2008. The principal researcher and the research team made every effort to maintain independence from the conservation project in the eyes of the local population, in order to establish a relationship of trust and enable hunters to talk openly about their changing hunting strategies, particularly illegal practices.

Working with trained research assistants, we conducted four participatory mapping exercises (Chambers 1994) and four group interviews, two of each with Kaka hunters, and two with Aka hunters. Participatory mapping was used to understand changes in where hunters hunt, including changes within the selection of the four hunting zones. Participatory mapping exercises focused on mapping the forest space - defined by local names of rivers, streams, and other features - local hunting zones, and changes in the use of these areas. Mapping exercises were not paper based but were conducted *in situ* in hunting camps or in the village, and used available local materials such as palm nuts and leaves (Riddell 2011). One research assistant acted as facilitator, while hunters themselves designed the map. The resulting map was used as a discussion tool to explore the nature of reported changes in wildlife populations and hunting. During the group interviews, there were more in-depth discussions about a) their perceptions of changes in populations of wildlife species over time, and b) their explanations for any observed changes. We elicited how they had adapted their hunting strategies in response to these changes, or to other socio-economic changes in the village. Resource-change timeline diagrams were used as tools to discuss changes in wildlife species relative to a locally-significant timeline, using large sheets of paper which the facilitator marked. Timelines were determined by identifying locally-significant events (e.g., change in the village chief, arrival of the conservation project and forestry road) rather than years, from which the conversation about resource changes could be marked. After the mapping exercises and group interviewing in June-July 2007, we then classified the reported changes in hunting strategy into four groups, including: i) day/night, ii) distance from village, iii) hunting zone, and iv) gun owner hunting by self or Aka hunter.

High-resolution offtake surveys

The high-resolution offtake survey was designed to provide an understanding of how hunting strategy influences prey profile, to improve the interpretation of the long-term offtake dataset and therefore improve reliability of inferences made about the sustainability of hunting. While some components of hunting strategy were already collected in the long-term offtake dataset (hunting zone and season), the high-resolution offtake survey differed in that two additional indicators of behaviour – distance of hunt from the village, and day or night hunts – were also included. Furthermore, actual time hunting was also included in this dataset, which allowed for a more accurate calculation of Catch Per Unit Effort data (CPUE; biomass caught per hour hunting), not possible with the long-term dataset. Multi-day hunting trips assumed an average hunt time of eight hours/day based on reported hunt time for day hunts around the village (mean=8.25hrs +/-3.12, N=228). Lastly, in this gun hunting system, where gun owners either hunt themselves, or provide their shotgun to hunters (most often Aka hunters), this factor (hunter ethnicity) was included as part of the hunting strategy, as hunters explained that the prowess of the hunter – for which Aka hunters are known in this region - was one of the main factors determining the outcome of a hunt. We evaluated data on these strategies to assess the degree to which hunting strategy affects offtakes, measured as prey numbers per hunt, biomass per hunt, prey profile per hunt and CPUE.

We conducted high-resolution offtake surveys over 12 months between June 2007 and June 2008 which included collecting data from 104 hunters. A trained research assistant recorded hunting products entering the village from hunters for twenty days a month, which was verified weekly by the first author. Data collected included the number of animals, species, sex, weight, hunting technique, hunt location, time hunter was away from the village (based on position of the sun), whether the animal was hunted at day or night, and socio-economic characteristics of all hunters involved in the hunt. Hunted animals arriving in the village were almost exclusively from gun-hunting (99%), which was also true for the long-term data set. Only the Aka use traditional methods, and most meat hunted with traditional methods is consumed in the forest by the Aka, and therefore these were not included.

Data analysis

Data analysis occurred in four stages, corresponding to the four hypotheses. Firstly, we graphically examined changes in bushmeat entering the village over the period of 1997 – 2006 based on the long-term offtake records. Annual change was measured through three indicators: numbers of animals hunted, biomass of animals hunted, and overall harvest prey profile (acknowledging that total offtake at the village level will be increasingly underrepresented over time). The NNNP conservation project assigned hunted animals to four categories based on their functional group and size, and these were used for the purposes of analysis. They included: 1) small ungulates (blue duiker), 2) medium-large ungulates (other duiker species and wild pig), 3) primates, and 4) all other species which included rodents, carnivores, and birds. Overall harvest biomass for each category was obtained from carcass numbers and mean species and sex-specific weights (Kingdon, 2003).

