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**Data Access Statement:** No new data were generated as part of this study. For details on the spatial datasets, see Supplementary Table 2. The spatial datasets are available at <https://www.protectedplanet.net/en/> (PAs), <https://glad.earthengine.app/> (forest cover), <https://hub.worldpop.org/> (human population density), <https://malariaatlas.org/> (travel time to town), <https://www.forestintegrity.com/> (forest condition) and <https://globaldatalab.org/> (SHDI). Hunting data were extracted directly from published papers and from multiple original sources. Individual datasets from different sources (before processing) are being made available to download with restrictions through the WILDMEAT Data Portal (<https://explorer.wildmeat.org/>), which is stored in the CIFOR Dataverse. WILDMEAT is a new data sharing platform designed to house data on the hunting, consumption and trade of wildlife. Due to the highly sensitive nature of the data (locations of potentially vulnerable communities conducting illegal activities in some cases; locations of endangered species), each dataset is available under different data sharing conditions as determined by the original data owner through a Data User Agreement. This is to allow individual data providers to assess the use of the data against their ethical assessments and agreements. Information on wild meat indicators is freely available via the new toolkit at <https://www.wildmeat.org/toolkit/indicators/>. All of our analyses were conducted using the R statistical environment (v.4.1.1) through the open-access integrated development environment for R, R Studio (freely available at <https://posit.co/download/rstudio-desktop/>). The code used to develop the models is available via GitHub at <https://github.com/DJIngram/regional-hunting>.

**Enquiries:**

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# Regional patterns of wild animal hunting in African tropical forests

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Wildlife contributes to the diets, livelihoods and socio-cultural activities of people worldwide; however, unsustainable hunting is a major pressure on wildlife. Regional assessments of the factors associated with hunting offtakes are needed to understand the scale and patterns of wildlife exploitation relevant for policy. We synthesized 83 studies across West and Central Africa to identify the factors associated with variation in offtake. Our models suggest that offtake per hunter per day is greater for hunters who sell a greater proportion of their offtake; among non-hunter-gatherers; and in areas that have better forest condition, are closer to protected areas and are less accessible from towns. We present evidence that trade and gun hunting have increased since 1991 and that areas more accessible from towns and with worse forest condition may be depleted of larger-bodied wildlife. Given the complex factors associated with regional hunting patterns, context-specific hunting management is key to achieving a sustainable future.

Biodiversity loss is occurring at an unprecedented rate globally<sup>1</sup>. Hunting has been identified as a major pressure on wild animals, and unsustainable hunting (overexploitation) can drive species towards extirpation or extinction<sup>2–5</sup>. The loss of species and populations (defaunation<sup>6</sup>) can lead to seemingly ‘empty’ habitats<sup>7–9</sup> and cascading effects on ecosystem services and functions<sup>10</sup>. Hunting, consumption and trade of wild animals are pervasive throughout much of the world, particularly in tropical regions<sup>11,12</sup>. Hunted animals contribute to village subsistence economies and offer revenues for those involved in trade. Declines

in wild animal populations caused by overexploitation can thus trigger increased food and economic insecurity among people relying on meat and other body parts of wild animals<sup>13,14</sup> (hereafter ‘wild meat’ refers to the meat of wild terrestrial and aquatic animals, excluding fish<sup>12</sup>) and can lead to increased land conversion to agriculture to provide new sources of food and income<sup>15</sup>. Furthermore, access to wild meat plays important socio-cultural roles in some human communities<sup>16–18</sup>, which declines in wild animals may negatively impact. Ensuring that all extraction of wild meat is sustainable is a key component of achieving several

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of the United Nations Sustainable Development Goals (for example, Goal 2 (Zero Hunger) and Goal 15 (Life on Land)<sup>12,19</sup>) and the Convention on Biological Diversity Global Biodiversity Framework targets (particularly Targets 5 and 9 (ref. 20)) and for slowing or even reversing the loss of biodiversity<sup>21</sup>.

Despite decades of research and increasing interest in global policy<sup>22</sup>, the governance and management of wild animal hunting and trade remain substantial global challenges, with little evidence of interventions that have achieved sustainable and equitable wild meat hunting in tropical regions<sup>12</sup>. These challenges are perceived to be severe in sub-Saharan Africa, where current impacts on wildlife from overexploitation are high and likely to grow given the expected doubling of the human population between 2019 and 2050<sup>23</sup>. West and Central African countries, which contain some of the most biodiverse ecosystems on Earth, are at risk of wildlife overexploitation given the current high levels of hunting pressure for wild meat, ultimately due to the need for food and income<sup>22,24</sup>. Over the past few decades, hunting practices have evolved, with traditional methods (for example, spears and nets) largely being replaced or accompanied by technologies that improve the efficiency of individual hunting such as wire snares<sup>25,26</sup>, guns<sup>27</sup>, mobile phones<sup>22</sup> and LED flashlights<sup>28</sup>. Given these rapidly changing pressures, there is a need to understand the spatial and temporal patterns of wild meat extraction to guide transitions to sustainable food systems at scale<sup>29</sup>.

