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Gun hunter behavior and success in the Tshuapa–Lomami–Lualaba landscape

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ABSTRACT
The behavior and success of commercial bushmeat gun hunters in the forest landscape between the Tshuapa and Lualaba rivers, Democratic Republic of the Congo, were studied to understand hunter practices and wildlife governance challenges through the lens of optimal foraging theory. Over a period of 4 months in 2016 to 2017 and 7 months in 2022, 242 hunter follows covering 3235 km were conducted. Hunting success increased with distance from the villages and was associated with wildlife encounter rates, the quality of guns and night hunting. Prey size and the type of encounter influence prey selectivity. The results indicate the limited applicability of optimal foraging theory to commercial bushmeat gun hunter behavior in the Lomami context, high hunting pressure on ungulates and primates, and the importance of the Lomami National Park to both protect biodiversity and as a source of wildlife for adjacent forests.

KEYWORDS
Democratic Republic of the Congo; gun hunter decision-making; human commercial wild species use; Lomami National Park; optimal foraging theory; protected species

Introduction

The hunting of wild species has resulted in population decreases of faunal resources, local species extinctions and defaunation of large forest tracts across the Congo basin (L. M. Coad, 2008; Fa & Brown, 2009; Kümpel et al., 2008; Wilkie et al., 2016), therefore jeopardizing the ecosystem integrity (L. Coad et al., 2013) and the survival of wild species of high conservation concern (Abernethy et al., 2013; Hart et al., 2008). Hunting for "bushmeat" ("viande de brousse" as known locally) is a main source of income for forest-dwelling people in the Democratic Republic of the Congo (DRC) and the wider Congo Basin (Fa & Brown, 2009; Harrison, 2011; Nasi et al., 2011; van Vliet & Nasi, 2008), including those adjacent to protected areas (Mavah et al., 2018). Unsustainable hunting eventually creates a vicious circle where decreased harvests of wildlife resources lead to decreased income and food security (L. Coad et al., 2018). These developments are further exacerbated by population growth, migration, advances in hunting technologies and improved accessibility to forest areas (L. Coad et al., 2018).

The Tshuapa–Lomami–Lualaba landscape (TL2 landscape) located between the rivers Tshuapa and Lualaba, the core of which is protected by the Lomami National Park (LNP) situated in the provinces of Maniema and Tshopo in the Central–Eastern

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DRC, has been highly impacted by hunting of commercial wild species (Batumike et al., 2021; USFWS-Great Ape Conservation Fund, 2009). Several wildlife policies have implications for hunting in the TL2 landscape, including temporary provincial-level hunting bans in Maniema (July–September) and Tshopo (August–November) with associated management measures (Hart et al., 2022), prohibition of all hunting in the LNP, and the protection status of wildlife regulated by a national legislation and the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES).

Hunter behavior is determined by prey choice, hunter effort and success and hunting techniques as a consequence of hunter decision-making (L. M. Coad, 2008; Kümpel, 2006). Optimal foraging theory, an "approach to the study of foraging behaviour that uses the techniques of mathematical optimization to make predictions about this critical aspect of animal behaviour" (Pyke et al., 1977), in the context of human hunting has been shown as useful to predict hunter behavior and decision-making (M. S. Alvard, 1993; L. M. Coad, 2008; Kümpel, 2006; Fa et al., 2022). The investigation of hunting patterns can be used to estimate wildlife abundance through wildlife encounter rates (Kümpel et al., 2008) and hunter off-take (Rist et al. 2008) and has enabled conservation scientists to improve the understanding of human–wildlife interactions in conservation landscapes.

Knowledge of hunting systems is essential to inform conservation strategies that address social institutions to reduce poaching (de Merode et al., 2007) and law enforcement patrolling to protect primates (Wiafe & Amoah, 2012). It can also inform governance and management schemes promoting sustainable hunting regimes (Fa et al., 2022; van Vliet et al., 2010). Studies addressing hunter behavior and the characteristics of hunting systems in Gabon, Equatorial Guinea and the Republic of the Congo showed the links between hunting systems, hunting success, the effect of seasonality on hunter behavior and socio-economic factors influencing local hunter behavior and decision making and have mostly focussed on trappers (L. M. Coad, 2008; L. Coad et al., 2013). Studies on hunting in the DRC described the transition to commercial hunting among the Mbuti (Hart, 1978) and the impacts of human hunting on bonobos (Hart et al., 2008) and demonstrated the ineffectiveness of wildlife protection laws in the absence of enforcement in the Northern DRC (Rowcliffe et al., 2004).