The second stage of data analysis aimed to examine whether there were significant changes in prey profile over time, using the long-term dataset. We used the presence or absence of animals of the different size/ functional group categories in each hunt as an indicator of prey profile. This accounts for the difference in monitoring across years and hunters by analysing at the level of the hunt. In addition to the effect of time, we explored other factors which potentially affect prey profile including the season (dry or rainy season), the ethnicity of the hunter (Aka or Kaka), and the hunting zone (Loundoungou, Sombo or Gomo; Appendix 1). As all these factors were only available for the years between and including 2001 and 2007, six years of data were analysed. Generalized mixed effects models (GLMMs) were used to explore the relationship between a response variable and independent variables (fixed effects). Models were run in the R v2.9.2 (R Development Core Team 2009), using the lme4 package (Bates et al. 2015). In all models, hunter ID was used as a random effect to account for non-independence of repeated measures of the same hunter. Assessments of likelihoods using binary data were modelled using a binomial error distribution and logit link function (Bolker et al. 2008). Models were compared using the Akaike information criterion (AIC) which allows comparison of predictive ability between models with all combinations of factors. Models were run for three of the four prey profile categories (medium-large ungulate, small ungulate and primates). The 'other' category was not analysed because it made a very small contribution to the total offtake (<3%).

The third stage involved analysing the results from the participatory techniques. This had already been partly carried out in the field when the main reported hunting strategy changes were categorised by themes (Aronson 1994). Thematic analysis was also used to pick out prominent themes concerning hunters' perceptions of changes of wildlife populations, and their reasons for any adaptations to their hunting strategies.

The last step of the analysis aimed to understand the relationship between hunting strategy and offtake. We used the four principal hunter strategies which hunters reported had changed because of the new road and associated socioeconomic changes as factors in linear mixed models and generalized mixed effect models (LMMs and GLMMs), to test whether offtake per hunt (hunt offtake) as reported in the 2007-8 high-resolution offtake surveys related to reported hunting strategy. The strategies included in the models were i) choice of hunting zone, ii) distance from the village, iii) day or night, iv) the ethnicity of the hunter, and v) the season (Appendix 1). Again, hunter ID was included as a random effect.

RESULTS

Long-term offtake records

Change in harvest numbers and biomass over time

Overall harvest numbers and biomass increased slightly between 1997 and 2000, when all animals hunted by the village was recorded (Figure 3). In 2001, there is a marked increase in prey numbers, because of the increased number of animals hunted from Sombo hunting zone, although this increase is less marked for biomass. From 2001, we recognise that because the number of hunters increased relative to survey effort, total offtake at the village level will be increasingly underrepresented over time and should be interpreted with caution. Despite survey effort staying the same, we still observed a slight increase in prey numbers in 2002, due to the increased number of animals hunted from Loundoungou hunting zone. This is followed by a marked increase in overall prey numbers and overall harvest biomass in 2003, the majority of which originated from Sombo and Loundoungou hunting zones. This increase corresponds to the arrival of 200 in-migrants, looking for forestry employment, in Makao-Linganga. In the same year hunting products from Bundi hunting zone stopped arriving in Makao-Linganga. This was because as hunters from Makao-Linganga passed near the forestry site on their return from hunting (Figure 2), they sold or exchanged bushmeat, rather than bringing it back to the village.

Between 2004 and 2005, the in-migrants, along with 65 Aka, relocated to Sombo forestry town, which corresponded to a slump in prey numbers and biomass arriving in Makao-Linganga in these years (Figure 3). However, the arrival of the second road in 2006 corresponded with another peak in the number and total biomass of hunted animals. This was the result of the creation of the new bridge across the Motaba River, permitting hunters direct access to Loundoungou hunting zone, without need for a canoe. There were also 20-30 road construction workers living in Makao-Linganga in 2006, and an increase in people passing through the village. This led to increases in the number and biomass of animals from Loundoungou hunting zone, which made up the majority of the overall harvest by 2006. This increase in offtake from Loundoungou masked the reduction in the number of animals originating from Sombo hunting zone since 2003 (Figure 3).

Change in harvest prey profile over time

Prior to the opening of the road, the harvest was dominated by medium-large ungulates, with small contributions from other size/functional categories (Figure 4). However, the proportion of medium-large ungulates in the overall harvest decreased suddenly with the new forestry road in 2001, and continued to decline until 2006 (Figure 4). Correspondingly, the proportion of small ungulates increased in 2001, and continued to increase over time, while offtake of primates and other species remained steady. The increase in small ungulates in the overall harvest explains the sharp increase in the number of hunted animals and yet marginal increase in total biomass in 2001.