For decades, many researchers have quantified the number of wild animals hunted for meat during a given period (that is, offtake) at individual sites across West and Central Africa, predominantly to understand local hunting patterns and drivers<sup>30,31</sup>. By collating and analysing these studies, we aim to better understand the scale, magnitude and patterns of wild meat offtake across the region. Past efforts to investigate wild meat offtake patterns by analysing site-level hunting studies<sup>14,32–35</sup> have been limited by the number of sites that were included (14–33 sites, excluding hunting camps), survey effort (including very low effort,  $\leq 10$  days), data compatibility (including opportunistic sampling) and the analytical methods used (not accounting for study differences). Here we collate and analyse data from 83 studies, representing 115 settlements, to investigate the socio-cultural, economic and landscape variables associated with key components of wild meat offtake, using a Bayesian modelling approach that accounts for differences among studies. We investigate factors associated with variation in (1) wild meat offtake rate per hunter (mean kg per hunter per day), (2) the proportion of hunted animals that are sold (as a proxy for the use of wild meat for income versus food within hunter households), (3) the proportion of all hunted animals killed by gun hunting (a measure of hunting technology use) and (4) four taxonomic composition metrics of the offtake (as proxies for wild animal depletion). Throughout, we also investigate the influence of hunting technology and survey effort (measured as both the number of hunters surveyed and the number of monitoring days) on our results. By improving our understanding of the scale and patterns of wild meat hunting, our results can inform relevant sustainability policy in the region, especially by providing insights for monitoring and intervention design.

## Results

### Summary of studies

In total, we collated data from 83 hunter offtake studies conducted in 78 sites across seven countries in West and Central Africa between 1991 and 2020 (Fig. 1, Extended Data Fig. 1 and Supplementary List 1). The sites accounted for data from 115 settlements; the number of settlements per site, including single villages, grouped villages and towns, ranged from 1 to 14. The studies monitored a mean of  $23 \pm 20$  hunters for a mean of  $178 \pm 173$  days (mean  $\pm$  s.d.). Across all studies, 85,214 individual animals from 143 unique species and 33 orders were reported to be captured, accounting for a total live wild animal mass of >837,900 kilograms hunted over 462,435 hunter-days (including

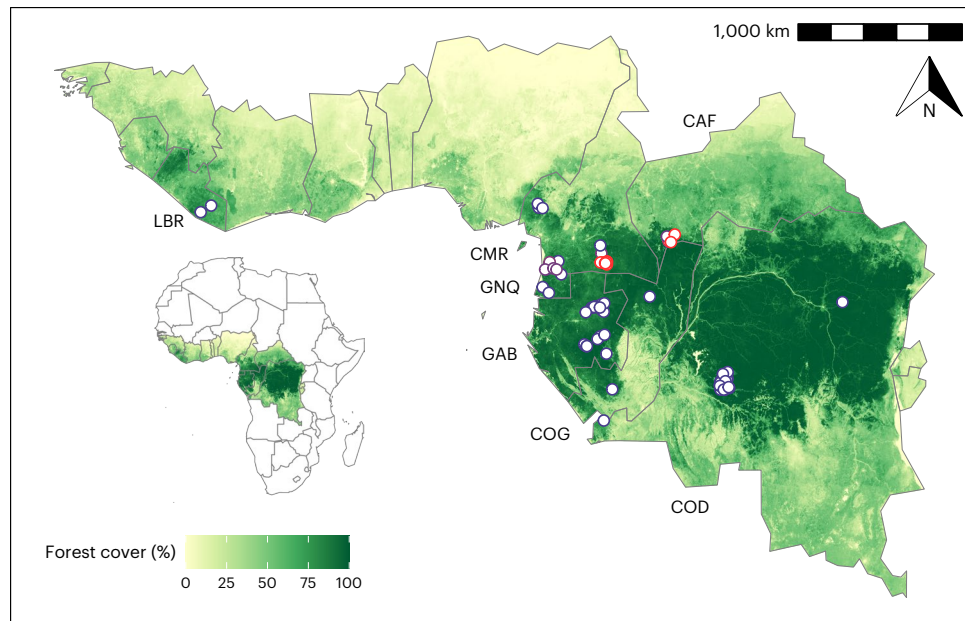
elephants). Mammals were the most frequently hunted taxa, accounting for a mean of  $93 \pm 5\%$  of the total number of animals hunted in each study, with the remainder comprising reptiles ( $4 \pm 4\%$ ), birds ( $2 \pm 2\%$ ) and amphibians ( $>0 \pm 0\%$ ). Across all studies, hunters sold a mean of  $57 \pm 17\%$  of the animals hunted (range, 17–94%). The studies were biased towards areas with greater forest cover: the mean forest cover within 20 km of sites was  $90 \pm 8\%$  (Fig. 1), whereas the mean forest cover across the study region was  $50 \pm 33\%$ . The study sites were located closer to protected area (PA) boundaries ( $35 \pm 30$  km away) compared with the mean across the study region of 48 km (excluding points inside PAs), and in areas with lower human population density ( $7 \pm 13$  individuals per km<sup>2</sup>) than the mean across the study region of  $40 \pm 86$  individuals per km<sup>2</sup> in 2020 (excluding urban areas).