Commercial hunting has been shown to have significant impact on species extirpation locally (Abernethy et al., 2013). However, despite the increasingly widespread use of firearms due to their increasing availability (L. Coad et al., 2018) and empirical evidence that gun hunting leads to unsustainable hunting regimes and biodiversity loss in tropical forests and the overall bushmeat crisis in Central Africa (van Vliet & Nasi, 2008), few studies have addressed commercial shotgun hunting. Night hunting with shotguns, a method indicated as particularly effective (Bowler et al., 2020), has not been well studied in the Congo Basin. This study contributes to addressing these gaps. The aim was to understand the behavior and success of commercial bushmeat gun hunters and their use and interactions with unprotected and protected wildlife in the TL2 landscape, Central–Eastern Democratic Republic of the Congo, by understanding hunter decision-making, prey choice and night hunting using optimal foraging theory. Consequently, this study helps to advance the discussion on the applicability of optimal foraging theory to commercial gun hunting and informs local conservation management and governance of the TL2 landscape.

Optimal Foraging Theory and Hunter Behaviour

Optimal foraging theory (OFT) has been shown as relevant for the study and management of hunting (Fa et al., 2022; Koster & Venegas, 2012; Winterhalder & Lu, 1997), including bushmeat hunting in Central Africa (L. M. Coad, 2008; Kümpel, 2006; Rowcliffe et al., 2004). The theory has been successfully applied to human hunting in a broad range of geographical settings, while mis-matches between model predictions and hunter decision-making in empirical studies have been linked to the cultural aspects of prey choice (Fa et al., 2022). Critique of OFT also includes deficiencies in testability due to ad-hoc modifications of models, as models are based on parameters that are difficult to estimate (Fa et al., 2022). Building on mathematical models of costs and benefits, the theory has been applied to understand and predict the behavior of foragers, including human hunters in terms of prey choice, foraging location and time, where foragers attempt to maximize return rates in relation to foraging effort (Fa et al., 2022). The models that anticipate how human hunters behave and make decisions within their spatial environment include the optimal diet model and the central place foraging model (Koster & Venegas, 2012; Orions and Pearson, 1979).

The optimal diet model is related to prey choice, ranking prey according to profitability – usually weight or economic value of prey, and predicts that more profitable species are hunted more often than less profitable species (M. Alvard, 1995; Kümpel, 2006; Rowcliffe et al., 2004). This concept has mainly studied hunting methods characterized by selectivity, including gun hunters in Peru (M. S. Alvard, 1995, 1993) and commercial hunters in the DRC (Rowcliffe et al., 2004).

Central place foraging concerns animals that hunt from a fixed location and has been applied to human hunters in tropical forests (L. M. Coad, 2008; Levi et al., 2011). The model predicts that a forager will maximize calorific returns and thus increasingly target larger bodied prey with increasing distances from the central place to balance increased travel costs (Kümpel, 2006; Levi et al., 2011).

Methods

Study Area

The TL2 landscape is dominated by tropical forests, including riverine and lowland humid forest with edaphic grass savanna mosaics in the South. The core of the landscape is protected by the Lomami National Park, which was established in 2016, covering 8874 km^2. The wider landscape covers roughly 29.000 km^2 and contains around 330 villages and temporarily settlements (LNP management plan, unpublished).

Data on village-based gun hunter behavior were collected in 14 villages located in three administrative *collectivités* in the forested landscape around the LNP, shown in Figure 1, between 2016 and 2017 ($n = 44$) and 2021 and 2022 ($n = 198$). As seasonality affects hunting practices, the study was conducted in October–December during the rainy season in the Maniema province, in January and February during the dry season in the Tshopo province in 2016–2017, in February to June 2022 (dry and rainy season in Tshopo), and from March to July 2022 (dry and rainy season in Maniema) and coincided with formally regulated open hunting seasons. The village survey data were collected between November 2020–June 2021 and February–July 2022.

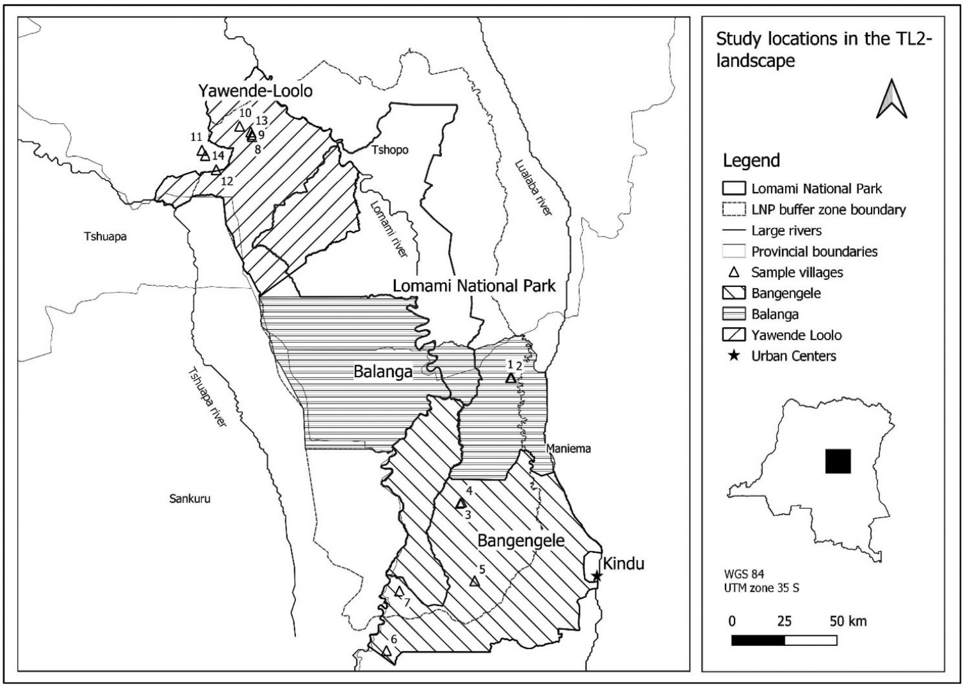

Figure 1. Study locations in the Tshuapa–Lomami–Lualaba landscape (TL2).