Change in prey profile per hunt

Using data from 2001 to 2006 our GLMMs found strong support for the role of hunting zone and hunter ethnicity in the likelihood of a medium-large ungulate being caught in a hunt (i.e., the hunt harvest; Table 2; Appendix 2). The proportions of hunts containing medium-large ungulates from different hunting zones matched known hunting pressure on these zones: Gomo, the most distant zone with low historic and current hunting pressure, had the highest proportion of hunts containing medium-large ungulates (76% of hunts); Loundoungou had low historic and increasing current hunting pressure (61% of hunts); and Sombo had high historic and current hunting pressure (44% of hunts containing medium-large ungulates; Figure 5).

Hunting zone also explained the proportion of hunts with primates in the harvest, with Sombo zone hunts containing a higher proportion of hunts with primates than other zones. For small ungulates, there was a significant interactive effect between year and zone (Table 2). This is likely because of the increase in the number of hunts returning with small ungulates from Loundoungou and Gomo after the new road in 2001, although the proportion of hunts with small ungulates was already high in Sombo zone prior to the road.

Ethnicity of the hunter influenced the likelihood of a medium-large ungulate or primate in the hunt. This was particularly pronounced for medium-large ungulates, which occurred in 63% of Aka hunts, and only 31% of Kaka hunts.

Hunters' response to the road and wildlife depletion

Participatory mapping and group interviews revealed that hunters perceived a reduction in the abundance of wildlife that could be hunted legally around Makao-Linganga since the new road in 2001. This was particularly true of previously common large-medium mammal species, such as red-river hog, and Peter's duiker, which hunters reported to be their preferred game. The consensus was that Sombo hunting zone, particularly within a return-day's walk (up to 10-15km from the village) were especially affected, whereas distant hunting sites, such as Gomo zone, were unaffected.

Hunters attributed this local wildlife depletion to: 1) increased gun-hunting as a result of the increased accessibility of cartridges, new demand for bushmeat, and increased engagement of Aka hunters in gun-hunting, 2) the growth of Sombo forestry town, including the increased disturbance from the sawmill, and 3) increased gun and wire-snare hunting by commercial hunters in Sombo which is adjacent to Sombo forestry town (Figure 2).

Hunters reported changing their strategies over time in a variety of ways. We classified these changes in hunting strategies into four groups: i) increase in night hunting, ii) increased distance travelled for gun-hunting, iii) increased use of Loundoungou zone, and iv) increase in proportion and number of hunts where Aka hunters are provided with the gun to hunt. The first three strategies are primarily driven by hunters' need to maintain a high CPUE in the face of prey depletion and increased demand for bushmeat, while strategy iii) was also prompted by the bridging of the Motaba river, and strategy iv) represents a social change as a result of forestry and conservation – reducing the time Aka spend living in the forest, increasing the time spent living in the village, and increasing engagement with the village and forestry economy (Riddell 2013). If offtake is linked to hunting strategy, as indicated by the analysis of the long-term dataset, then changes in hunting strategies over time could result in trends in bushmeat offtake which appear to be as a result of changes in wildlife abundance, but are in fact purely as a result of changes in hunting strategy.

High-resolution offtake surveys

Considering that hunters reported that their strategies had changed over the course of the long-term monitoring, we sought to understand how hunting strategy is linked to four hunting sustainability indicators: number of animals, biomass, prey profile, and CPUE.

Number of animals caught per hunt

We found strong support for the role of hunting zone, day or night hunts, and distance from the village, in the likelihood of having more than one animal per hunt (Appendix 2). Although there was no apparent difference between Loundoungou and Gomo zones, a lower proportion of hunts contained more than one animal in Sombo hunting zone. A higher proportion of those hunts far from the village contained more than one animal, while night hunts were more likely to contain more than one animal (75%) than day hunts (39%). Support for the interaction between hunting zone and distance occurred because hunts close to the village in Sombo hunting zone were more likely than distant hunts to contain more than one animal, while in Gomo and Loundoungou all hunts had a similar likelihood of containing more than one animal. This anomaly in the Sombo hunting zone is related to the fact that hunters rarely use Sombo zone for camp hunting as a result of wildlife depletion, but instead prefer to hunt close to the village.

