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RESEARCH ARTICLE



Fluid hunter motivation in Central Africa: Effects on behaviour, bushmeat and income

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Abstract

- 1. Individual motivation for the rural use of common-pool resources (CPRs) can be fluid, with the line between subsistence and commercial often unclear and in flux.
- 2. Implications of fluid motivation are understudied yet important for socialecological systems (SESs), such as bushmeat hunting throughout Central Africa that is essential to local protein/nutrition, income and culture.
- 3. Making locally informative predictions of multiple SESs nested within a landscapescale SES has been historically difficult, but community-driven participatory approaches provide new kinds and quantities of data, opening previously inaccessible doors for research and governance.
- 4. We apply hierarchical Bayesian structural equation modelling to a novel dataset of 910 hunts from 111 gun and trap hunters across nine villages in Gabon, generated in a participatory process whereby hunters conducted GPS self-follows in conjunction with paraecologist surveys of their motivation, behaviour and offtake. We (i) establish the human behaviour driving gun-hunting and trapping success and predict its effect on offtake across villages and (ii) link fluid motivation of gun hunters to their behaviour, number of animals hunted, biomass yielded and income earned.
- 5. Gun hunts across villages yielded more animals during the night than the day, and when hunters brought high amounts of ammunition and walked far distances from villages. Gun hunts were less successful when coupled with trapping while perhunt success of trapping itself was generally low and difficult to predict. Fluid gun hunters hunted fewer animals when motivated strictly by subsistence, despite no

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reduction in ammunition brought or distance walked, while offtake from strictly commercial versus mixed motivation was the same. Numbers of animals hunted, biomass and income were tightly linked. We discuss the implications of these results for the ecological sustainability of hunting and participatory forecasting in bushmeat research and policy.

KEYWORDS

common-pool resource, community hunting management, Gabon, human ecology, paraecology, rural livelihoods, social-ecological system, wild meat

1 | INTRODUCTION

The hunting of wild animals is 'one of the most fundamental and enduring of human-wildlife relationships', revealing cultural, economic and ecological dimensions of human behaviour and the socialecological systems (SESs) with which we coevolve (Kurz et al., 2021). Why and how people hunt changes with the conditions of a given SES over time. There is a widespread interest in how the politics of colonization and capitalism and their related phenomena such as urbanization, rural migration patterns, development, land tenure and resource rights, logging, climate change and conservation influence hunting and its impacts on human culture and well-being, biodiversity and ecosystem functioning (Ingram, 2020; Ingram et al., 2021). Much has been written about the increasing commercialization of hunting and implications for sustainability, especially in the rainforests of Central Africa, a region of abundant biodiversity and 'bushmeat' (from the French viande de brousse) hunting, trade and consumption (Abernethy et al., 2013). Yet the modern line between subsistence and commercial hunting-as with the rural use of a vast range of other common-pool resources (CPRs)-is blurred (Atheull et al., 2009; Carroll et al., 2003; Chauhan et al., 2008; Clark et al., 2002; Coad et al., 2019; Dahdouh-Guebas et al., 2000; Gombay, 2006; Ingram et al., 2021; Joly et al., 2019; Lacuna-Richman, 2002; Muth et al., 1996; Poe et al., 2015; Staddon, 2009). Animals are not hunted only for consumption or sale, but often for both (as well as for other reasons, such as protecting crops or cultural ceremonies).

Most research on hunter motivation has examined clear contrasts or gradients such as the probability of hunting versus not (lbbett et al., 2020; Nuno et al., 2013; Silvestre et al., 2021) or the degree of commercialization of hunting in relation to economic drivers (Bachmann et al., 2019; Brashares et al., 2011). In West Africa, Bachmann et al. (2020) further explored the effects of motivation, finding that commercially motivated hunters travelled long distances to hunt duiker in forested protected areas whereas more subsistence hunters focused on rodents in agricultural areas near villages. Similar outcomes due to cultural variation were found in the Amazon, where Indigenous hunters targeted larger-bodied species in more distant and intact forests versus non-Indigenous hunters who stayed closer to villages hunting smaller species (Constantino et al., 2021). Still, the more subtle implications of motivation remain underexplored. Many bushmeat SESs entail hunters of the same ethnicity hunting for both income and food (to varying degrees) across the same relatively contiguous landscape. In this common scenario, could the motivation of an individual hunter change from hunt to hunt, and if so, how might this affect their behaviour (technology use, effort across space and time and social dynamics) and offtake (beyond the above mentioned changes in prey profiles)? One could expect that such an individual fluid hunter, on a more commercially motivated hunt, would mirror the changes many (though not all) hunting SESs have undergone as they commercialize: increased hunting effort and higher offtake.

Offtake refers to 'the quantities of meat harvested' (Coad et al., 2019). How should bushmeat research define and measure these quantities? The total number of animals hunted, especially of threatened species, may be of greatest interest to conservation scientists or government environmental officials, whereas the total biomass or money earned may be of greatest importance to hunters and their families. Rather than a single definition or metric, offtake should be considered in ecological, alimentary and economic terms, and links made between them. Robust insight into the sustainability of hunting requires coupling data on offtake with hunter behaviour (Riddell et al., 2022).

Data on offtake from the last few decades of bushmeat hunting research are abundant, and social data increasingly so (though Nana et al. (2022) highlight the dearth of attention to noneconomic cultural factors). Yet we still lack a holistic understanding of the drivers of hunter behaviour and its effects on offtake; for example, what are the causes and results of hunting in the night versus the day, and of using guns versus wire snares (hereafter 'traps'; Dobson et al., 2019)? Although a few empirically rich case studies have tracked changing use of guns and traps over time (Coad et al., 2013; Gill et al., 2012), it is difficult to directly compare the efficiency of the two hunting methods (Dobson et al., 2019; Marrocoli et al., 2019). Individuals may also combine gun-hunting and trapping, though their relationship in this context is hitherto unexplored (Kumpel et al., 2009). The relationship between motivation and behaviour also depends on technology. Motivation and behaviour could change from hunt to hunt for gun hunters. For trap hunters, changes occur over a longer time period, as traps remain active for long periods, sometimes many months, with hunters laying more traps or changing their location at specific, infrequent moments for various reasons.

How can we link hunter motivation, behaviour and offtake, and do so in a way that is useful to the governance and management of bushmeat hunting? Intensive studies of specific locations provide detailed insight into hunting behaviour and the composition and level of offtake, but it can be hard to generalize results from sitespecific studies across regions (Balvanera et al., 2017; Villamayor-Tomas et al., 2020). Meta-analyses or big data approaches are valuable for general insight, but are not in-depth or locally relevant enough to inform proposed future directions in sustainable hunting initiatives such as community adaptive management (Coad et al., 2019). Scale mismatches thus appear to be a problem that is difficult to address in both theory and practice. The explicit spatial delimitation of a focal SES is rarely clear; SESs are generally nested and can be analysed at the local, regional and global scale (Martín-López et al., 2017). Bushmeat hunting of a single community can be viewed as a single SES, nested within a landscape SES containing multiple community SESs, affected by and interacting through wider social-ecological conditions. For example, even discrete hunting catchments may be linked through shared source populations of wildlife (Antunes et al., 2016; Mockrin & Redford, 2011; Novaro et al., 2000) that could in turn be mutually impacted by external factors, such as the expansion of logging (Poulsen et al., 2009; Riddell et al., 2022). High quality and quantity of local data across a landscape SES would yield locally useful understanding of community SESs, the comparisons of which would yield an aggregate understanding of the landscape SES. A particular advantage to such data would be enabling the explicit forecasting of alternative management strategies-including predicting future human behaviour and its consequences under different scenarios to proactively prepare for change and adapt to it over time (Travers et al., 2019).

Participatory approaches such as hunter self-monitoring and paraecology (a paraecologist is a 'resident professional with local knowledge who lacks formal academic training [but has] fulltime employment underpinned by extensive [on site] training'; Schmiedel et al., 2016) enable the collection of data designed with and collected by communities that can link information and make predictions across different scales (e.g. hunt, hunter, community, landscape). When data are collected by local people, many sites can be simultaneously studied, and informed through in-depth local social-ecological knowledge, versus the limited time and understanding of an outside research team (Danielsen et al., 2021). New technology like simple GPS units now enables the local collection of hunt-level spatially explicit information of a previously unimaginable quantity (Fa et al., 2021; Froese et al., 2022). Participatory monitoring allows us to simultaneously address multiple, sometimes interacting, aspects of bushmeat hunting SESs. Further advantages abound: devolving power in science, local data ownership and use for autonomous decision-making, creating opportunities for knowledge coproduction, boundary spanning between rights holders and policy decision-makers, and high-quality participatory mapping vital to customary land tenure rights needed for just and sustainable hunting governance and management (Camino et al., 2020;

Constantino et al., 2018; Froese et al., 2022; Malmer et al., 2020; Norstrom et al., 2020; Reed et al., 2019; Villaseñor et al., 2016).

Here, we link hunter motivation, behaviour and offtake by applying hierarchical Bayesian structural equation modelling to a dataset of novel origin, quantity and depth generated by paraecologists and participating hunters. Specifically, we: (i) establish the human behaviour driving gun-hunting and trapping success and predict its effect on offtake across villages and (ii) link fluid motivation of gun hunters to their behaviour, number of animals hunted, biomass yielded and income earned. We discuss implications for the ecological sustainability of hunting and participatory forecasting in bushmeat research and policy.