Hunter Follows and Household Survey

Data were collected from two data sources. 242 gun hunter follows were conducted with 54 different gun hunters of which 25 were in Maniema and 29 were in Tshopo, covering a total of 3235.25 hunting km and >1532 hunting hours. A village household survey sampling all households was carried out in 11 of the 14 participating villages.

The village household survey yielded supplementary data on the importance of commercial hunting for household income and the count of active gun hunters within each household. The household survey interviews were carried out in a private environment and questions were asked to the responsible household head in either Swahili or Lingala, the regional languages. This study makes use of household data from a broader village survey carried out in the TL2 landscape in 2021/22 and a study of hunter behavior in Balanga in 2016/17. The absolute number of present gun hunters could be determined in 9 of the participating villages to estimate the sample size.

Hunter follows are a useful method to assess territory use, effort, and success and other characteristics of hunter behavior (L. M. Coad, 2008; Kümpel, 2006; Rist et al., 2008). In the hunter follows, the hunter was asked why they hunt to determine commercial or subsistence hunting as a primary motivation and was accompanied during a hunting trip, and information about their behavior and decision-making was recorded. The number of follows per individual hunter was balanced to avoid skewing of data toward particular individuals (mean (M) = 4.48 follows per individual hunter; median (MED) = 3.5). Information on the hunter's age, hunting experience in years, the number of cartridges, and gun type were recorded before each follow. All data points from hunter follows were recorded in a log book and were spatially referenced using a GPS. Tracklogs were recorded for the duration of the follow to measure the overall hunting trip distance to determine hunter effort in km (Rist et al., 2008). Each wildlife encounter, where the hunter either saw or heard the animal, was recorded and the species was identified, based on the assessment of the hunter. Subsequently, the pursuit behavior, attempted shots and pursuit outcomes were recorded for encounters with commercial species. Hunter's qualitative and explanatory comments regarding their decision-making were also noted. Records of small mammals including squirrels (*Sciuridae*) and galagos (*Galagidae*) and birds, with the exception of Guinea fowls (*Numidiae.*) and Congo peafowls (*Afropavo congensis*), were excluded.

The research was guided by the Wageningen University Code of Conduct for scientific practice. The principles of informed consent, autonomy, confidentiality, anonymity and no harm were applied in all aspects of study, acknowledging the sensitivity of hunting. For this reason, village names are anonymized and respondents are anonymous. Local village administrative and customary authorities and hunters were asked for permission to conduct the study prior to any research based on informed consent. Hunters showed initial suspicion, despite agreeing to collaborating with the research team, and the data are thus skewed with hunters who were willing to participate.

Data Analysis

The village survey data were analyzed in Microsoft Excel. The village survey yielded quantitative data pertaining to the relevance of hunting as a commercial activity for household income. The absolute number of households for which commercial hunting is a relevant economic activity in relation to the total number of households sampled supported percentage values for each of the villages.

Hunter follow data were entered in Microsoft Excel and GIS shapefiles (hunter follows) and analyzed using SPSS and QGIS3. We calculated catch per unit effort (CPUE) for each follow dividing hunting offtake in kilograms by hunting hours, suing time as a measure for hunter effort (RIst et al., 2008;), shown in Table 1. The offtake weight was estimated based on the average male specimen weight using Kingdon´s field guide to African mammals (2015). CPUE measured in kg estimated offtake weight divided by hunting distance (kilometers) was complementarily used in several figures.

Wildlife encounter rates were calculated dividing the number of wildlife encounters by hour. Wildlife pursuit rates were determined dividing the number of pursuits per follow by the number of wildlife encounters. Hunts were categorized into day and night hunts, as well as village-based, camp-based and transit hunts (when hunters travel between their village and hunting camps) based on Rist et al. (2014), emphasizing this is an important factor due to variability in time that hunters spend actively hunting. Hunters were grouped according to gun type: 1) original brand 12 gauge shotguns (OBS), 2) city-manufactured shotguns (CMS) and 3) village-manufactured shotguns (VMS) – to investigate hunting success based on equipment, a further distinction as studies in Central Africa have demonstrated the increased effectiveness of shotguns and military rifles (Rowcliffe et al., 2004; Hart et al., 2008).