### Modelling offtake and composition

Our analyses showed that studies with more hunters surveyed were associated with lower estimates of offtake (kg per hunter per day; Fig. 2, Extended Data Fig. 2a and Supplementary Table 1). Within the range of data in the model, studies that surveyed 84 hunters produced mean per-hunter offtake estimates less than one sixth the size of those that surveyed 2 hunters, when all other variables were held at means or medians. We found that studies with larger mean daily hunter offtakes were associated with a greater proportion of animals sold (that is, hunting for income)—a change from 17% to 94% of animals sold was associated with a more-than-four-times increase in mean daily hunter offtake (Fig. 3a). Mean daily hunter offtake was greater in areas with better forest condition (that is, lower forest degradation from infrastructure, agriculture or deforestation), such that the average hunter removed over six times more wild meat per day at sites with healthy forests (10/10 forest intactness index) than at sites with degraded forests (3.7/10; Fig. 3b). Mean daily hunter offtakes from studies that monitored only village hunters (traditionally agricultural rural communities—for example, many Bantu peoples) were nearly double those of studies that monitored only traditionally mobile forest hunter-gatherers (for example, Aka and Baka; Fig. 3c). Furthermore, hunter offtakes more than doubled farther away from towns (population >10,000 people) across the range of our data (Fig. 3d). We also found marginal support (89% uncertainty interval (UI)) for mean daily hunter offtakes being greater closer to PAs. While not quite at the marginal 89% level of support, our model showed some evidence suggesting that lower levels of individual hunter offtake per day may be correlated with higher levels of subnational human development (estimate,  $-0.13$ ; lower UI bound,  $-0.28$ ; upper UI bound, 0.01).

Our model showed that the mean proportion of animals sold within studies increased from 34% to 72% of the total offtake between 1991 and 2020 (Fig. 3e). The proportion sold was also shown to be greater among village hunters than among forest hunter-gatherers—a mean of 61% of the total catch was sold in studies that monitored only village hunters compared with 42% in studies that monitored only forest hunter-gatherers (Fig. 3f). The model showed marginal support for a positive association between the number of monitoring days and the proportion sold.

We found that the proportion of animals killed by guns was twice as high in studies of village hunters than in those of forest hunter-gatherers. Our model provides marginal statistical support for an increase in the proportion of animals hunted by guns over time, as well as marginal support for an interaction between time and the proportion of monitored hunters that were village hunters (Fig. 2). Specifically, the increasing trend in the proportion of animals killed by guns over time was most evident in studies where all the hunters monitored were village hunters, in which it increased from 25% to 76% between 1991 and 2020 (Fig. 4). Our model also marginally supported a negative association with the number of hunters surveyed and a positive association between gun-hunting and the proportion of animals that were sold.



**Fig. 1 | Geographical distribution of sites where hunting data were collected.** Map of West and Central Africa, showing forest cover (green shading) and sites where hunting data were collected (white circles). Circle edge colours indicate the proportion of hunters monitored that were village hunters (with a gradient from orange to purple representing only forest hunter-gatherers to only village hunters, respectively). The data were collated from seven countries in West and

Central Africa and represent hunters from 115 settlements at 78 sites. Forest cover data are from Hansen/UMD/Google/USGS/NASA<sup>119</sup>. The country outlines were obtained using the `wrld_simpl` data in the `maptools` R package<sup>105</sup>. Three-digit country codes denote countries with studies available: Cameroon (CMR), Central African Republic (CAF), Democratic Republic of the Congo (COD), Equatorial Guinea (GNQ), Gabon (GAB), Liberia (LBR) and the Republic of the Congo (COG).