2 | METHODS

2.1 | Study system and participatory data collection

Rural hunters from nine villages (five Kota and four Fang) near the town of Makokou, provincial capital of the Ogooué-Ivindo Province, Gabon, collected data via the Nsombou Abalghe-Dzal project's participatory bushmeat hunting monitoring programme coupling paraecology with hunter GPS self-follows (Froese et al., 2022; https://nadagabon.org). The study area is characterized by low human population density and relatively intact forests and wildlife; yet it is under increasing disturbance from logging, mining and associated access (more information in Froese et al., 2022). Study villages represent around half of the total villages ~50km from Makokou along the three national roads that join the town, randomly selected with stratification for, ethnicity, road and population size in an earlier phase of the project (Beirne et al., 2019; Froese et al., 2022). In each village, the paraecologist (authors BB, SDN, JE, JE, SEK, JLM, CM, IN and EN) conducted pre- and posthunt surveys with participating hunters (up to five each month, rotating monthly with the order of participation selected at random in a communitywide meeting and the frequency of participation evened out over time; we set an upper monthly limit of five participating hunters due to the number of available GPS units). All hunters who wished to participate did, and we emphasized that the project did not define hunting strictly as walking long distances with a gun at night, but that for the project hunting included any form of killing an animal, even just checking a few traps in a backyard plantation.

In each survey, paraecologists asked participating hunters a suite of social, ecological and economic questions and weighed all animals hunted. Questions included asking about the behaviour we considered in this study: if the hunt was conducted during the day and/or night, the amount and type of ammunition taken on the hunt, whether hunters went alone or with porters and/or other hunters, and the number of traps they checked and how long it had been since they checked them. Before each hunt, motivation was learned by paraecologists who asked each participating hunter: why are you going hunting? See Supplementary Material 1 for an English translation and the original French data sheets, data sheets, protocol and instructions. Hunters carried simple GPS units (Mobile Action® i-gotU GT-600) to quantify their spatial behaviour. The bushmeat hunting SESs in the study area, process of our engagement in community-driven research and methodological specifics of hunter GPS self-follows are described in detail in Froese et al. (2022).

'We obtained authorization to conduct research in Gabon through the Institut de Recherche en Ecologie Tropicale (IRET) within the Centre National de la Recherche Scientifique et Technologique (CENAREST) (N°AR0057/18/MESRS/CENAREST/ CG/CST/CSAR and N°AR004/20/MESRTT/CENAREST/CG/CST/ CSAR). Our research with human subjects was further approved by Duke's Institutional Review Board (IRB; Protocol Number: Froese 2019-0047). We followed the principle of free, prior and informed consent (FPIC) at both the community and individual level (Ibbett & Brittain, 2020). Communities gave oral FPIC during meetings before any research was conducted; individual hunters gave oral FPIC in response to a written FPIC statement read aloud to them. Hunters understood (a) how the data would be used, (b) that they could refuse to participate without experiencing negative consequences, (c) that they could cease participating without giving a reason at any time, (d) that they could see their personal data at any time, (e) that they could ask us to delete their data at any time, (f) the process by which we anonymized identifiable data, (g) that we did not have the desire or right and would not share data identifiable to either villages or hunters with any outside parties including the Gabonese government and (h) that they could contact us and ask questions at any time. Only adult (>18 years old) hunters participated. We do not include village names or identifiable maps in publications'. (Froese et al., 2022).

2.2 | Modelling approach

The processes by which bushmeat is harvested, and the factors which influence such processes, differs by hunting method (here guns vs. traps). Therefore, we modelled the animals hunted using each technology separately, for both gun hunts (including when also trapping) and trap hunts (including when also gun-hunting). To predict how human behaviour drives gun-hunting and trapping success across multiple villages, we fit generalized linear mixed models (GLMMs; Section 2.3 below). To link fluid motivation of gun hunters to their behaviour, number of animals hunted, biomass yielded and income earned, we fit a multivariate response generalized linear mixed piecewise structural equation model (mvGLMpwSEM; Section 2.4 below).

We included all continuous behavioural predictors (see Section 2.3) deemed important from the literature and our knowledge of the study site, and statistically sensible to include together based on causal theory (Pearl, 2009)—as well as the potentially important factors of weather (rainy or not during the hunt), hunting period (night, day or both) and wet versus dry season. We fit varying intercepts of hunter and village. In reality, each unique hunter was confined to a unique village, suggesting a nested approach. But we did not specify it as such when fitting models in order for hunters to be compared to the total pool of hunters across villages (assuming that a skilled hunter in village A is more similar to a skilled hunter in village B than he is to a less skilled hunter in village A). Regardless, this should not tangibly change inference (McElreath, 2020). We did not use global intercepts, because we prioritized making predictions at the village level and comparing them across villages.

We formatted all categorical predictors as index variables, as we were interested in individual categories rather than in comparison to a reference. The lone exception was weather, formatted as a dummy/binary/indicator variable, because rainy hunts were rare (6% of hunts) and can be seen as different from the norm.

We quantified a suite of metrics representing hunter effort in terms of space and time: hours hunting, total km (distance) walked, size of area hunted, max km (from) village and mean km village. These could all influence hunter offtake in various ways. For example, the farther a hunter walked, the more likely he (all hunters were male) is to cross an animal's path (but he could also circle around his house all day and get nothing). Likewise, the larger the area the hunter searches, the more likely he will overlap the home ranges of more animals. The Euclidean distance from the village is likely important, given that wildlife in the study area is more abundant farther from villages (Beirne et al., 2019; Koerner et al., 2017). Increased time hunting also increases potential for animal encounters, regardless of distance or area. Causal relationships between these metrics are not clear, and the direction of causality could change within a hunt. We chose to include only one space-time metric in models, max km village, because it captures both hunter effort and potential reduction in the local abundance and/or occupancy of hunted species (defaunation) and is the most tangibly perceived and thus potentially useful metric for community hunting management decision-making. Furthermore, as expected, all these metrics were highly correlated, and max km village was the most highly correlated across all metrics (Figure S1). A principal components analysis (PCA) showed that >75% of total variation was captured by the first component, to which max km village contributed slightly more than the other metrics (Figure S2).

We centred (subtracted from the mean) and scaled (divided by the standard deviation) all continuous predictors to facilitate model convergence and comparison of effects across predictors. We formatted variables that acted as both responses and predictors in the model of fluid gun hunter motivation (see below) in their original values as responses, log-transformed for kg (biomass) and money to improve fit given high variation in values, and centred and scaled them as predictors.

We modelled count responses using a Poisson rather than a gamma-Poisson (negative binomial) distribution, as exploratory modelling demonstrated that gamma-Poisson estimates contained extreme and unrealistic maximum values, overestimated dispersion, and had a very high values of the shape parameter (indicating similarity to a pure Poisson process). Furthermore, variance was explicitly modelled by nesting by village and hunter. Parameter estimation was the same using both distributions. For the fluid gun hunter motivation model, we used a gamma distribution for continuous responses (or a normal distribution if log-transformed) and a Bernoulli distribution for binary responses.

We quantified uncertainty with 92% intervals—the midpoint between the arbitrary 95% (which should be avoided should it evoke erroneous comparisons to p-values) and the increasingly en vogue though equally arbitrary 89% (McElreath, 2020). Regardless, we used posterior predictions to more fully understand uncertainty rather than simply including or excluding parameters based on whether their uncertainty interval overlaps zero.

All models were Bayesian, fit through the Stan probabilistic programming language via the R package brms (Burkner, 2017; Stan Development Team, 2022). We used prior predictive checks to identify uninformative yet reasonable priors; those for fixed variable coefficients and standard deviations of varying intercepts were coincidentally the same as the first bushmeat paper to use brms (Jones et al., 2020). We ran models with four chains of 3000 iterations each (1500 warm-up), giving posterior distributions of 6000 estimates. We assessed model fit through visual MCMC diagnostics and graphical posterior predictive checks using the R package bayesplot as outlined in Gabry et al. (2019). Models fit well. Input data and reproducible scripts of data exploration, prior predictive checks, model fitting, model checking (including an HTML file showing all plots) and posterior predictions and plotting are available at: https:// github.com/gradenfroese/fluidHunters.

2.3 | Establishing meaningful hunter behaviour to predict offtake across villages

Below we present the full gun model. The full trap model was structured the same, but without the behaviour predictors trap hunt (in addition to gun-hunting), nightday (hunting period), small ammo (number of 00 cartridges, suitable for most species and the most commonly used ammunition), large ammo (chevrotine, a larger shotgun shell used for larger animals, more expensive to purchase and less often used), porters (number accompanying the hunter to help carry bushmeat) and other hunters (number accompanying the hunter, with their own gun), and with the behaviour predictors gun hunt (in addition to trapping), traps checked (the total number) and trap days (since traps were last checked). Refined models retained meaningful predictors as determined by whether posterior predictions of responses changed along the range of the predictor in a clear direction-entailing posterior distributions of parameter estimates with little overlap with zero, without using arbitrary cut-offs-with a magnitude that could have real-world consequences (see Section 3). Animals refers to the total number of animals hunted, and threatened to the total of animals from species listed as Near Threatened, Vulnerable, Endangered or Critically Endangered on the IUCN red list.