Informed by M. S. Alvard (1993), L. M. Coad (2008) and Kümpel (2006), the variables wildlife encounter rate (n wildlife encounters/hour), wildlife pursuit rate (pursuits/encounter), gun type, hunt type, distance from the nearest village, hunting in the LNP, time of the

Table 1. Variables used in the analyses.

Variable	Explanation	Abbreviation
Hunter follows		
Hunt type and metadata		
Purpose of hunting	Commercial or subsistence	
Age of the hunter	Age of the hunter	
Experience of the hunter	Years of active hunting	
Time of the hunt	Day hunt or night hunt	
Duration of the hunt	Duration of the hunting trip in hours	
Hunting distance	Distance of the hunt trip in km	
Type of hunt	1) Village-based (departing from and returning to the village)	
	2) Camp-based (departing from and returning to a camp)	
	3) Transit (departing from a village and ending in a camp or departing from a camp and ending in a village)	
Gun type	1) Original brand 12 gauge shotgun	OBS
	2) City-manufactured shotgun	CMS
	3) Village-manufactured shotgun	VMS
Cartridges	Number of cartridges brought on the hunting trip	
Wildlife		
Wildlife encounters	Type, number and location of wildlife encounters per follow	
Species	Name of encountered, pursued and killed species	
Species size	Estimated body weight of encountered, pursued and killed species	
Wildlife pursuits	Number of pursuits per follow	
Wildlife encounter rates	Wildlife encounters per km hunt	
Wildlife pursuit rates	Pursuits per wildlife encounter	
Duiker encounter rates	Duiker encounters per km hunt	
Primate encounter rates	Primate encounters per km hunt	
Duiker pursuit rates	Duiker pursuits per encounter	
Primate pursuit rates	Primate pursuits per encounter	
Hunting success		
Catch per unit effort	Estimated kg of killed animals per hunting hour	CPUE
Village household survey		
Relevance of hunting		
Share of households where commercial hunting is a relevant source of household income	Percentage of total households per sampled village where commercial hunting is a relevant source of income	

hunt (night and day), hunter age, number of cartridges and shot attempts per pursuit were fitted to an inverse Gaussian generalized linear model (GLM) using a log link function with CPUE (kg/hour) as the response variable to test for the effect on hunting success. A unstandardized regression coefficient was used to interpret the effect size of the variables fitted to the model as the scale of the response variable CPUE is known and interpretable (Nakagawa & Cuthill, 2007).

To analyze hunting success in relation to the nearest village distance and represent hunts spatially in the forested landscape, centroid locations were calculated for each of the hunts in GIS based on the hunter follow tracklogs. Centroids in this case are the mean center of all x- and y- coordinates associated with the tracklog. This provided a hunt distance measure for each of the 242 hunter follows, which was then fitted to the generalized linear model. Subsequently, based on this measure for the hunt distance from the nearest village, hunter follows were categorized according to five distance ranges: (1) 0–5 km, (2) 5–10 km, (3) 10–15 km, (4) 15–20 km and (5) >20 km for visualizations associated with the distance variable. A logistic regression model was used to examine the relationship between hunter pursuit decision-making and the size of the prey. The average adult body weight of the encountered animal was fitted to the logistic regression model with Yes = pursuit or No = no pursuit as the binary response variable.

Results

Hunting Success

All participating hunters were male and stated to hunt for the primary purpose of income with subsistence as a secondary motivation. Hunters occasionally used specific body parts for self-consumption, particularly intestines and animal heads, while smoking commercially more valuable animal parts for sale. The share of kg offtake used for self-consumption could not be determined. Commercial hunting (including snaring) is a major source of monetary income for 63.8% of the 411 households sampled in 11 of the villages (61.66% in Maniema and 67.55% in Tshopo). On average, 53.54% of gun hunters from the nine villages where the absolute number of gun hunters could be determined took part in the study.

The intercept of the GLM was significant ($B = -1.058$, $SE = 0.296$, Wald χ^2 (1) = 12.745, $p < .001$, 95% CI [−1.639, −0.477]). Wildlife encounter rates ($B = 0.284$), day or night ($B = -0.475$), the type of gun ([OBS]$B = 0.547$), distance between the hunting location and the nearest village ($B = 0.015$), age of the hunter ($B = 0.027$), the wildlife pursuit rate ($B = 0.430$) and the attempted shot per pursuit rate ($B = 0.951$) were significant predictors of hunting success (Table 2).

Shot attempts per pursuit ($B = 0.951$), day or night ($B = -0.475$), original brand shotguns ($B = 0.547$), wildlife pursuit rates ($B = 0.430$) and wildlife encounter rates ($B = 0.284$) had a stronger effect size on hunting success than age ($B = 0.027$) and distance between the hunting location and the nearest village ($B = 0.015$; Figure 2). The type of hunt

Table 2. Generalized linear model output with parameter estimates for CPUE.