The taxonomic composition of the hunter offtake was associated with several variables (Fig. 2), depending on the metric under consideration. We found that hunted species richness more than doubled with the number of monitoring days, from 20 to 50 species over the range of the data (Extended Data Fig. 2b), holding other variables constant. The ratio of larger- to smaller-bodied duikers was positively associated with travel time to towns (with a fourfold increase in this duiker ratio as travel time increased from 0 to 15 hours; Extended Data Fig. 3) and was marginally negatively associated with the proportion of animals hunted by gun. The ratio of ungulates to rodents increased from 2.5 to 17.1 with an increasing proportion of animals hunted by guns (from 0% to 99%; Fig. 4) and from 0.33 to 17.1 with increasing forest condition index. Finally, the proportion of primates in the offtake nearly tripled to 20% as the proportion of animals hunted by gun increased (Fig. 4).

## Discussion

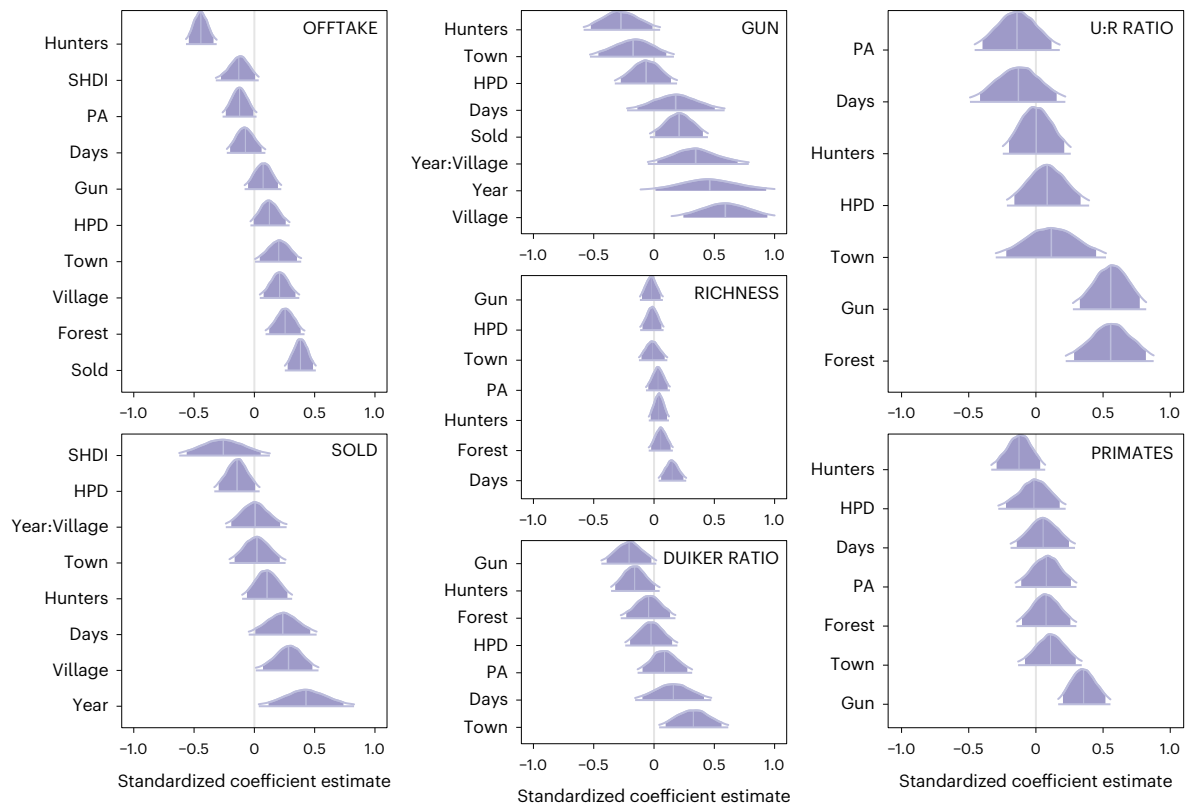
We analysed factors associated with regional hunting patterns across African tropical forests, which previously had been explored rigorously at only the local site level<sup>36,37</sup>. Using a large compilation of African hunting data, our analyses provide insights into regional patterns of the scale of wild meat hunting, possible wildlife depletion and effects of survey effort, which together have implications for wild meat monitoring, management and policy over large spatial scales.