In the notation for all models, α symbols indicate varying ('random') intercepts belonging to individual villages and hunters; and linear model coefficients for categorical predictor variables. For example, $\alpha_{\text{village}[h]}^{[m]}$ denotes the varying intercept for model *m* assigned to a village relevant to hunt *h*; the superscript *m* represents models for all animals and those for threatened in a common notation and distinguishes between them. β symbols denote linear model coefficients. The index *h* is frequently used to refer to separate hunts and the *p* index runs over different continuous and binary predictor variables. We used normal distributions for priors of predictor variables and varying intercepts, and exponential distributions for priors of standard deviations of varying intercepts.

animals_h ~ Poisson
$$\left(\lambda_h^{[1]}\right)$$

threatened_h ~ Poisson $\left(\lambda_h^{[2]}\right)$
 $p \in \{1, ..., 7\}$
 $m \in \{1, 2\}$

(p=1, ..., p=7) = weather, traphunt, max km village, small ammo, large ammo,

porters, other hunters

$$\log \left(\lambda_{h}^{[m]}\right) = \alpha_{\text{village}[h]}^{[m]} + \alpha_{\text{hunter}[h]}^{[m]} + \alpha_{\text{season}[h]}^{[m]} + \alpha_{\text{nightday}[h]}^{[m]} + \sum_{p=1}^{7} \beta_{p}^{[m]} X_{hp}$$
$$\alpha_{\text{season}}^{[m]}, \alpha_{\text{nightday}}^{[m]} \sim \text{Normal}(0, 0.5)$$
$$\beta_{p}^{[m]} \sim \text{Normal}(0, 0.5)$$

 $\alpha_{\text{village}}^{[m]} \sim \text{Normal}\left(0, \sigma_{\text{village}}^{[m]}\right)$ $\alpha_{\text{hunter}}^{[m]} \sim \text{Normal}\left(0, \sigma_{\text{hunter}}^{[m]}\right)$ $\sigma_{\text{village}}^{[m]}, \sigma_{\text{hunter}}^{[m]} \sim \text{Exponential}(2)$

To predict the effect of meaningful behaviour on offtake across villages, we varied slopes of predictor variables by village, using a bivariate normal distribution (MVNormal) parameterized in terms of a mean vector and covariance matrix. To complete a fully Bayesian model specification, we used the LKJ prior (LKJcorr) for the correlation matrix of the normal prior, with its single parameter set to 1. This is equivalent to a uniform prior over correlation matrices with entries residing in [0.0,1.0]; for a complete covariance specification we include additional scale parameters via the diagonal matrix **S**.

See below the gun model. The trap model is structured the same, but with different predictors.

animals_h ~ Poisson (λ_h)

$$p \in \{1,2\}$$

$$(p = 1, p = 2) = \max \text{ km village,}$$
 small ammo



2.4 | Linking fluid motivation of gun hunters to their behaviour and offtake

We tested if the number of animals hunted changed in response to hunter motivation, and if so, how this relationship was mediated by their modelled behaviour. To do so we compared three submodels within the mvGLMpwSEM (Figure 1). First, we fit a model assuming that motivation drives changes strictly through unknown and unobserved mechanisms with no mediation by modelled hunter behaviour. Second, we fit a partial mediation model testing the hypothesis that motivation drives changes in animals hunted in part through driving changes in modelled hunter behaviour; if so, we would expect to see a weaker influence of motivation through the unknown pathway. Third, we fit a full mediation model assuming that there is no unknown effect of motivation on animals hunted; here, a change in the influence of modelled behaviour on animals hunted would indicate dependence between modelled behaviour and the unknown mechanisms. We used the bivariate normal distribution (MVNormal) to estimate correlation of behaviour as multivariate responses within hunters (vs. its use to estimate varying slopes in above models).

For successful hunts, we used the mvGLMpwSEM to test how the number of animals hunted and max km village drive total kg. It is clear that hunting more animals should yield higher total biomass; from our previous research we can further hypothesize that animals hunted farther from the village will be more sensitive, larger-bodied species, increasing total biomass even given the same number of animals hunted (Beirne et al., 2019; Koerner et al., 2017).

We further used the mvGLMpwSEM to test whether the probability of hunters selling some bushmeat directly mapped to their original motivation, and if it was dependent on kg: if a hunter's intention was strictly to eat, but he had unexpectedly high offtake, we would expect him to sell something, as stomachs fill faster than pockets. We also tested the probability of selling all bushmeat, for which we would expect kg to be less important, because if a hunter shot many animals he may want to keep some to eat. Lastly, when some bushmeat was sold, we investigated the relationship between money earned and kg, and whether original motivation influenced money earned.

> small ammo_h ~ Poisson $\left(\lambda_{h}^{[1]}\right)$ maxkm village_h ~ Gamma $\left(a, \lambda_{h}^{[2]}\right)$ animals_h ~ Poisson $\left(\lambda_{h}^{[3]}\right)$



FIGURE 1 Top: directed acyclic graph (DAG) of multivariate response generalized linear mixed piecewise structural equation model (mvGLMpwSEM) linking fluid gun hunters motivation, behaviour, and offtake. For 342 hunts, wh = why hunt (eat, sell, or both), km = max km village, sa = small ammo brought on hunt, ?= unobserved and unknown mechanisms, and <math>an = animals hunted. For 186 successful hunts (an > 1, grey circles) kg = biomass, ss = probability of some bushmeat being sold, and as = probability of all bushmeat being sold. For 143 hunts with some bushmeat sold (dark grey circle) mo = money earned. h refers to a single hunt, the unit of observation. Bottom: sub-models testing different possible mediation pathways of behaviour.

and many subjects to cover during subsequent visits to and meetings in villages). Villages had ~10-50 total hunters, though never present in a given village at the same time. Estimating the number of active hunters in a village is difficult because it can vary greatly even within brief periods, but in the four smaller villages generally ~60%-70% of hunters participated in GPS self-follows and in the five larger villages participation was ~35%-50%. Thirty hunters used exclusively guns, four were exclusively trappers, and 77 used both techniques. They recorded 910 total hunts (479 using a gun, 198 using traps and 233 using both techniques) and 1331 animals hunted from 43 total species (Froese et al., 2022). Two hundred and ninety-seven of the animals hunted were from 12 threatened species. Fifty-nine per cent of animals hunted were sold. Of these sold animals, 85% were for sale at the village (71% of these were hung up along the roadside for sale to passing cars, 23% were sold to others in the village such as neighbours, friends and family members, and 5% were sold to merchants). Regarding sales to cars, traffic was both to and from Makokou, and we do not know what percentage purchased was consumed by the buyer versus resold or gifted. Of the 14% of sold animals brought to Makokou for sale, 53% were sold at the bushmeat market, 29% to merchants, 7% for ceremonies, 6% to a hotel on a single occasion and 3% for a marriage on a single occasion. Of the 41% of animals which were eaten, we did not collect data on potential variation in consumption patterns as our sampling protocol explicitly avoided bothering people when preparing or eating food.

We a priori excluded eight hunts longer than 48 h from models, as they represent a different process than those we aimed to understand (often hunting in preparation for ceremonies, rather than for daily needs of food and money). Final models with the full suite of predictor variables included 623 gun hunts and 368 trap hunts. We explored imputation of missing predictor variables which occurred in ~13% of hunts, but it was unreliable, and we had sufficient data. Anonymized GPS tracks and associated hunter data can be explored with our Shiny participatory mapping app: https://gradenfroese.shinyapps.io/carto_ex_EN/.

3.1 | Offtake across behaviour and villages

For gun hunts, the full model of behaviour estimated that the number of animals hunted increased with max km village and small ammo, as well as with large ammo to a lesser degree (Figure 2). Other hunters and porters had no effect on the number of animals hunted, though raw data showed that hunts with porters had more animals hunted along with higher max km village and small ammo (Figure S3). For trap hunts, the number of animals hunted was estimated to increase with the number of traps checked, and to slightly decrease with max km village and days since traps checked. Trends for threatened species mirrored all animals (excepting evidence for a negative effect of other hunters), but parameter estimates were more uncertain.

Both trapping and gun-hunting during the day was predicted to yield on average <1 animal per hunt, versus >1 animal per hunt in gun hunts during the day and night or night alone (Figure S4).

 $\log(kg)_h \sim \text{Normal}\left(\mu_h^{[4]}, \sigma^{[4]}\right)$ some sold_h ~ Bernoulli $\left(p_{h}^{[5]} \right)$ all sold_h ~ Bernoulli $(p_{h}^{[6]})$ when some sold = = 1 $\log(\text{money})_h \sim \text{Normal}\left(\mu_h^{[7]}, \sigma^{[7]}\right)$ $\log \left(\lambda_{h}^{[1,2]}\right) = \alpha_{\text{village}[h]}^{[1,2]} + \alpha_{\text{hunter}[h]}^{[1,2]} + \alpha_{\text{whyhunt}[h]}^{[1,2]}$ $\log \left(\lambda_{h}^{[3]}\right) = \alpha_{\text{village}[h]}^{[3]} + \alpha_{\text{hunter}[h]}^{[3]} + \alpha_{\text{whyhunt}[h]}^{[3]} + \beta_{1}^{[3]} \max \operatorname{km village}_{h} + \beta_{2}^{[3]} \operatorname{small ammo}_{h}$ $\mu_{h}^{[4]} = \alpha_{\text{village}[h]}^{[4]} + \alpha_{\text{hunter}[h]}^{[4]} + \beta_{1}^{[4]} \operatorname{animals}_{h} + \beta_{2}^{[4]} \operatorname{max km village}_{h}$ $\operatorname{logit}\left(p_{h}^{[5,6]}\right) = \alpha_{\operatorname{village}[h]}^{[5,6]} + \alpha_{\operatorname{hunter}[h]}^{[5,6]} + \alpha_{\operatorname{why hunt}[h]}^{[5,6]} +$ $\beta_1^{[5,6]}$ kg $\mu_{h}^{[7]} = \alpha_{\text{village}[h]}^{[7]} + \alpha_{\text{hunter}[h]}^{[7]} + \alpha_{\text{why hunt}[h]}^{[7]} + \beta_{1}^{[7]} \text{kg}_{h}$ $\alpha_{\text{why hunt}}^{[1,2,3,5,6,7]} \sim \text{Normal}(0,0.5)$ $\beta_1^{[3,...,7]}, \beta_2^{[3,4]} \sim \text{Normal}(0,0.5)$ $\alpha_{\text{village}}^{[1,\ldots,7]} \sim \text{Normal}\left(0,\sigma_{\text{village}}^{[1,\ldots,7]}\right)$ $\left[\alpha_{\text{hunter}}^{[1]} \right] \sim \text{MVNormal}(\mathbf{0}, S)$ $\alpha_{\rm hunter}^{[2]}$ $\alpha_{\text{hunter}}^{[3,...,7]} \sim \text{Normal}\left(0, \sigma_{\text{hunter}}^{[3,...,7]}\right)$ $\Sigma = SRS$ $\mathbf{S} = \begin{bmatrix} \sigma_{a_{\text{hunter}}^{[1]}} & \mathbf{0} \\ \mathbf{0} & \sigma_{a_{\text{hunter}}^{[2]}} \end{bmatrix}$ $\sigma_{\text{village}}^{[1,...,7]}, \sigma_{\alpha_{\text{humber}}^{[1,2]}}, \sigma_{\text{humber}}^{[3,...,7]}, \sigma^{[4,7]} \sim \text{Exponential}(2)$ $a \sim \text{Gamma}(4,0.8)$

3 | RESULTS

One hundred and eleven hunters from nine villages conducted GPS self-follows from 10 June 2019 to 9 March 2020. We excluded a small amount of data from: a month of pilot collection in a single village, a tenth village (fifth Fang village) in which hunter GPS self-follows began but were soon stopped due to a lack of interest, and in two villages where there were some problems with paraecologist data collection (where we retained data after the problem was resolved). Participating hunters were all male and ranged from 20 to 79 years old (mean = 42, SD = 12). The majority of hunters, though not all, present during initial meetings decided to participate, and some others that were not present at that time later joined (which we encouraged though did not actively promote due to limited time

 $\mathbf{R} \sim LKJcorr(1)$



FIGURE 2 Mean and 92% uncertainty intervals (UI) summarizing posterior distributions of standardized coefficient estimates of hunter behaviour (β) on gun-hunted and trapped animals.