Parameter	B	Std. Error	95% Wald Confidence Interval		Hypothesis Test		
			Lower	Upper	Wald Chi-Square	df	Sig.
(Intercept)	−1.058	.2963	−1.639	−.477	12.745	1	.000
Day or night (day)	−.475	.1442	−.758	−.192	10.855	1	.001
Day or night (night)	0[a]	.	.	.	.	.	.
In LNP	.071	.1835	−.289	.431	.149	1	.699
In and out LNP	−.379	.2815	−.931	.173	1.814	1	.178
Outside LNP	0[a]	.	.	.	.	.	.
Gun type OBS	.547	.1375	.277	.816	15.813	1	.000
Gun type CMS	−.018	.0959	−.206	.170	.035	1	.851
Gun type VMS	0[a]	.	.	.	.	.	.
Village-based	.169	.1244	−.075	.413	1.841	1	.175
Transit	.049	.0992	−.145	.244	.246	1	.620
Camp-based	0[a]	.	.	.	.	.	.
Distance between village and hunting location	.015	.0073	.001	.030	4.412	1	.036
Age	.027	.0058	.016	.039	22.536	1	.000
Shotgun shells	.004	.0069	−.010	.018	.333	1	.564
Wildlife pursuit rate	.430	.1926	.053	.807	4.988	1	.026
Wildlife encounter rate	.284	.0903	.107	.461	9.909	1	.002
Shot attempts/pursuit	.951	.1385	.679	1.222	47.146	1	.000
(Scale)	.129[b]	.0124	.107	.155			

Note. Dependent variables: CPUE; independent variables include day or night, PNL, gun type, type follow, distance hunting location-village, hunter age, *n* shotgun shells, wildlife pursuit rate, wildlife encounter rate, and shot attempts per pursuit.
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nt. Maximum likelihood estimate.

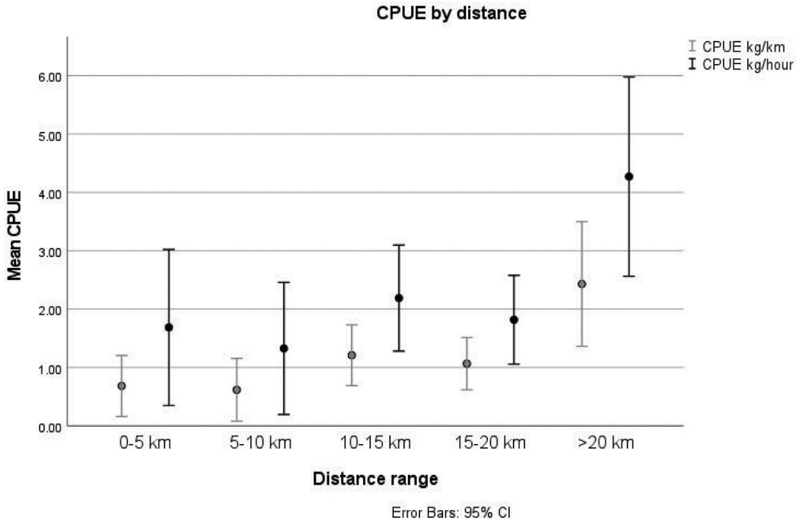

Figure 2. Wildlife catch per unit effort by distance.

(village-based, camp-based or during transit), the number of cartridges brought on the hunt and hunting in the LNP were not significant predictors for hunting success in the GLM. Original brand shotguns (OBS) were used by 14 hunters (59 follows), city manufactured guns were used by 13 hunters in (81 follows) and village manufactured guns were used by 27 hunters (102 follows). OBS hunters are significantly more successful than artisanal gun users, having similar wildlife pursuit rates but a higher shot kill per shot attempt ratio (0.83) than city (0.66) and village (0.45) manufactured gun users (Table 3).

There was no relationship between the wildlife encounter rate and distance ($r = 0.094$, $p = .147$). Encounter rates with larger-bodied species, including larger primates (Tshuapa red colobus, Angola colobus, and black-crested mangabey) ($r = 0.309$, $p < .001$) and duikers ($r = 0.344$, $p < .001$), increased with distance. The wildlife pursuit rate ($r = 0.246$, $p < .001$) and the attempted shots per wildlife pursuit ratio ($r = 0.374$, $p < .001$) increased with distance (Figure 3).

Table 3. Comparison of the performance of original brand shotguns, city-manufactured shotguns and village-manufcatured shotguns.

	OBS[a] hunt ($n = 59$)	CMS[b] hunt ($n = 81$)	VMS[c] hunt ($n = 102$)
Wildlife pursuit rate	0.70	0.67	0.64
Primate pursuit rate	0.71	0.65	0.72
Shots per km	0.17	0.15	0.24
Shots per direct encounter	0.52	0.41	0.48
Shots per pursuit	0.63	0.53	0.73
Shot hit escape/attempt	0.05	0.03	0.15
Shot kill/attempt	0.83	0.66	0.45
Primate shot kill/attempt	0.79	0.61	0.44
CPUE (kg/km)	1.92	0.84	0.83
CPUE (kg/hour)	3.86	1.53	1.57

[a]Original brand shotguns
[b]City-manufactured shotguns
[c]Village-manufactured shotguns