Biomass per hunt

Our results show strong support for the effect of hunting zone, hunter ethnicity, and distance from the village on the biomass of the harvest (Appendix 2). Hunts occurring in Gomo zone had the highest biomass per hunt, followed by Loundoungou and then Sombo. Hunts by Aka hunters had a higher biomass than those by Kaka hunters. However, Aka hunter biomass per hunt at night was not significantly different to Kaka hunter biomass per hunt. Lastly, the biomass harvested also increased with distance from the village, and an interaction between distance and day or night hunts occurred as distant day hunts (15km+) contained a higher biomass than distant night hunts, the opposite was found for close and medium hunts (0-5km, 6-15km).

Prey profile per hunt

All four hunting strategies considered in the analysis appeared to affect the likelihood of all three size/functional groups in the hunt harvest (Appendix 2).

The effect of hunting zone on the likelihood of a hunt containing a medium-large ungulate was the same as in the long-term monitoring dataset, with a higher proportion of hunts from Gomo, then Loundoungou and then Sombo, containing medium-large ungulates, although the difference between Loundoungou and Sombo in 2007-8 is not as pronounced as results from the long-term dataset. Fewer hunts from Gomo returned with small ungulates in the harvest compared to the other hunting zones, although there was no apparent difference between the proportion of hunts including a primate between zones. However, a higher proportion of Aka day hunts from Sombo included a primate compared to other zones.

Overall, 59% of day hunts by Aka hunters contained medium-large ungulates, compared to only 16% of day hunts by Kaka hunters (Figure 6). This supports claims by Kaka hunters that the Aka's superior hunting skills make them more able to hunt medium-large ungulates. However, this difference is not apparent when lamping at night, where hunting a medium-large ungulate requires less skill than during the day.

Similarly, Aka return with a marginally higher proportion of small ungulates during the day compared to the Kaka, although this difference was not apparent at night. Kaka instead often returned with primates, present in 66% of Kaka hunts, compared to only 36% Aka hunts.

Day or night affected the likelihood of primates and small ungulates in the hunt harvest, but not medium-large ungulates. There was also strong support for the role of distance, with proportions of hunts with medium-large ungulates increasing with distance, and the proportion of primates declining with distance (Figure 7).

An effect of season only appeared in the closest hunts to the village (0-5km), and in Sombo hunting zone, where we would expect wildlife to be the most depleted. Primates were more likely to be included in hunt harvests in the zone closest to the village during the dry season, possibly because ungulates are difficult to hunt at this time (partly as a result of dry undergrowth which reduces hunter stealth), and are more depleted around the village. There was also an increased proportion of small ungulates in Sombo hunting zone in rainy season hunts, as they are easier to hunt in the rainy season, and medium-large ungulates are depleted in this zone.

Catch Per Unit Effort (CPUE)

The strongest support for hunting strategy affecting CPUE (kg/hour) was for hunting zone, day and night hunts, and distance (Appendix 2). CPUE was only significantly different between Loundoungou (1.9kg/hour) and Sombo (1.5kg/hour). Night hunts yielded a higher CPUE (2.3kg/hour) compared to day hunts (1.7kg/hour), which confirms hunters' reports that night hunts are more efficient as a result of the use of lamps. There was also some support for the role of season, with dry season hunts having a lower CPUE (1.6kg/hour) than rainy season hunts (2.0kg/hour), possibly as a result of hunter visibility and limited stealth in the dry season.

DISCUSSION

Using a unique combination of datasets, we demonstrate that changes in hunting offtake can reflect hunting strategies as well as the underlying wildlife population. We illustrate how using offtake data alone as a proxy for wildlife abundances may lead to erroneous inferences about hunting sustainability if changes in hunting strategies are not simultaneously understood. The analysis allowed us to evaluate the impact of two commercial logging roads on hunters' behaviour. By combining these datasets, we can make inferences on hunting sustainability in the case study village in northern Congo, illustrating that in one hunting zone (Sombo) there was evidence for wildlife depletion.

Contribution of each dataset to inferences about sustainability

Our results support our first hypothesis that new roads and associated socioeconomic developments increase hunting levels (number of animals, total biomass), but without accounting for hunting strategy it is only possible to make provide limited inferences about sustainability. Changes in offtake numbers and biomass were closely linked to the human population and settlement patterns in and around Makao-Linganga, corresponding to two new roads. However, caution should be used when interpreting the trends in the long-term offtake data because data on total offtake at the village level was incomplete. Nevertheless, had total biomass and prey numbers been analysed without considering the hunting zone where the animals were caught, the decline in prey numbers originating from Sombo hunting zone would have been masked by the corresponding increase from Loundoungou zone, as hunters shifted to this more profitable site. As in other village offtake surveys (see Mockrin et al. 2011), our study illustrates the importance of spatially stratifying data collection and analysis.