These partial effects were conditional on unchanging behaviour, and so the difference was due to unmodelled behaviour and/or social-ecological context, such as animals being easier to hunt at night using LED headlights (Bowler et al., 2020). Given equivalent modelled behaviour, hunting during both the day and night was not predicted to increase the number of prey over strictly night hunts. In the raw data such an increase was observed, as hunters went farther from the village during hunts that occurred over the day and night (Figure S4). Neither gun nor trap hunting yielded different numbers of animals across seasons. This was also the case for the raw data. The number of animals hunted decreased on rainy gun hunts; rain had no effect on trap hunts (Figure S5).

The majority (68%) of combined gun and trap hunts occurred strictly during the day. During these combined day hunts, gunhunting was predicted to yield half as many animals as a gun-only day hunt, while trapping success was similar whether or not in conjunction with gun-hunting (Figure 3). Combined offtake from gunhunting and trapping was virtually the same as strictly gun-hunting.

We refined models to include only meaningful behaviour as predictors—max km village and small ammo for gun hunts, number of traps checked and traps days for trap hunts—with the number of animals hunted as the sole response given the similar trends and high uncertainty in threatened species. Refined models predicted similar numbers of animals hunted to the full model (Figure S6). As varying intercepts were more variable across villages than hunters (Figure S7), we then created a gun and trap model with refined predictors varying slope by village. All models retained varying intercepts by both village and hunter. The effect of behaviour on animals hunted was highly consistent across villages in gun hunts, and diverse in trap hunts, though estimates in the latter were highly uncertain (Figure 4 and Figure S8).

The number of animals hunted were predicted to increase with max km village, and this relationship strengthened with increasing small ammo (Figure 4). In observed data, ~25% of hunts were <2 max km village, ~50% were between 2 and 5 and ~25% were >5; the maximum was 17. For small ammo, 2 was the 18th percentile, 4 the 54th and 6 the 86th; the maximum was 18. The amount of small ammo has an influence beyond simply limiting the maximum number of animals that could be shot because hunters sometimes miss (the mean wasted small ammo per hunt ranged from 0 to 1.1 across villages). At far distances with low ammunition, impossible values could be predicted, but this combination of behaviour rarely occurs (in only 11 of 704 hunts did hunters have <3 small ammo and walked >5 km from their village). There was no evidence of a relationship between traps checked and animals hunted (Figure 4), regardless of the number of days since traps checked, for which 2 days was the 24th percentile, 4 the 65th and 6 the 85th; the maximum was 49. This finding stands



FIGURE 3 Left: mean predicted number of animals yielded during day hunts by gun and trap, with 92% uncertainty intervals (UI). OR refers to only one method being used during a hunt; AND refers to both being used. The horizontal gray line and shaded area represents the summed mean and 92% UI of gun and trap offtake during combined hunts.

in contrast to the similar standardized coefficient estimates between traps checked for trap hunts and max km village and small ammo for gun hunts (Figure 2). But all predictors were centred and scaled, and an increase of 1 translates to an increase of ~50 traps checked (a large amount; the mean traps checked was 54, and the maximum was 255) in contrast to an increase of ~2.5 max km village and ~2 to 4 small ammo (much more common changes).

3.2 | Fluid motivation of gun hunters

Hunters usually responded that they intended to both eat and sell their bushmeat. Of 106 gun hunters in our data, 51 were monotypic, always giving the same motivation: 41 hunters always hunted for both reasons, six just to eat, and four just to sell. But 54 hunters were fluid: sometimes stating both reasons, sometimes just to eat, and sometimes just to sell, and very rarely for other reasons, like protecting their fields or preparing for a ceremony (we believe that hunters' varying responses robustly reflect fluid motivation, given that a full response to the simple question of 'why are you going hunting?' did not require deep energy or engagement, and that there is no reason to think these fluid hunters would only sometimes fully engage with the same question that they generally engaged with). We retained 342 hunts of fluid gun hunters in the mvGLMpwSEM, removing one extreme outlying hunt that had very high biomass (145 kg, vs. the second highest observed value of 79 kg) and money earned (117,000 XAF, vs. the second highest observed value of 56,000 XAF). Motivation in 199 of these hunts was to eat and sell versus 54 strictly to eat and 89 strictly to sell.

When a hunter's a priori motivation was strictly to eat, he was predicted to hunt ~1 less animal than if his motivation was to eat and sell (Figure 5). A strict intention to sell did not change the predicted number of animals hunted relative to eat and sell. This was the case with and without behaviour included in the model, evidence that the mechanism through which motivation to eat reduced animals hunted was not through reduced max km village or small ammo (neither of which were predicted to change with motivation to eat). The motivation to sell predicted no change in small ammo, and a mean ~1 farther max km village walked by hunters, although this latter estimate was highly uncertain. Within hunters, there was a predicted correlation between max km village and small ammo, despite no global or within-hunter correlations in the raw data (Figure S9).

At the observed mean during successful hunts of 4.2 max km village, total kg was predicted to strongly increase with an increasing number of animals hunted; at the observed median during successful hunts of two animals hunted, total kg was not predicted to change with increasing max km village (Figure S10). This implies that, while going farther from villages increased the chance of hunting more animals (Figure 4), the biomass of individual animals was consistent across varying distances. Inference did not change when including the outlying hunt.

At very low kg, hunters with strictly commercial intentions were predicted as more likely to sell some offtake than those with dual intentions (~70% vs. ~55%; Figure 6). Regardless of original motivation, the probability of selling bushmeat rapidly rose with increasing kg, and was virtually guaranteed by 50 kg. The probability of selling all bushmeat was predicted as higher given a motivation of sell versus eat and sell (~70% vs. ~50%), and did not change with increasing kg. Money earned was predicted to increase with kg irrespective of motivation, though the maximum estimated income was ~1.5–2.5 times greater than realistic. Income was well-predicted for most hunts, but not for highly successful hunts (biomass of \gtrsim 40 kg: ~nine blue duiker, three medium duiker or a large red river hog). When including the outlying hunt, predicted income of high biomass hunts was even more unrealistic; inference on probabilities of sale did not change (Figure S11).

4 | DISCUSSION

We linked motivation of bushmeat hunters to their behaviour and offtake across nine villages, by applying hierarchical Bayesian structural equation modelling to a novel dataset gathered through community monitoring coupling paraecology with participating hunter GPS self-follows. Gun-hunting success across villages increased during the night and with more ammunition and farther



FIGURE 4 Top: predicted gun-hunted animals across observed max km village conditional on small ammo. Bottom: predicted trapped animals across observed number of traps checked conditional on days since traps checked. Gray lines represent fitted slopes from 500 posterior distributions in refined global models (thick lines = means). Coloured lines represent mean slopes across the 9 villages in the varying slopes models; their uncertainty is not shown for plot readability (but see Figure S8). Length of lines vary by village with their range of observed predictors. Dashed horizontal lines represent the maximum possible number of animals that could be hunted given small ammo.

from villages, and decreased when coupled with trapping. Trapping success was lower than gun-hunting and more difficult to predict. Fluid gun hunters hunted fewer animals when motivated by bushmeat consumption alone, though not due to modelled hunter behaviour (no reduction in ammunition brought or distance walked), while offtake from strictly commercial versus mixed motivation was the same. Different forms of offtake–numbers of animals hunted, biomass and income–were tightly linked. Below we consider our findings in more detail and discuss implications for the ecological sustainability of hunting and participatory forecasting in bushmeat research and policy.

4.1 | Drivers of gun hunter behaviour and offtake

Increasing ammunition and the maximum distance from the village drove higher offtake. This is an unsurprising but new insight nonetheless—little research has been conducted on gun-hunting



FIGURE 5 Mean predicted change with 92% uncertainty intervals (UI) of number of animals hunted, max km village, and small ammo in gun hunts by fluid hunters with an intention strictly to eat or sell versus a baseline of both, shown as estimated by the no (motivation alone) versus partial (+ behaviour) mediation models (Figure 1).

success in relation to ammunition and spatial effort. Importantly, this relationship was consistent across nine villages, indicating that our results could be used to extrapolate to other community SESs within the study landscape SES (~20 total villages) to generate more general inference. As simple GPS tracking and participatory approaches grow in use, our results should be compared to both seemingly similar and divergent bushmeat hunting SESs.