### Socio-economic variables associated with hunter offtake

Our results show that the proportion of offtake sold is positively correlated with daily hunter offtake levels. Mean daily hunter offtakes were also positively correlated with the proportion of hunters who were village hunters, as opposed to traditional forest hunter-gatherers. Village hunters typically sold a greater proportion of their offtake than traditional hunter-gatherers. These results could be because village hunters (probably including hunters coming from elsewhere specifically to hunt) tend to be more integrated into the market economy than traditional forest peoples, and have better access to modern

sales technologies such as mobile phones and mobile money<sup>25,38,39</sup>. Furthermore, though we acknowledge that our dataset is not longitudinal across the same hunters/sites, our model suggests that the proportion of animals sold has increased over time. This result could be because the demand for wild meat, particularly in urban areas, also drives the proliferation of commercial hunters and encourages some subsistence hunters to hunt for income<sup>22</sup>. These results are probably comparable to those in other parts of the tropics such as in African savannahs where wild meat is sold for income<sup>8</sup>, and in East, South and Southeast Asia<sup>40</sup> and Latin America<sup>22</sup> where wild meat is openly sold in markets. As urban areas are a major destination for traded wild meat<sup>12</sup>, initiatives to reduce consumer demand and the price of wild meat in urban areas could disincentivize commercial hunting and in turn ease pressure on wildlife<sup>41</sup>. However, given that one outcome of reducing urban demand would be to reduce the immediate economic viability of hunting in rural areas, campaigns targeting urban areas will probably need to be conducted together with initiatives to develop other, more sustainable sources of rural income<sup>42</sup>. Where rural communities have legal rights to hunt wildlife, a substantial challenge to local hunting management and sustainability could be that communities have no legal means of excluding external commercial hunters, who may target areas with intact forest and/or close to PAs.

While more data are needed to understand whether there is a concrete relationship between hunting and development, development assistance focusing on building resilient local economies that are not dependent on wild meat hunting (for example, by raising health, standard of living and education levels), coupled with increased access to and diversification in employment and alternative proteins, may reduce hunting pressure over time. This will depend on trends in urbanization, consumer preferences, wealth and human population density. However, future development could lead to unintended impacts such as increased ecosystem degradation due to increasing agriculture, species declines<sup>43</sup>, industrial expansion, logging roads and potentially new markets for wild meat if it becomes a luxury commodity<sup>44</sup>.



**Fig. 2 | Variables tested for associations with components of wild meat hunter offtake.** Bayesian generalized linear multilevel model standardized coefficient estimates and posterior density curves across the following response variables: mean daily hunter offtake (OFFTAKE; kg per hunter per day), the proportion of total animals that were sold (SOLD), the proportion of animals hunted by gun (GUN), species richness (RICHNESS), the ratio of larger to smaller duikers (DUIKER RATIO), the ratio of ungulates to rodents (U:R RATIO) and the proportion of total animals that were primates (PRIMATES). Possible explanatory variables, on the basis of a priori hypotheses, are the number of hunters surveyed (Hunters), the Subnational Human Development Index (SHDI), the distance to a protected area (PA), the number of monitoring days (Days), the proportion of animals hunted by gun (Gun), the mean human population density within 20 km

(HPD), the travel time to the nearest town >10,000 people in minutes (Town), the proportion of monitored hunters who were village hunters rather than traditional forest hunter-gatherers (Village), the mean forest condition within 20 km (Forest; index from poor condition (0) to good (10)), the proportion of animals that were sold (Sold), the year (Year) and an interaction between year and the proportion of village hunters (Year:Village). For each variable, the vertical line shows the mean estimate, the outer light purple line represents the 95% uncertainty interval (UI) and the darker purple shaded area represents the 89% UI. Possible variable associations are not well supported in the model when the UI overlaps with 0 (the vertical light purple line). The variables are ordered by mean coefficient estimate within each model, from negative to positive.