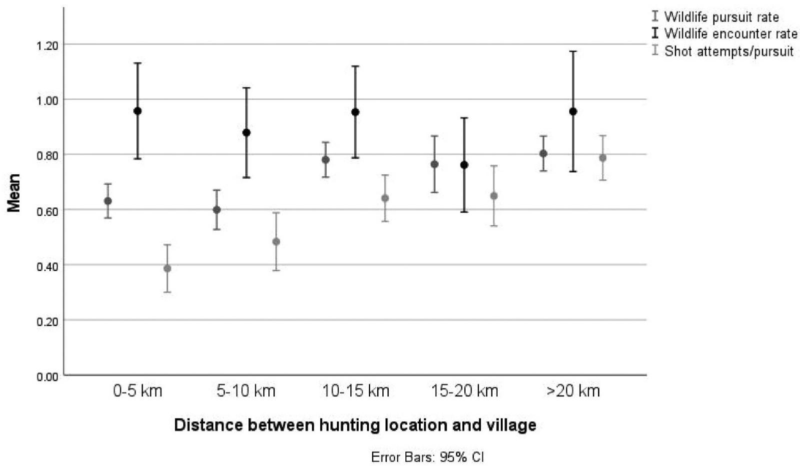

Figure 3. Wildlife pursuit rates, wildlife encounter rates and shots per pursuit ratio by distance.

Prey Choice

Primates and duikers accounted for 85% of offtake. Primates accounted for 70.98% of all wildlife encounter situations ($n = 1163$) and were mostly detected by their vocalizations or noise (78% of encounters). 69% of primate encounters were followed by a pursuit by the hunter. Duikers accounted for 11.5% of all wildlife encounters and were pursued in 85.9% of cases. Hunters attempted shots on duikers in 73% of pursuits compared to 33% in primate pursuits. 51% of duiker encounters resulted in a killing, compared to 20% of primate encounters, 26% of antelope and buffalo encounters and 11% of hog encounters. The logistic regression model revealed that there was no statistical relationship between the pursuit decision making and the size of the animal ($B = 0.003$). This indicates that changes in the weight of the largest species in the group are not associated with changes in the pursuit rate. Average pursuit rates of duikers (0.83 pursuits per encounter) and monkeys (0.81 pursuits per encounter) are similar and higher than for antelopes and hogs (0.69 pursuits per encounter). Smaller primates such as juveniles were repeatedly not targeted as hunters frequently returned from stalks stating "they were too small." Very small and reportedly not hunted mammals of no commercial value – such as squirrels – were excluded from the analysis. Adults of large species such as bongos (*Tragelaphus eurycerus*) and African forest buffalos (*Syncerus caffer nanus*) were reported as not hunted by hunters using village-manufactured guns and reportedly difficult to hunt with commonly used shot pellets or slugs by original brand shotgun hunters, partially attributed to risks of confrontation with a wounded and/or aggressive animal. 6.7% of shot attempts on red river hogs by VMG hunters were successful, while in the majority of cases, hogs were not hit fatally and escaped. 42.86% of shot attempts by CMS hunters on either hogs or sitatunga resulted in the killing of the animal as opposed to 77.78% successful attempts by OBS users on either sitatunga, hogs or yellow backed duikers.

The primate pursuit rate increased with the distance from the village ($r = 0.179$, $p = .012$). The highest pursuit rate was observed in hunting locations more than 20 kilometres away from the nearest village (0.84) compared to a pursuit rate of 0.71 (pursuits per encounter) at distances of 0–5 kilometres and 0.59 pursuits per encounter at distances of 5–10 kilometers. However, this trend was not evident for smaller-sized species, such as the red-tailed monkey and the wolf's mona monkey, where there was no significant relationship between the pursuit rate and distance ($r = -0.130$, $p = .135$). Bonobos were pursued in one out of five direct encounters.

Other nationally protected species including golden cats (*Caracal aurata*), sitatunga (*Tragelaohus spekii*), water chevrotains (*Hyemoschus aquaticus*) and tshuapa red colobus monkeys (*Procolobus tholloni*) had relatively high pursuit rates.

Night Hunting

Night hunting targeted nocturnal species. 30% of the sampled hunters were followed in the night. As the hunter walks, he scans the undergrowth with his headlamp to spot the reflective eyes of wildlife. As soon as an animal was spotted, it is spotlighted and the hunter tries to get closer to reach a suitable shooting position. Ambush hunting was also often used at night where the hunter mimics the calls of duikers and antelopes to lure them in the dark. If the hunter hears noises in the thicket as a result of his calls, he switches on the lamp to scan the undergrowth. Night hunting was a significant predictor of hunting success in the generalized linear model. Predominantly terrestrial species, such as duikers and water chevrotains, were more susceptible to nighttime hunting, with night hunts accounting for 77.37% of the total duiker offtake in terms of estimated weight (kg). Duiker encounter rates were higher during night follows, shown in Table 4, and 55.36% of duiker encounters occurred at night time. The Mann–Whitney U test revealed that the average encounter rate of larger mammals, such as antelopes, was significantly higher at night ($U = 5710.50$, $n = 242$, $p < .001$) compared to during the day and five out of seven antelope kills occurred at night. There was no difference in the hog encounter rate between day and night hunts ($U = 4975.00$, $n = 242$, $p = .614$). During daytime pursuits, preys were successfully killed in 30% of pursuits, but during night pursuits, the success rate increased to 52% and the shots per kill ratio was lower. Village-based night hunts had a range of up to 15.1 km from the village. 35 night hunts were camp-based. More than 50% of recorded hunts in the park were night hunts, comparing to 18% for outside-LNP hunts. Several hunters, particularly in the South of the landscape, reported preference to hunt inside the LNP in the night because the perceived risk of encountering law enforcement patrols and arrest was considered lower.