There was also support for hypothesis 2, that new roads and associated socio-economic developments affect prey profile as medium-large animals are hunted out around the village (halo effect) and small ungulates, primates, and other prey increase in the hunt profile, but without accounting for hunting strategy we can only provide limited inferences about sustainability. The seemingly unexplainable and immediate shift in prey profile between 2000 and 2001, when all animals were analysed together, was identified as unlikely to reflect changes in wildlife abundance alone. Although assessing overall prey profile of the total offtake in a given area is commonly used as an indicator to infer hunting sustainability (see for example Gill et al. 2012; Coad et al. 2013), when we analysed prey profile in terms of presence or absence of each size/functional group at the hunt level, the findings were far more revealing. Comparisons of both medium-large ungulates and primates between zones matched our expectations considering the historical and current hunting pressures in each zone: that Sombo would have the least proportion of hunts with medium-large ungulates, and Gomo, the most distant zone, the most. In addition, this analysis illustrated that Sombo had a high proportion of hunts with small ungulates prior to the forestry road compared to other hunting zones, indicative of historic hunting pressure in this zone. However, there was a rapid increase in small ungulates in Gomo hunts over time, despite the fact that Gomo is distant from the village. These findings suggest that the long-term dataset is a reflection of multiple processes other than simply changes in wildlife populations alone.

Hunters provided strong evidence for hypothesis 3, that hunters can clearly articulate how they respond to changing abundance of wildlife and local socio-economic changes and these changes can be incorporated into the design of offtake surveys. The results from the participatory techniques supported the results from the long-term monitoring data: hunters reported a reduction in medium-large ungulates in Sombo hunting zone, and reported that they increasingly used Loundoungou zone. Although hunters were not able to provide us with the quantitative data generated by the long-term monitoring dataset, the general conclusions based on the findings of both methods would have been the same. The additional advantages of the participatory techniques in this case were their ability to describe changes in hunter strategies, and give explanations for these changes, and this understanding is vital to informing management. PRA techniques should be seen as a useful tool to complement long-term scientific data collection, involve hunters in sustainability assessments, and therefore community management of wildlife.

We find strong evidence for hypothesis 4, that wildlife offtake is linked to hunting strategy, when including hunting strategy (identified from the participatory techniques) in the analysis of the high-resolution offtake data. Only through use of this dataset are some of the trends in this long-term monitoring dataset explainable. For example, the sudden prey profile shift at the time of the new road (Figure 4), and the increase in the number of animals hunted without a similar increase in biomass (Figure 3), can be explained by the initiation of night hunting: night hunts have a higher likelihood of containing small ungulates and more than one animal than day hunts. In addition, based on low CPUE and a low proportion of medium-large ungulates hunted when hunts occurred close to the village, the high-resolution offtake dataset was able to provide some evidence for a ‘halo’ of depletion around Makao-Linganga. Based on this knowledge, and the fact that hunters reported increasing their travel distance over the years, it is highly likely that the long-term dataset is suffering from hyperstability. However, the lack of monitoring of these behavioural factors in the long-term dataset means it is impossible to quantify the effect of these factors. Nevertheless, by showing that hunting strategy affects offtake, and providing qualitative data indicating that hunting strategy has changed over time, the high-resolution offtake dataset has helped us understand that the long-term dataset is compounded by changes in hunting strategy. Despite this, the comparisons of prey profile between the three principal hunting zones using the different datasets all reached the same general conclusion.

The question remains as to which offtake metrics are the most accurate indicators of sustainability. Kümpel *et al.* (2010) argue that changes in prey profile and CPUE are the most accurate. In our case study, CPUE yielded a different result from prey profile data. This is possibly due to the measure of effort we used, which assumed that hunters hunt for an average of eight hours for every hunt, regardless of their distance from the village. However, Rist *et al.* (2008) demonstrate that CPUE is sensitive to the measure of effort used: the authors illustrate that the proportion of total time spent hunting actually decreases with increasing distance from a village in Equatorial Guinea. Importantly, it is evident from our findings that the likelihood of catching each prey size/functional group was influenced by different processes. For example, the ethnicity of the hunter during day hunts influenced the likelihood of catching medium-large ungulates, while the likelihood of catching small ungulates and primates was instead influenced by whether the hunt was conducted during the day or night. However, the presence or absence of medium-large ungulates in hunt harvests yielded the same results for all three methods of assessment. Medium-large ungulates are preferred prey species in this region, and preferred species are killed when encountered by hunters, and therefore are more likely to represent wildlife densities than non-preferred species. Hunters based the quality of different hunting zones based on their perceptions of the abundance of medium-large ungulates, indicating this is a locally significant indicator of sustainability. Ultimately, however, accurate indicators of sustainability from offtake data may vary between sites, but must be one which represents local processes that are understood, e.g., in this example the dynamics between Aka and Kaka hunters.