### Landscape variables associated with hunter offtake

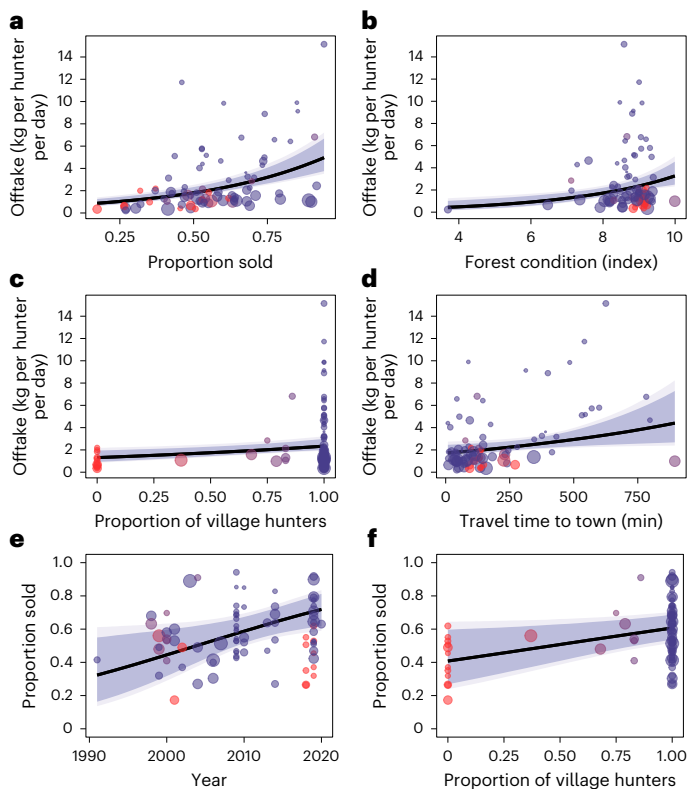
At the regional scale, we found greater mean daily hunter offtake in areas with better forest condition. This result could be caused by hunters in areas with better forest condition hunting more because they have fewer alternative sources of meat and income and/or because areas with better forest condition are less depleted of wildlife, so hunters can hunt larger-bodied species. We found that mean daily hunter offtakes were greater in more remotely located sites and closer to PAs (although the latter relationship was marginally significant), mirroring the local-scale patterns for greater levels of hunting<sup>45</sup> and wild meat consumption recorded in East Africa<sup>46</sup>. This suggests that remote areas or PAs may have a role as refuges and source areas for wild animals<sup>47</sup>, and/or that PAs are established in more remote intact landscapes where hunters may rely more on wild meat for food and income, and/or that these areas have yet to reach the depleted state of more accessible sites. Our results underscore the need to sustainably manage functional forest ecosystems and PAs, which provide local people with potentially renewable natural resources.

### Implications of gun hunting

Our results suggest that village hunters are increasingly using guns to hunt animals rather than other methods, albeit at marginal statistical significance (see 'Limitations'). This could result from multiple factors,

including increased access to guns by village hunters<sup>26,48,49</sup>, increased access to aerial and arboreal animals that guns provide to hunters, and the increased selectivity of guns relative to traps, making guns the preferred weapon for those who hunt for income<sup>26</sup>. Furthermore, our results suggest that where hunters use guns proportionally more than other methods, they also sell a greater proportion of the offtake. This association could be because guns are the weapon of choice for commercial hunters, so that they can target commercially viable species, and because guns require financial investment, which is more likely to be possible for commercial hunters.

Increasing gun use over time is likely to impact fauna in different ways. Our results show that when hunters catch a greater proportion of animals by gun, the proportion of primates in the catch and the ungulate:rodent ratio increase. Consumers prefer ungulates and primates in some countries, and these taxa are commonly offered for sale at urban wild meat markets<sup>50–52</sup>. While gun hunting is usually more selective than trapping and could therefore be considered better for wildlife generally (for example, fewer carnivores are killed with guns than by traps<sup>53</sup>, and fewer animals are wasted<sup>54</sup>), increased gun hunting has implications for the conservation and management of ungulates and arboreal and aerial animals<sup>55</sup>. Primates, for example, may be particularly vulnerable to overhunting using guns and can be the target of specialized primate hunters given their high value<sup>56</sup>. In many



**Fig. 3 | Variables associated with hunter offtake and proportion sold.**

**a–f**, Bayesian generalized linear multilevel model predicted effects of an association between hunter offtake and the proportion of animals sold (**a**), forest condition (**b**), the proportion of village hunters (**c**) and the travel time from a site to the nearest town with a population >10,000 (**d**). The proportion of offtake that is sold is associated with year (**e**) and the proportion of village hunters (**f**). The purple ribbons show the 89% (dark purple) and 95% UIs (light purple), while the black line shows the global average marginal effect. The points show individual studies (scaled by the number of hunters surveyed) and are coloured according to the proportion of hunters monitored that were village hunters (with a gradient from orange to purple representing only forest hunter-gatherers to only village hunters, respectively). The points are semi-transparent to show point density.

cases, gun hunting without the correct permits (gun permit and game quotas) is already illegal, but quotas are extremely difficult to enforce, and hunting law is in general inadequately enforced. The scale of hunting for income, as well as gun proliferation, self-manufacture and use, means that purely enforcement-based management is likely to be challenging, especially in post-conflict areas<sup>55</sup> and in areas where the rule of law is weak. Efforts to ensure that wildlife use is sustainable should simultaneously focus on enforcing laws that regulate the hunting of threatened species, including ensuring their survival in PAs, while also investigating and co-developing ways for local communities to manage wildlife sustainably, where possible<sup>57</sup>. Shifting the focus to spatial hunting management (for example, the rotation of hunting zones over time) may be more locally appropriate and resilient to changes within the hunting system (for example, changes in hunting technology).