Table 4. Comparison of day and night hunting.

	Day n = 191	Night n = 51
Wildlife encounter rate (n/hour)	0.90	0.75
Duiker encounter rate	0.03	0.15
Wildlife pursuit rate	0.66	0.66
Shot attempts per encounter	0.39	0.52
Shot attempts per pursuit	0.55	0.65
Kills per pursuit	0.30	0.52
Kills per attempt	0.56	0.77
Kg duiker offtake	208	711.25
CPUE (kg/hour)	1.45	4.46
CPUE (kg/km)	0.83	2.11

Discussion

Original brand shotgun hunters had higher CPUE than artisanal gun users, likely related to the better overall quality, less technical errors, range and power of the gun, and faster recharge. Users of artisanal guns seem to have to get closer to prey than original brand shotgun hunters to have similar chances of success. Distinguishing between models of shotguns is a relevant further differentiation of gun hunting in Central Africa (Rowcliffe, de Merode & Cowlishaw 2004, Hart et al., 2008), and related variation of hunting success suggests that gun hunters have different impacts on fauna, depending on the gun type. Deepening the understanding of the technology–hunter interface is relevant to understand local and regional faunal trends and decline or resilience of particular wild species due to hunting (Kümpel et al., 2008; van Vliet & Nasi, 2008) and relating to law enforcement and gun control. The hunter age, shown as a relevant predictor for individual success among trappers in Gabon (L. M. Coad, 2008) and Equatorial Guinea (Kümpel, 2006), had a significant effect on hunting success of gun hunters in TL2. The number of shotgun shells did not predict hunting success in hunter follows, but the distance of the hunting location to the nearest village is a significant predictor of hunting success where hunting success increases with increasing distance, which corresponds to central place foraging predictions (M. S. Alvard, 1993; Levi et al., 2011). Wildlife encounter rates were not correlated with distance; however, duikers and larger primates were more frequently encountered in locations further away, indicating that larger bodied prey are relatively more depleted closer to villages, similar to observations in the Republic of the Congo (Mavah et al., 2018). This pattern corresponds with predictions of central place foraging models (M. S. Alvard, 1993; Levi et al., 2011). Increasing hunting success in relation to the increasing distance from the village seems to be furthermore associated with higher wildlife pursuit rates and shot attempts per pursuit, which increase with village distance. This behavior may support the survival of certain species around villages and might be associated with more open-access hunting systems in distant locations and competition, which would require further empirical investigation.

The size of commercially relevant prey was not a statistical determinant of the pursuit behavior of hunters, which suggests equal selection of smaller and larger commercial prey alike and similar targeting of wildlife within the commercial species range. Monkeys, low-ranked species in diet-breadth models in tropical environments with availability of larger bodied species (Hawkes et al., 1982), similar to Lomami, had similar pursuit rates as larger bodied duikers and higher pursuit rates than antelopes and hogs. High pursuit rates of smaller primate species, in the Lomami context, seem to be associated with the commercial nature of hunting. Very large mammals like bongos and African forest buffalos were not pursued by artisanal gun hunters due to the constraints of artisanal guns combined with a perceived high risk of being attacked. A substantial share of larger bodied ground dwelling species such as sitatunga and red river hogs observed in Kindu bushmeat markets (Batumike et al., 2021) seems to be caught by trapping rather than gun hunting. Primate-specific pursuit rates ranged between 0.4 and 1, suggesting that certain primates seem to be more attractive prey – regardless of the mean primate body size – which could be related to different levels of meat quality and possibly is linked to primate behavior and perceived odds for success in pursuits, and the nature of the encounter probably has an influence too.

Species that are known for their loud vocalizations might have been sometimes overlooked and not pursued due to their distance, regardless of their size.

Distance to the village does not influence hunters' decision-making in primate pursuit behavior, contradicting predictions of central place foraging where hunters would be expected to increasingly neglect smaller-sized species and specialize on larger species the further they go from a central place (M. S. Alvard, 1993; Kümpel, 2006; Orions & Pearson, 1979). Hunters invest similar efforts in pursuing and stalking smaller bodied primates in distant forests and locations nearby villages alike, different to subsistence hunters in Peru (M. S. Alvard, 1993). Possible variation in this decision-making between different hunter populations would require further investigation.