In this work, like much of the (albeit sparse) bushmeat hunting research that draws on SES theory, we did not conduct analyses through Elinor Ostrom's (and others afterwards) proposed general framework for analysing SESs (Ostrom, 2009; Smith et al., 2018). For more explicit engagement of bushmeat hunting research with CPR and SES theory, the 'continued development of diagnostic frameworks that balance local context with generalizability will require increased communication and engagement among scholars outside the established silos of wildlife and commons scholars' (Smith et al., 2018). Special attention in such frameworks must be paid to indices of the 'resource unit' variable-what culturally grounded indicators can give direct insight into the state of the resource itself, the wildlife that is hunted (Hongo et al., 2022; Ingram et al., 2015; Ostrom, 2009; Sterling et al., 2017)? We found that income, a key form of offtake, was difficult to accurately predict when many animals were hunted.

Several predictors had little influence on offtake. The number of porters and other hunters was inconsequential—hunting in our study SESs can thus currently be analysed at the individual hunter level with community-level insights made through additive logic, rather than considering social dynamics during hunts. It is unknown if this is the norm or an exception, as there is currently little research on relationships between hunters, though work on hunter-trader relationships is increasing (e.g. Jones et al., 2019).

Surprisingly, offtake was not predicted to vary across seasons (conditioned on other predictors being held constant). This differed from local perceptions; participatory data exploration with communities show diverse monthly trends across species and villages-and a wealth of local knowledge on drivers-that may not be capable of producing signals when aggregating noise from 12 months into two seasons and >50 species into 'animals'. Seasonal differences in offtake could also be due to changes in hunting behaviour, though we did not explicitly test this (e.g. raw data showed higher offtake in gun hunts during the dry season, along with higher small ammo and max km village). Models further showed that rain does not have a strong direct effect on offtake, though the small number of rainy hunts, even during the rainy seasons, indicates it influences the decision to go hunting in the first place. Local perceptions are that climate is changing fast in our study SES, with increasingly unpredictable weather. While the relationship between bushmeat hunting and climate change is little studied (but see Bodmer et al., 2018), and is currently considered to be less important than changing rural social dynamics and increasing extractive industry, the influence of climate on hunting dynamics could increase in the decades to come.



FIGURE 6 Predicted probability across observed total kg of bushmeat gained during successful hunts of selling some offtake (top left), selling all offtake (bottom left), and predicted money earned when some offtake sold (right; $4e+04 \text{ XAF} \approx 65 \text{ USD}$). Lines represent fitted slopes from 500 draws of posterior distributions (thick lines=mean), coloured by a priori hunter motivation to strictly sell or both eat and sell.

Varying intercepts of hunters showed little influence on the number of animals hunted. This, along with the fact that most hunters used both gun and traps, seems in contrast to research in West Africa showing more economically reliant hunters targeting duiker with guns in forests, and more nutritionally reliant hunters targeting rodents by trapping fields (Bachmann et al., 2020). Forest cover is largely contiguous across our study landscape SES (like much of Central Africa, though forest disturbance varies greatly), which could limit the potential to specialize hunting based on habitat; though a very small number of trap hunters were motivated to protect crops as seen in West Africa (Duonamou et al., 2021), agricultural fields in Gabon are generally small. Important differences between hunters may also manifest in their modelled behaviour, such that varying intercepts of hunters were less important because their behaviour was accounted for. Or hunters may vary in how often they hunt (which we did not study), versus their skills or strategies while hunting (e.g. Riddell et al., 2022). Indeed, a common trend is that a small number of hunters hunt a disproportionately high amount of a community's total offtake (Coad, 2007; Jones et al., 2020). More specific work on hunters themselves would shed light on these ideas, all untested in this study.

Gun hunts motivated by bushmeat consumption alone had lower offtake for reasons unknown, while strictly commercial versus mixed motivation did not affect offtake. This suggests that on a hunt in which a fluid hunter was not intending to sell any bushmeat he would initially exert a similar effort (walk just as far from the village with just as much ammo) until successful, and once getting enough to eat would go home. More work on in-hunt decision-making would be needed to confirm this, but exploration of raw data indeed shows that hunts motivated by subsistence alone were around one hour shorter than mixed motivation hunts. The generally low prevalence of strictly commercial hunters and hunts suggests that van Vliet and Nasi's (2008a) finding from our study area that 'there appears to be no clear tendency to abandon subsistence hunting for commercial hunting as in other regions of Africa' remains the case over 15 years later. Ethnographic research could help better understand underlying hunting motivation and how they are changing (or not) over longer time scales and across social-ecological conditions not addressed in this study (Blaser, 2009; Gibson, 2020; Moon et al., 2019; Shaffer et al., 2018; Wade & Malone, 2021). Further and more broadly, contextualizing detailed linkages like those our models provide here with theory on human motivation and behaviour could provide a foundation for longer-term predictions of changes in subsistence-commercial gradients of CPR use over time.

4.2 | Trapping success: Counterintuitive and complex

We expected that when a hunter checked more traps he would have higher offtake. This was not the case (despite standardized coefficient estimates indicating an effect, highlighting the importance of making posterior predictions over interpreting model coefficients alone). Trapping success per hunt was generally low, so perhaps there was simply not enough variation in offtake for prediction. Or perhaps analysing trapping on a per hunt basis is not appropriate: if few animals occur in a relatively small trapped area, high numbers of traps could initially be more productive after being set, but even a small number of traps could catch the total available animals over time, giving similar offtake when calculated as per-hunt averages across long periods. Dobson et al. (2019) identified the 'influence of the spatial arrangement of snares on capture success' as a future research direction. Our data did not permit pursuing that idea, but paraecology coupled with participating hunters could be used to scale up spatially and temporally explicit monitoring of trapping such as that of Coad (2007). Regardless, in our study SES trap use is decreasing over time (van Vliet & Nasi, 2008a) and only 24% of animals hunted are trapped (Froese et al., 2022), so trapping may be of less importance than gun-hunting for sustainability. Yet the dramatic reduction in gunhunting success when trapping also occurred shows that legacy effects may be occurring-areas trapped are typically done so for long periods, so even if trap efficiency is low wildlife populations could be depleted over time.

4.3 | Assessing and increasing hunting sustainability

The ecological sustainability of bushmeat hunting is notoriously difficult to ascertain (van Vliet & Nasi, 2008b; Weinbaum et al., 2013). and this study cannot do so. Nor did it attempt to estimate overall offtake, though integrating the data here with village-wide paraecologist bushmeat transects enables estimating total offtake by villages across the landscape SES (Froese et al., 2022). The relatively high amount of hunters conducting GPS self-follows, ~35%-70% of hunters across study village, gives a robust interpretation of typical village-based hunts. Hunter self-follow data were local in kind: while hunting camps were used, as they often are across Central Africa (Abernethy et al., 2013), this was rare: only 86 of the 910 total hunts. Still, participating hunters may conduct other important forms of hunting across the landscape SES not captured by this study. For example, four of the eight hunts excluded from models for being longer than 48h were hunts preparing for ceremonies in a single village, during which hunters on average stayed 4 days in the forest a max 15km from the village, were accompanied by three porters and two other hunters, brought 22 small and two large ammo, and returned with 16 animals hunted (though <1 threatened)-figures vastly larger than village-based averages. The frequency of such ceremonial hunts across the landscape SES is unknown and likely fluctuates year-to-year with social dynamics. Many hunters from villages, Makokou, and elsewhere also spend large amounts of time in gold mining camps both close to and far from villages. Hunting

associated with these camps is unknown, and given the diffuse, transient and oft-clandestine nature of gold mining, would be far more difficult to conduct participatory research on at scale. Hunting by loggers in the region is equally difficult to assess, as is that of urban hunters (these classifications are not necessarily mutually exclusive: in one village, most hunters now live in Makokou, but go back to the village a few times a week to hunt). While forms of hunting not based in villages may have relatively small direct impacts of wildlife populations within village hunting catchments, they could have strong influence on source–sink dynamics so important to ecological sustainability. Assessing sustainability becomes even more complex when considering its social, economic and political dimensions (O'Connor, 2006).

Still, coupling our detailed drivers of hunt-level offtake with our more general results from our data sources of defaunation gradients (Beirne et al., 2019; Koerner et al., 2017) and community-level hunting dynamics (Froese et al., 2022) should provide a fertile playground (Mastandrea & Pericàs, 2021) for exploring potential patterns of defaunation and ways to understand it in our study SESs. It is striking that individual animal biomass did not increase farther from villages. Overall patterns in offtake are likely driven by a small number of most hunted species—such as blue and medium duiker, small porcupines and pangolin, and common monkeys-and rare larger-bodied species of conservation interest whose abundance/occupancy of forest is known to increase farther from villages, such as chimpanzees and gorillas, may not have much influence in the data. Griffiths et al. (2022) found that closer to villages animals were better at escaping hunters; drivers of not only human but also wildlife behaviour merit further work. This should be coupled with explicit considerations of source-sink dynamics: mapping spatial patterns of overall hunting pressure was not our focus here, but hunter GPS self-follows are a strong method for doing so.

Although participatory monitoring alone cannot resolve the many difficulties of assessing sustainability, it can increase it. We designed our methods not only to answer our research questions but also to provide a platform for community ownership of data and engagement informing self-determined hunting management. As of June 2023, three of the nine study communities have launched community hunting management (the governance, form and effects of communities' management and its relationship to their participatory monitoring is beyond the scope of this article). High-quality maps of village territories produced by hunters can help strengthen community land tenure rights and wildlife conservation (Constantino et al., 2018). Progress in the sustainability of community SESs can ripple out to others, amplifying impact in the landscape SES through "'incrementalism', whereby individual projects have only a small impact, but collectively the impact is large." (Scholes et al., 2013). Local progress in a given community SES does not provide a direct blueprint for scaling up, but lessons learned can inform pathways to doing so (Balvanera et al., 2017). Lessons from this work can contribute to the government of Gabon's current 'revising [of] their wildlife legislation' (Nana et al., 2022).