### Proxy-based evidence of depletion

Our results suggest that hunted fauna may be more depleted in areas more accessible from towns and in areas of worse forest condition. For example, the duiker ratio was lower in areas that are more accessible from towns, possibly indicating that the larger *Cephalophus* duikers have become more depleted in these areas<sup>58,59</sup>. This is corroborated by our findings that daily hunter offtake and the ungulate:rodent ratio were greater in areas with better forest condition. In depleted areas,

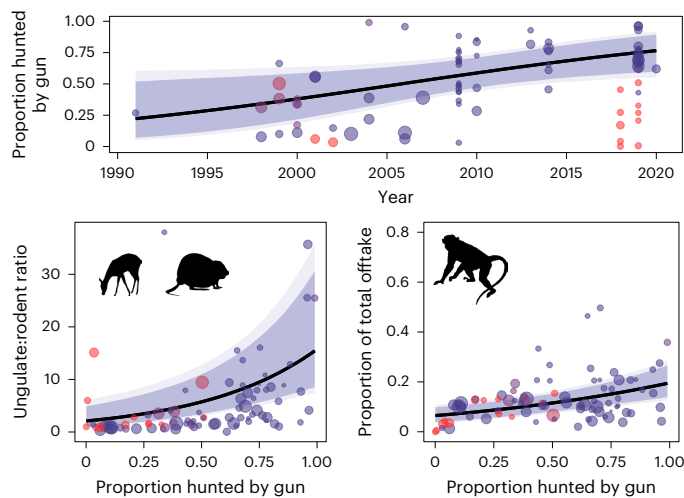
we cannot discern whether the offtake has reached a post-depletion sustainability state in which fast-reproducing species are being hunted sustainably<sup>60,61</sup>. Together, and assuming that offtakes reflect the local abundance of wild animals to some extent<sup>55,62–65</sup>, these results underscore the role of remote areas with good forest condition as refuges for wildlife. Furthermore, Forest Stewardship Council (FSC)-certified logging concessions in Central Africa have been shown to hold much higher numbers of large-bodied animals than non-FSC certified concessions<sup>66</sup> and thus are of great importance for sustainable hunting management across much of forested Africa<sup>67</sup>. Given that poor forest condition is characterized by greater levels of infrastructure, agriculture and deforestation, the effects of hunting pressure and forest degradation may be conflated in our models. However, this would not change the premise that remote areas serve as refuges for wildlife and possibly source populations for hunted areas.

### Limitations

Our results have the following limitations. First, due to the disparate nature of our dataset, our results largely focus on past drivers and hunting patterns. In the future, hunting patterns may be influenced by other factors, which would make it challenging to predict them from this dataset. However, we suspect that many factors will remain important in the future, such as (1) accessibility and distance to PAs, given that they will probably remain an important refuge for wildlife; (2) forest integrity, due to the importance of source–sink dynamics and the cumulative effect of multiple stressors on wildlife; and (3) the proportion of wild meat sold, given increasing access to markets and the cash-based economy. Furthermore, it was not possible to include important contextual information that was not reported in our data sources, such as hunter typology (for example, commercial and/or migrant hunters travelling long distances), use of hunting camps, indicators of wealth or prosperity, governance, regulation, conflicts and PA effectiveness. Another limitation is that, given the absence of time-series studies at multiple locations across the region<sup>68</sup>, our analyses use space-for-time substitution out of necessity and therefore assume that comparisons across space represent trends over time (we recognize that correlation does not imply causation). Finally, while our results cannot be used to determine the sustainability of hunting practices at individual sites directly (see the discussions in ref. 69), they do provide important context for developing local sustainable management and monitoring plans. Given the now substantial catalogue of evidence regarding the drivers and impacts of hunting achieved over 20 years of research<sup>12</sup>, we urge researchers and practitioners to focus their efforts on identifying and implementing ways to sustainably manage wildlife.

### Research, policy and action

The analyses presented here are an important step towards better understanding some of the factors associated with offtake patterns and could be used to guide policy, monitoring and management strategies. For example, we identified that a substantial proportion of offtake is destined for trade, which suggests a role for policies and actions to reduce demand in urban areas and to regulate wild meat supply chains. However, fundamental moral and ethical implications should be considered when designing related national policies or local interventions. We suggest that where local communities rely on wild meat for nutrition, and where hunting builds resilience in the local economy and remains an important component of cultural identity, management efforts should focus on attaining sustainable offtake under local governance, protecting threatened species and developing an effective hunting monitoring framework. Furthermore, given that we highlight how gun hunting may disproportionately impact primates, research is needed to conduct sustainability and population assessments of hunted primate species, followed by appropriate management and policy. We present evidence of wild animal depletion in areas accessible from towns and in areas with poor forest condition, which emphasizes the importance