The price of shotgun shells could be a factor for such decision-making, as observed among gun hunters in Ecuador (Sirén & Wilkie, 2016), Peru (M. S. Alvard, 1993) and Equatorial Guinea (Kümpel et al., 2008), and seems to be a selective factor among gun hunters, reflected by their ignoring very small primate specimen and juveniles. Ammunition price dynamics are likely to have an effect on the threshold of species falling into the prey range (Sirén & Wilkie, 2016), which in turn can affect wildlife population dynamics.

The protection status of an animal partly influences prey choice, different to observations in Northern DRC (Rowcliffe et al., 2004), which is attributed to awareness-raising and wildlife law enforcement. Bonobos were pursued though not killed in one out of five encounters. Other nationally protected species such as African golden cats, Tshuapa red colobus and water chevrotains were pursued and killed. While we acknowledge that the researchers presence might have influenced hunter behavior in particular situations, this indicates the hunters' general confidence in collaboration with the research team to some degree, while varying levels of awareness regarding the protection status of species less prominent than bonobos and sitatunga and lower perceptions of risks and associated sanctions in the case of killing and sale could be factors. There were few encounters and only one kill with the endemic and protected dryas monkey, and accordingly, it cannot be confirmed whether hunter decision-making corresponds with the reports from villagers, who state that dryas is not hunted due to its small size (Alempijevic et al., 2021). There were no absolute species hunting taboos at the village level, congruent with other places where wildlife is commercialized (Rowcliffe et al., 2004; Kümpel et al., 2008). Lower encounter rates of duikers and larger primates around villages indicate the hunting effects on fauna similar to patterns near the Odzala National Park in the Republic of Congo (Mavah et al., 2018) and correspond with central place foraging predictions (Levi et al., 2011). On the other hand, hunting in the LNP did not predict hunting success, suggesting prey availability in the park's surroundings. Particular species are likely more impacted by hunting than others (van Vliet & Nasi, 2008) and focusing attention on both animal and hunter behavior could reveal the underlying mechanisms of hunter–prey interaction that can explain the detrimental effects of commercial hunting on certain species, and resilience among others (Fournier et al., 2023; Kümpel et al., 2008, Linder & Oates, 2011). Sparing primate juveniles and small specimen and source potential of the LNP and the low efficiency of artisanal guns could contribute to the resilience of particular species toward gun hunting and sustainability of particular hunting systems.

Night hunting was a significant predictor for hunting success in the regression model and CPUE was higher during night hunts, attributed to the larger average body size and related higher commercial value of most duikers, compared to primates that constitute most of the prey obtained during the day, similar to Robinson & Remis. The higher number of kills per shot ratio in night hunts is attributed to the short range at which duikers are encountered and their freeze response when dazzled by torchlight (Newing, 2001). Smaller arboreal species, including palm civets and pottos, are targeted only opportunistically, similar to Laurance et al.'s (2008) findings in Gabon. While hunters in Gabon hunted at less than 5 km from villages (van Vliet & Nasi, 2008), night hunters in the TL2 landscape ranged up to 15 km from the village, practiced camp-based night hunting and entered the LNP in the night with more than 50% of recorded hunts in the LNP being night hunts, based on a perception of lower risk of encountering law enforcement patrols and being arrested. Gun hunters in TL2 used conventional flashlights at the time of the study; however, the introduction of LEDs and rechargeable batteries increased night hunting and the effectiveness of night hunters (Bowler et al., 2020) and has negative impact on fauna.

Conclusions and Conservation and Management Implications of Gun Hunting in TL2

This study provides empirical evidence to understand the behavior and success of commercial gun hunters and their use and interactions with unprotected and protected species in the Lomami landscape, Central–Eastern DRC, by understanding hunter decision-making, prey choice and night hunting using optimal foraging theory. There were limitations in explaining prey choice and hunter decision-making of commercial gun hunters in the Lomami context, particularly concerning central place foraging, although the prey body size did not predict pursuit rates. The results show varying levels of hunting success according to the type of shotgun, suggesting that economic and regulatory mechanisms affecting access to good quality guns might reduce the hunting pressure, especially on primates. Night hunting is profitable and thus of concern for conservation. Illegal hunting in the park could be curbed by increased patrol team presence at night. A comprehensive analysis of the interactions between faunal trends, spatial-temporal aspects of LNP patrols and law enforcement, and hunter behavior over time could support a more holistic understanding of how the LNP is affected by hunting and inform management and communities on how to deal with hunting and community livelihoods.

Hunter decision-making, in terms of pursuit behavior and prey choice, indicates that protected species are targeted by gun hunters with the exception of bonobos and dangerous large mammals such as buffalos and bongos. Relatively lower wildlife encounter rates of larger bodies species around villages indicate the sink character of these areas and the importance of the LNP as a source to sustain wildlife and consequently local income opportunities, food and nutritional needs of local communities in its vicinity.

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Disclosure Statement

No potential conflict of interest was reported by the author(s).

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Data Availability Statement

The data that support the findings of this study are available from the corresponding author, Maximilian Graefen, upon reasonable request.

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