4.4 | Participatory forecasting for community adaptive bushmeat hunting governance and management

Increasingly accessible and popular, hierarchical Bayesian modelling greatly improves our ability to deal with complex data and thus our 'capacity to more directly apply [social-]ecological understanding' to decision-making (Clark, 2005; insertion ours). Meanwhile, lured by the prospect of getting closer to causality, researchers across disciplines are turning towards structural equation modelling (SEM; Laughlin & Grace, 2019; Pearl, 1998). But as in bushmeat hunting research, these parallel developments have been largely in isolation: hierarchical SEM is 'powerful yet unexplored' (Fan et al., 2016) despite the flexibility Bayes offers SEM being pointed out almost 20 years ago by Clark (2005). We brought these worlds together, and our models are better for it-and could potentially be further improved through nonlinear functions such as in Koster et al. (2020) and integration with agent-based modelling for generating predictions via the accumulation of individual simulated hunts rather than aggregate inference-but will still always have limits. These limits can be traversed by knowledge-coproduction weaving quantitative understanding with local knowledge and qualitative insight (Collins et al., 2021; Malmer et al., 2020; Norstrom et al., 2020).

Here our monitoring was participatory but our modelling was not. A logical next step is to build our estimated posterior distributions into a participatory forecasting tool, one that values and uses local knowledge (e.g. as informative priors for differences in wildlife abundance across local areas) and simulates the effects on offtake of potential community management actions. Iterative forecasts could be made by communities over time, with accuracy tested and posteriors becoming new priors (Banner et al., 2020). A key outstanding unknown is the use—and usefulness—of such knowledge in community decision-making of hunting governance and management.

AUTHOR CONTRIBUTIONS

Graden Z. L. Froese, Alex Ebang Mbélé, Christopher Beirne and John R. Poulsen conceived the ideas and designed the methodology with inputs refining ideas and methods prior to data collection from Blaise Bazza, Sylvain Dzime N'noh, Jovin Ebeba, Jocelin Edzidzie, Serge Ekazama Koto, Jonas Landry Metandou, Clotaire Mossindji, Irma Ngoboutseboue and Eric Nzemfoule; Blaise Bazza, Sylvain Dzime N'noh, Jovin Ebeba, Jocelin Edzidzie, Serge Ekazama Koto, Jonas Landry Metandou, Clotaire Mossindji, Irma Ngoboutseboue and Eric Nzemfoule collected the data with supervision and computer entry and cleaning from Graden Z. L. Froese and Alex Ebang Mbélé; Graden Z. L. Froese analysed the data with contributions from Alex Ebang Mbélé, Christopher Beirne, Daniel J. Ingram, Christopher Krapu, Abhishek Baral, Srishti Saha and John R. Poulsen; Graden Z. L. Froese led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare that there is no conflict of interest.

DATA AVAILABILITY STATEMENT

Input data and reproducible scripts of data exploration, prior predictive checks, model fitting, model checking and posterior predictions and plotting are available at: https://github.com/gradenfroese/fluid Hunters. Shiny participatory apps in English and French, and forthcoming apps and updates, can be found at: https://nadagabon.org.

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REFERENCES

- Abernethy, K. A., Coad, L., Taylor, G., Lee, M. E., & Maisels, F. (2013). Extent and ecological consequences of hunting in central African rainforests in the twenty-first century. *Philosophical Transactions* of the Royal Society B: Biological Sciences, 368(1631), 20130494. https://doi.org/10.1098/rstb.2013.0494
- Antunes, A. P., Fewster, R. M., Venticinque, E. M., Peres, C. A., Levi, T., Rohe, F., & Shepard, G. H. (2016). Empty forest or empty rivers? A century of commercial hunting in Amazonia. *Science Advances*, 2(10), e1600936. https://doi.org/10.1126/sciadv.1600936
- Atheull, A. N., Din, N., Longonje, S. N., Koedam, N., & Dahdouh-Guebas, F. (2009). Commercial activities and subsistence utilization of mangrove forests around the Wouri estuary and the Douala-Edea reserve (Cameroon). Journal of Ethnobiology and Ethnomedicine, 5(35). https://doi.org/10.1186/1746-4269-5-35
- Bachmann, M. E., Junker, J., Mundry, R., Nielsen, M. R., Haase, D., Cohen, H., Kouassi, J. A., & Kühl, H. S. (2019). Disentangling economic, cultural, and nutritional motives to identify entry points for regulating

a wildlife commodity chain. *Biological Conservation*, 238, 108177. https://doi.org/10.1016/j.biocon.2019.07.022

- Bachmann, M. E., Nielsen, M. R., Cohen, H., Haase, D., Kouassi, J. A., Mundry, R., & Kuehl, H. S. (2020). Saving rodents, losing primates— Why we need tailored bushmeat management strategies. *People* and Nature, 2(4), 889–902. https://doi.org/10.1002/pan3.10119
- Balvanera, P., Calderón-Contreras, R., Castro, A. J., Felipe-Lucia, M. R., Geijzendorffer, I. R., Jacobs, S., Martin-Lopez, B., Arbieu, U., Speranza, C. I., Locatelli, B., Harguindeguy, N. P., Mercado, I. R., Spierenburg, M. J., Vallet, A., Lynes, L., & Gillson, L. (2017). Interconnected place-based social-ecological research can inform global sustainability. *Current Opinion in Environmental Sustainability*, 29, 1–7. https://doi.org/10.1016/j.cosust.2017.09.005
- Banner, K. M., Irvine, K. M., & Rodhouse, T. J. (2020). The use of Bayesian priors in ecology: The good, the bad and the not great. *Methods in Ecology and Evolution*, 11(8), 882–889. https://doi. org/10.1111/2041-210X.13407
- Beirne, C., Meier, A. C., Mbele, A. E., Menie, G., Froese, G., Okouyi, J., & Poulsen, J. R. (2019). Participatory monitoring reveals villagecentered gradients of mammalian defaunation in Central Africa. *Biological Conservation*, 233, 228–238. https://doi.org/10.1016/j. biocon.2019.02.035
- Blaser, M. (2009). The threat of the Yrmo: The political ontology of a sustainable hunting program. *American Anthropologist*, 111(1), 10–20. https://doi.org/10.1111/j.1548-1433.2009.01073.x
- Bodmer, R., Mayor, P., Antunez, M., Chota, K., Fang, T., Puertas, P., Pittet, M., Kirkland, M., Walkey, M., Rios, C., Perez-Peña, P., Henderson, P., Bodmer, W., Bicerra, A., Zegarra, J., & Docherty, E. (2018). Major shifts in Amazon wildlife populations from recent intensification of floods and drought. *Conservation Biology*, 32(2), 333–344. https:// doi.org/10.1111/cobi.12993
- Bowler, M., Beirne, C., Tobler, M. W., Anderson, M., Dipaola, A., Fa, J. E., Gilmore, M. P., Lemos, L. P., Mayor, P., Meier, A., MenieMenie, G., Meza, D., Moreno-Gutierrez, D., Poulsen, J. R., Jesus, A. d. S., Valsecchi, J., & Bizri, H. R. E. (2020). LED flashlight technology facilitates wildmeat extraction across the tropics. *Frontiers in Ecology and the Environment*, 18(9), 489–495. https://doi.org/10.1002/fee.2242
- Brashares, J. S., Golden, C. D., Weinbaum, K. Z., Barrett, C. B., & Okello, G. V. (2011). Economic and geographic drivers of wildlife consumption in rural Africa. *Proceedings of the National Academy of Sciences* of the United States of America, 108(34), 13931–13936. https://doi. org/10.1073/pnas.1011526108
- Burkner, P.-C. (2017). brms: An R package for Bayesian multilevel models using Stan. Journal of Statistical Software, 80(1), 1–28. https://doi. org/10.18637/jss.v080.i01
- Camino, M., Scientific, N., Thompson, J. J., Matteucci, S. D., & Altrichter, M. (2020). Using local ecological knowledge to improve large terrestrial mammal surveys, build local capacity and increase conservation opportunities. *Biological Conservation*, 244, 108450. https:// doi.org/10.1016/j.biocon.2020.108450
- Carroll, M. S., Blatner, K. A., & Cohn, P. J. (2003). Somewhere between: Social embeddedness and the spectrum of wild edible huckleberry harvest and use. *Rural Sociology*, *68*(3), 319–342. https://doi. org/10.1111/j.1549-0831.2003.tb00140.x
- Chauhan, K. V., Sharma, A. K., & Kumar, R. (2008). Non-timber forest products subsistence and commercial uses: Trends and future demands. *International Forestry Review*, 10(2), 201–216. https://doi. org/10.1505/ifor.10.2.201
- Clark, B. M., Hauck, M., Harris, J. M., Salo, K., & Russell, E. (2002). Identification of subsistence fishers, fishing areas, resource use and activities along the south African coast. South African Journal of Marine Science, 24, 425–437. https://doi.org/10.2989/0257761027 84528574
- Clark, J. S. (2005). Why environmental scientists are becoming Bayesians. *Ecology Letters*, *8*, 2–14. https://doi.org/10.1111/j.1461-0248. 2004.00702.x