Implications for sustainability assessments

To answer our original question, 'do the sustainability assessments based on traditional offtake surveys, and hunter focused participatory surveys with local knowledge of hunting strategy, result in different conclusions?', we argue that the general conclusions are the same, although the use of participatory and high-resolution offtake methods allowed us to qualify the degree to which the long-term dataset was representative of wildlife abundance or hunting strategy. The lack of information about hunting strategy in the long-term dataset prevented us from quantifying the effect of behaviour. If inferences about sustainability were based solely on the immediate change in offtake prey-profile in the long-term dataset in 2001, without an understanding of hunter strategies, the data would be interpreted as representing a dramatic change in wildlife abundance. By using information on hunting strategies to help interpret the long-term offtake dataset, a more comprehensive understanding emerges, in which changes are not solely attributable to changes in wildlife abundance.

Our analyses provide further evidence for the dynamic nature of hunting systems, illustrating the need to monitor hunting and hunting behaviour over time, which when taken into account can help to inform whether offtake-based indicators of sustainability are likely to be reliable. The evidence for wildlife depletion in Sombo hunting zone (all data sources), and close to the village (participatory and high-resolution data sources), may not necessarily mean that the overall hunting system around Nouabale-Ndoki National Park and surrounding logging concessions is unsustainable. Finding a 'halo' of depletion around settlements is relatively common, and not necessarily indicative of unsustainable use (e.g., Alvard et al. 1997). For example, Novaro *et al.* (2005) show that spatial heterogeneity in hunting pressure, with lower prey densities close to hunter population centres, and increasing densities with increasing distance away from these centres, can lead to a source-sink scenario. However, where the hunting haloes of villages are overlapping, or at least in close proximity, as is often the case in Central Africa, viable "source" populations of wildlife may be limited (Coad 2007). The northern Republic of the Congo is an area where overall hunting pressure may be still low enough to maintain wildlife in the long-term (see Abernethy et al 2016; Grantham et al 2020), as long as careful hunting management is practised.

CONCLUSION

Interpretation of offtake data, when used to make inferences about sustainability, requires an understanding of the degree to which offtake reflects the relative abundance of wildlife populations. Put simply, changes in hunters' behaviour can mask changes in wildlife abundance as hunters adapt their hunting strategies to evolving socio-economic contexts and wildlife depletion. We have shown how hunters adapted their strategies in light of the arrival of a commercial forestry road, and that including data on these hunting strategies in offtake monitoring protocols provided a qualitative understanding of the effect of hunting strategy, therefore providing explanations for offtake trends in the long-term low-resolution monitoring data. Incorporating hunting strategy into data collection protocols, and using participatory techniques to understand changes in hunting strategy, is one way to control for the effect of hunting strategy. We believe this method provides a valuable way to increase the reliability of inferences about sustainability made from offtake data, and could easily be incorporated into community-based hunting monitoring efforts and management.

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Figure captions:

Figure 1. Location of Makao-Linganga village in relation to NNNP, Sombo forestry town 6km north, and the two forestry roads, one from the north (2001) and one from the south (2006).

Figure 2. Extent of hunting zones used by Makao-Linganga population. Bundi-Bossiani hunting zone is no longer used by hunters from Makao-Linganga.

Figure 3. Total biomass and number of animals hunted per year and per hunting zone. The number of animals hunted are presented by hunting zone to highlight the change in contribution of each hunting zone to overall harvest over time, while key events are also indicated to assist interpretation

Figure 4. Percentage contribution of different size/functional animal groups to the overall harvest per year.

Figure 5. Proportion of hunts within each hunting zone that contained one of three size/functional animal groups (long-term low-resolution offtake dataset).

Figure 6. Comparison of the proportion of day and night hunts by Kaka and Aka hunters containing medium-large ungulates.

Figure 7. Prey profile of hunts by distance from Makao-Linganga village.

DATA AVAILABILITY STATEMENT

Research data are not shared.