- Coad, L. (2007). Bushmeat hunting in Gabon: Socio-economics and hunter behaviour [Doctoral dissertation]. University of Cambridge.
- Coad, L., Fa, J. E., Abernethy, K. A., van Vliet, N., Santamaria, C., Wilkie, D. S., Bizri, H., Ingram, D. J., Cawthorn, D., & Nasi, R. (2019). Towards a sustainable, participatory and inclusive wild meat sector (tech. Rep.). https://doi.org/10.17528/cifor/007046
- Coad, L., Schleicher, J., Milner-Gulland, E. J., Marthews, T. R., Starkey, M., Manica, A., Balmford, A., Mbombe, W., Diop Bineni, T. R., & Abernethy, K. A. (2013). Social and ecological change over a decade in a village hunting system, central Gabon. *Conservation Biology*, 27(2), 270–280. https://doi.org/10.1111/cobi.12012
- Collins, C., Nuno, A., Benaragama, A., Broderick, A., Wijesundara, I., Wijetunge, D., & Letessier, T. B. (2021). Ocean-scale footprint of a highly mobile fishing fleet: Social-ecological drivers of fleet behaviour and evidence of illegal fishing. *People and Nature*, 3(3), 740– 755. https://doi.org/10.1002/pan3.10213
- Constantino, P., Benchimol, M., & Antunes, A. P. (2018). Designing indigenous lands in Amazonia: Securing indigenous rights and wildlife conservation through hunting management. *Land Use Policy*, 77, 652-660. https://doi.org/10.1016/j.landusepol.2018.06.016
- Constantino, P. d. A. L., Valente-Neto, F., Nunes, A. V., & Campos-Silva, J. V. (2021). Culture still matters: Conservation implications of hunting by ethnolinguistic groups in southwestern Amazonia after centuries of contact. *Biodiversity and Conservation*, 30, 445–460. https://doi.org/10.1007/s10531-020-02099-y
- Dahdouh-Guebas, F., Mathenge, C., Kairo, J. G., & Koedam, N. (2000). Utilization of mangrove wood products around Mida Creek (Kenya) amongst subsistence and commercial users. *Economic Botany*, 54(4), 513–527. https://doi.org/10.1007/BF02866549
- Danielsen, F., Enghoff, M., Poulsen, M. K., Funder, M., Jense, P. M., & Burgess, N. D. (2021). The concept, practice, application, and results of locally based monitoring of the environment. *Bioscience*, 71(5), 484-502. https://doi.org/10.1093/BIOSCI/BIAA021
- Dobson, A. D., Milner-Gulland, E. J., Beale, C. M., Ibbett, H., & Keane, A. (2019). Detecting deterrence from patrol data. *Conservation Biology*, 33(3), 665–675. https://doi.org/10.1111/cobi.13222
- Duonamou, L., Konate, A., Xu, J., & Humle, T. (2021). Temporal evolution of bushmeat traded in high Niger National Park, Guinea, West Africa. *Oryx*, 55(5), 717-724. https://doi.org/10.1017/S0030605319001443
- Fa, J. E., Ros Brull, G., Avila Martin, E., Okale, R., Fouda, F., Farfan, M. A., Cain, B., Fisher, R., Coad, L., & Funk, S. M. (2021). Hunting territories and land use overlap in sedentarised Baka Pygmy communities in southeastern Cameroon. *Scientific Reports*, 11(1), 3503. https:// doi.org/10.1038/s41598-021-83223-y
- Fan, Y., Chen, J., Shirkey, G., John, R., Wu, S. R., Park, H., & Shao, C. (2016). Applications of structural equation modeling (SEM) in ecological studies: An updated review. *Ecological Processes*, 5, 19. https://doi.org/10.1186/s13717-016-0063-3
- Froese, G. Z. L., Ebang Mbélé, A., Beirne, C., Atsame, L., Bayossa, C., Bazza, B., Bidzime Nkoulou, M., Dzime N'noh, S., Ebeba, J., Edzidzie, J., Ekazama Koto, S., Imbomba, S., Mandomobo Mapio, E., Mandou Mabouanga, H. G., Mba Edang, E., Landry Metandou, J., Mossindji, C., Ngoboutseboue, I., Nkwele, C., ... Poulsen, J. R. (2022). Coupling paraecology and hunter GPS self-follows to quantify village bushmeat hunting dynamics across the landscape scale. *African Journal of Ecology*, *60*(2), 229–249. https://doi.org/10.1111/aje.12956
- Gabry, J., Simpson, D., Vehtari, A., Betancourt, M., & Gelman, A. (2019). Visualization in Bayesian workflow. *Journal of the Royal Statistical Society: Series A (Statistics in Society)*, 182(2), 389–402. https://doi. org/10.1111/rssa.12378
- Gibson, L. (2020). Bycatch of the day: Wild meat consumption, ecological knowledge, and symbolic capital among indigenous maroon parrot hunters of Jamaica. *Journal of Ethnobiology*, 40(2), 167–182.
- Gill, D. J. C., Fa, J. E., Rowcliffe, J. M., & Kümpel, N. F. (2012). Drivers of change in hunter offtake and hunting strategies in Sendje,

Equatorial Guinea. *Conservation Biology*, *26*(6), 1052–1060. https://doi.org/10.1111/j.1523-1739.2012.01876.x

- Gombay, N. (2006). From subsistence to commercial fishing in northern Canada: The experience of an Inuk entrepreneur. *British Food Journal*, 108(7), 502–521. https://doi.org/10.1108/0007070061 0676343
- Griffiths, B. M., Bowler, M., Kolowski, J., Stabach, J., Benson, E. L., & Gilmore, M. P. (2022). Revisiting optimal foraging theory (OFT) in a changing Amazon: Implications for conservation and management. *Human Ecology*, 50, 545–558. https://doi.org/10.1007/s1074 5-022-00320-w
- Hongo, S., Dzefack, Z. C., Vernyuy, L. N., Minami, S., Mizuno, K., Otsuka, R., Hiroshima, Y., Djiéto-Lordon, C., Nakashima, Y., & Yasuoka, H. (2022). Predicting bushmeat biomass from species composition captured by camera traps: Implications for locally based wildlife monitoring. *Journal of Applied Ecology*, 59(10), 2567–2580. https:// doi.org/10.1111/1365-2664.14257
- Ibbett, H., & Brittain, S. (2020). Conservation publications and their provisions to protect research participants. *Conservation Biology*, 34(1), 80–92. https://doi.org/10.1111/cobi.13337
- Ibbett, H., Keane, A., Dobson, A., Griffin, O., Travers, H., & Milner-Gulland, E. J. (2020). Estimating hunting prevalence and reliance on wild meat in Cambodia's Eastern Plains. Oryx, 55(6), 878-888. https://doi.org/10.1017/S0030605319001455
- Ingram, D. J. (2020). Wild meat in changing times wild meat in changing times. Journal of Ethnobiology, 40(2), 117–130. https://doi. org/10.2993/0278-0771-40.2.117
- Ingram, D. J., Coad, L., Collen, B., Kumpel, N. F., Breuer, T., Fa, J. E., Gill, D. J., Maisels, F., Schleicher, J., Stokes, E. J., Taylor, G., & Scharlemann, J. P. (2015). Indicators for wild animal offtake: Methods and case study for African mammals and birds. *Ecology and Society*, 20(3), 40. https://doi.org/10.5751/ES-07823-200340
- Ingram, D. J., Coad, L., Milner-Gulland, E., Parry, L., Wilkie, D., Bakarr, M. I., Benítez-López, A., Bennett, E. L., Bodmer, R., Cowlishaw, G., Bizri, H. R. E., Eves, H. E., Fa, J. E., Golden, C. D., Midoko Iponga, D., Văn Minh, N., Morcatty, T. Q., Mwinyiali, R., Nasi, R., ... Abernethy, K. (2021). Wild meat is still on the menu: Progress in wild meat research, policy, and practice from 2002 to 2020. Annual Review of Environment and Resources, 46, 1–19. https://doi.org/10.1146/annur ev-environ-041020-063132
- Joly, F., Tulganyam, S., & Hubert, B. (2019). Subsistence or market economy? Assessment of a pastoral system of Mongolia twenty years after the fall of socialism. *Nomadic Peoples*, 23(1), 106–142. https:// doi.org/10.3197/np.2019.230106
- Jones, S. C., Papworth, S., Keane, A., St John, F., Smith, E., Flomo, A., Nyamunue, Z., & Vickery, J. (2019). Incentives and social relationships of hunters and traders in a Liberian bushmeat system. *Biological Conservation*, 237, 338–347. https://doi.org/10.1016/j. biocon.2019.06.006
- Jones, S. C., Papworth, S. K., St. John, F. A., Vickery, J. A., & Keane, A. M. (2020). Consequences of survey method for estimating hunters' harvest rates. *Conservation Science and Practice*, 2(12), e315. https://doi.org/10.1111/csp2.315
- Koerner, S. E., Poulsen, J. R., Blanchard, E. J., Okouyi, J., & Clark, C. J. (2017). Vertebrate community composition and diversity declines along a defaunation gradient radiating from rural villages in Gabon. *Journal of Applied Ecology*, 54(3), 805–814. https://doi. org/10.1111/1365-2664.12798
- Koster, J., Mcelreath, R., Hill, K., Yu, D., Shepard, G., Jr., Vliet, N. V., Gurven, M., Trumble, B., Bird, R. B., Bird, D., Gallois, S., Napitupulu, L., Ellen, R., Ziker, J., & Nielsen, M. R. (2020). The life history of human foraging: Cross-cultural and individual variation. *Science Advances*, 6(26), eaax9070. https://doi.org/10.1126/sciadv.aax9070
- Kumpel, N. F., Rowcliffe, J. M., Cowlishaw, G., & Milner-Gulland, E. J. (2009). Trapper profiles and strategies: Insights into sustainability

from hunter behaviour. Animal Conservation, 12(6), 531–539. https://doi.org/10.1111/j.1469-1795.2009.00279.x

- Kurz, D. J., Saikim, F. H., Justine, V. T., Bloem, J., Libassi, M., Luskin, M. S., Withey, L. S., Goossens, B., Brashares, J. S., & Potts, M. D. (2021). Transformation and endurance of Indigenous hunting: Kadazandusun-Murut bearded pig hunting practices amidst oil palm expansion and urbanization in Sabah, Malaysia. *People and Nature*, 3(5), 1078–1092. https://doi.org/10.1002/pan3.10250
- Lacuna-Richman, C. (2002). The socioeconomic significance of subsistence nonwood forest products in Leyte, Philippines. *Environmental Conservation*, 29(2), 253–262. https://doi.org/10.1017/S037689290 2000152
- Laughlin, D., & Grace, J. (2019). Discoveries and novel insights in ecology using structural equation modeling. *Ideas in Ecology and Evolution*, 12, 28–34. https://doi.org/10.24908/iee.2019.12.5.c
- Malmer, P., Centre, S. R., Masterson, V., & Austin, B. (2020). Mobilisation of indigenous and local knowledge as a source of useable evidence for conservation partnerships. https://doi.org/10.1017/9781108638210.006
- Marrocoli, S., Reinhardt, M., Morgan, D., Loon, T. V., Kulik, L., & Kuhl, H. (2019). Using wildlife indicators to facilitate wildlife monitoring in hunter-self monitoring schemes. *Ecological Indicators*, 105, 254– 263. https://doi.org/10.1016/j.ecolind.2019.05.050
- Martín-López, B., Palomo, I., García-Llorente, M., Iniesta-Arandia, I., Castro, A. J., García Del Amo, D., Gómez-Baggethun, E., & Montes, C. (2017). Delineating boundaries of social-ecological systems for landscape planning: A comprehensive spatial approach. *Land Use Policy*, 66, 90–104. https://doi.org/10.1016/j.landu sepol.2017.04.040
- Mastandrea, M. M., & Pericàs, M. A. (2021). Photoredox dual catalysis: A fertile playground for the discovery of new reactivities. *European Journal of Inorganic Chemistry*, 2021(34), 3421–3431. https://doi. org/10.1002/ejic.202100455
- McElreath, R. (2020). Statistical rethinking: A Bayesian course with examples in R and Stan (2nd ed.). Chapman, Hall/CRC. https://doi. org/10.1201/9780429029608
- Mockrin, M. H., & Redford, K. H. (2011). Potential for spatial management of hunted mammal populations in tropical forests. *Conservation Letters*, 4(4), 255–263. https://doi.org/10.1111/j.1755-263X.2011.00173.x
- Moon, K., Blackman, D. A., Adams, V. M., Colvin, R. M., Sherren, K., Davila, F., Evans, M. C., Januchowski-hartley, S. R., Bennett, N. J., St, F. A. V., Lorrae, J., Carina, V. K., & Moon, K. (2019). Expanding the role of social science in conservation through an engagement with philosophy, methodology, and methods. *Methods in Ecology and Evolution*, 10, 294–302. https://doi.org/10.1111/2041-210X.13126
- Muth, R. M., Daigle, J. J., Zwic, R. R., & Glass, R. J. (1996). Trappers and trapping in advanced industrial society: Economic and socio cultural values of furbearer utilization in the northeastern United States. *Sociological Spectrum*, 16(4), 421–436. https://doi. org/10.1080/02732173.1996.9982144
- Nana, E. D., Njabo, K. Y., Tarla, F. N., & Tah, E. K. (2022). Putting conservation efforts in Central Africa on the right track for interventions that last. *Conservation Letters*, 15(6), e12913. https://doi. org/10.1111/conl.12913
- Norstrom, A. V., Cvitanovic, C., Löf, M. F., West, S., Wyborn, C., Balvanera, P., Bednarek, A. T., Bennett, E. M., Biggs, R., Bremond, A. D., Campbell, B. M., Canadell, J. G., Carpenter, S. R., Folke, C., Fulton, E. A., Gaffney, O., Gelcich, S., Jouffray, J.-B., Leach, M., ... Österblom, H. (2020). Principles for knowledge co-production in sustainability research. *Nature Sustainability*, 3, 182–190. https:// doi.org/10.1038/s41893-019-0448-2
- Novaro, A. J., Redford, K. H., & Bodmer, R. E. (2000). Effect of hunting in source-sink systems in the Neotropics. *Conservation Biology*, 14(3), 713-721. https://doi.org/10.1046/j.1523-1739.2000.98452.x
- Nuno, A., Bunnefeld, N., Naiman, L. C., & Milner-Gulland, E. J. (2013). A novel approach to assessing the prevalence and drivers of illegal

Bushmeat hunting in the Serengeti. Conservation Biology, 27(6), 1355-1365. https://doi.org/10.1111/cobi.12124

- O'Connor, M. (2006). The "four spheres" framework for sustainability. Ecological Complexity, 3(4), 285–292. https://doi.org/10.1016/j. ecocom.2007.02.002
- Ostrom, E. (2009). A general framework for analyzing sustainability of social-ecological systems. Science, 325, 419-422. https://doi. org/10.1126/science.1172133
- Pearl, J. (1998). Graphs, causality, and structural equation models. Sociological Methods & Research, 27(2), 226-284. https://doi. org/10.1177/0049124198027002004
- Pearl, J. (2009). Causal inference in statistics: An overview. Statistics Surveys, 3, 96-146. https://doi.org/10.1214/09-SS057
- Poe, M. R., Levin, P. S., Tolimieri, N., & Norman, K. (2015). Subsistence fishing in a 21st century capitalist society: From commodity to gift. Ecological Economics, 116, 241–250. https://doi.org/10.1016/j.ecole con.2015.05.003
- Poulsen, J. R., Clark, C. J., Mavah, G., & Elkan, P. W. (2009). Bushmeat supply and consumption in a tropical logging concession in northern Congo. Conservation Biology, 23(6), 1597-1608. https://doi. org/10.1111/j.1523-1739.2009.01251.x
- Reed, J., Barlow, J., Carmenta, R., Vianen, J. V., & Sunderland, T. (2019). Engaging multiple stakeholders to reconcile climate, conservation and development objectives in tropical landscapes. Biological Conservation, 238, 108229. https://doi.org/10.1016/j.biocon.2019.108229
- Riddell, M., Maisels, F., Lawrence, A., Stokes, E., Schulte-Herbrüggen, B., & Ingram, D. J. (2022). Combining offtake and participatory data to assess the sustainability of a hunting system in northern Congo. African Journal of Ecology, 60(2), 250–267. https://doi.org/10.1111/aje.13001
- Schmiedel, U., Araya, Y., Bortolotto, M. I., Boeckenhoff, L., Hallwachs, W., Janzen, D., Kolipaka, S. S., Novotny, V., Palm, M., Parfondry, M., Smanis, A., & Toko, P. (2016). Contributions of paraecologists and parataxonomists to research, conservation, and social development. Conservation Biology, 30(3), 506-519. https://doi.org/10.1111/cobi.12661
- Scholes, R. J., Reyers, B., Biggs, R., Spierenburg, M. J., & Duriappah, A. (2013). Multiscale and cross-scale assessments of socialecological systems and their ecosystem services. Current Opinion in Environmental Sustainability, 5(1), 16–25. https://doi.org/10.1016/j. cosust.2013.01.004
- Shaffer, C. A., Milstein, M. S., Suse, P., Marawanaru, E., Yukuma, C., Wolf, T. M., & Travis, D. A. (2018). Integrating ethnography and hunting sustainability modeling for primate conservation in an indigenous Reserve in Guyana. International Journal of Primatology, 39, 945-968. https://doi.org/10.1007/s10764-018-0066-2
- Silvestre, S. M., Calle-Rendón, B. R., De Toledo, J. J., & Hilario, R. R. (2021). Drivers of hunting in the savannahs of Amapá: Implications for conservation. Oryx, 55(2), 268-274. https://doi.org/10.1017/ \$0030605319000085
- Smith, H., Marrocoli, S., Lozano, A. G., Basurto, X., & Marine, D. (2018). Hunting for common ground between wildlife governance and commons scholarship. Conservation Biology, 33(1), 9-21. https://doi. org/10.1111/cobi.13200
- Staddon, C. (2009). Towards a critical political ecology of human-Forest interactions: Collecting herbs. Transactions of the Institute of British Geographers, 34, 161-176. https://doi. org/10.1111/j.1475-5661.2009.00339.x
- Stan Development Team. (2022). Stan modeling language users guide and reference manual, 2.29. https://mc-stan.org

- Sterling, E., Kipa, T., Brian, K., Makino, N., Authority, I., Cullman, G., & Burrows, K. (2017). Culturally grounded indicators of resilience in social-ecological systems. Environment and Society: Advances in Research, 8, 63-95. https://doi.org/10.3167/ares.2017.080104
- Travers, H., Selinske, M., Nuno, A., Serban, A., Mancini, F., Barychka, T., Bush, E., Rasolofoson, R. A., Watson, J. E. M., & Milner-gulland, E. J. (2019). A manifesto for predictive conservation. Biological Conservation, 237. 12-18. https://doi.org/10.1016/i.biocon.2019.05.059
- van Vliet, N., & Nasi, R. (2008a). Hunting for livelihood in Northeast Gabon: Patterns, evolution, sustainability. Ecology and Society, 13(2), 33-88. https://doi.org/10.2193/2007-149
- van Vliet, N., & Nasi, R. (2008b). Why do models fail to assess properly the sustainability of duiker (Cephalophus spp.) hunting in Central Africa? Oryx, 42(3), 392-399. https://doi.org/10.1017/S0030 605308000288
- Villamayor-Tomas, S., Oberlack, C., Epstein, G., Partelow, S., Roggero, M., Kellner, E., Tschopp, M., & Cox, M. (2020). Using case study data to understand SES interactions: A model-centered meta-analysis of SES framework applications. Current Opinion in Environmental Sustainability, 44, 48-57. https://doi.org/10.1016/j.cosust.2020.05.002
- Villaseñor, E., Porter-Bolland, L., Escobar, F., Guariguata, M. R., & Moreno-Casasola, P. (2016). Characteristics of participatory monitoring projects and their relationship to decision-making in biological resource management: A review. Biodiversity and Conservation, 25(11), 2001-2019. https://doi.org/10.1007/s10531-016-1184-9
- Wade, A. H., & Malone, N. (2021). Ecological, historical, economic, and political factors shaping the human-gorilla interface in the Mone-Oku Forest, Cameroon. Diversity, 13(4), 175. https://doi.org/10.3390/d13040175
- Weinbaum, K. Z., Brashares, J. S., Golden, C. D., & Getz, W. M. (2013). Searching for sustainability: Are assessments of wildlife harvests behind the times? Ecology Letters, 16(1), 99-111. https://doi. org/10.1111/ele.12008

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Supporting Information S1. Data sheets, protocol and instructions. Supporting Information S2. Figures.

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