**Fig. 4 | The winners and losers of gun hunting.** Top, Bayesian generalized linear multilevel model predicted changes in the proportion of the total number of individual animals caught that were hunted by gun over time, plotted as the interaction term when the proportion of hunters monitored that were village hunters is 1 (that is, purple points only). Bottom, modelled relationships of the proportion of animals hunted by gun with the ungulate:rodent ratio (left) and with the proportion of animals hunted that were primates (right). The purple ribbons show the 89% (dark purple) and 95% UIs (light purple), while the black line shows the global average marginal effect. The points show individual studies (scaled by the number of hunters surveyed) and are coloured according to the proportion of hunters monitored that were village hunters (with a gradient from orange to purple representing only forest hunter-gatherers to only village hunters). The points are semi-transparent to show point density. Credit: animal silhouettes, PhyloPic.org under a Creative Commons license [CC01.0](https://creativecommons.org/licenses/by/4.0/).

of active conservation efforts that protect and restore functioning ecosystems and that provide people with important natural resources.

Our results reflect hunting patterns in forested areas of West and Central Africa. In our analyses, the number of studies in several large countries (including the Democratic Republic of the Congo and the Central African Republic), in non-forest areas and in large areas of West Africa was limited. This means we cannot be certain about hunting patterns in these areas, so targeting future research in these areas will be valuable to fill these knowledge gaps. We highlight that longer-term monitoring of hunting activities, including ensuring representative samples of hunters, is needed to ensure robust conclusions about hunting patterns, species richness, sustainability and intervention effectiveness. While our results and others<sup>64,65,70</sup> suggest that the duiker ratio and the ungulate:rodent ratio may be useful proxies for wildlife availability and abundance, our results also suggest that the indicators are sensitive to changes in hunting technology (for example, switches from snaring to gun hunting), which needs to be considered when interpreting these indicators. Research across several biomes using standardized survey methods and indicators (for example, see [www.wildmeat.org](http://www.wildmeat.org)), where survey effort is incorporated into survey design, monitoring and evaluation, needs to be undertaken. The development of a transparent and rigorous regional wild meat hunting, consumption and trade monitoring network would provide standardized data over time that could be used to inform and monitor the impacts of national and regional strategies and policies for wild meat management and governance.

Together, our findings provide information at a scale that is relevant for decision-making across the region. Our study shows the strong need for robust monitoring and management frameworks for hunters and traders, which are currently lacking in most West and Central African countries and in other parts of the tropics. Without monitoring of hunted species populations and hunter offtakes, the sustainability of

hunting systems remains unknown. Such frameworks could also be supported through organizations such as the Central African Forests Commission (COMIFAC), an intergovernmental organization tasked with managing Central African forest sustainably. Assessing sustainability is key to monitoring progress towards Kunming-Montreal Global Biodiversity Framework Targets 5 and 9 on ensuring the sustainable use and management of wildlife by 2030, adopted by 196 countries in December 2022 (ref. 20). In conjunction with the necessary resources and suitable wild meat policies and legislation<sup>12</sup>, strong political and public will is crucial if such goals towards a more sustainable and just future for people and wildlife are to be achieved globally.

## Methods

### Wild meat data collation and inclusion criteria

Data on the number of animals caught by hunters in a given location (hereafter ‘hunter offtakes’) across West and Central Africa were extracted from published journal articles, grey literature (for example, non-governmental organization reports and university degree theses) and unpublished data (deemed suitable when they had been collected using published methods). Using the following methods, we searched for potential data sources between 1 August 2019 and 17 December 2021. Suitable sources were first identified from lists provided in two studies<sup>30,31</sup> that used systematic searching techniques. We then conducted regular additional literature searches using search engines and bibliographic databases (Google Scholar (including using alerts) and the ISI Web of Knowledge (All Databases)). We performed searches using Boolean logic with the following words: (bushmeat, game, gibier, hunt\*, offtake, poach\*, viande de brousse, wild meat, wildmeat) AND (Africa, Afrique centrale, Afrique de l’Ouest, Afrique occidentale, Bassin du Congo, Central Africa, Congo Basin, West Africa). While this method was effective at finding sources, we were able to find further sources mostly through subsequent searching of reference lists and contacting wild meat researchers (both akin to chain-referral sampling<sup>71</sup>). We did not exclude sources on the basis of the year or biome within which data were collected, or the ethnic group of the hunters monitored.

Sources may contain one study or more, in which hunter offtakes were monitored at sites (settlements including villages and towns), over a known period. For seven studies that monitored hunting at more than one settlement in a limited geographic area, data were unavailable for each settlement separately; thus, some sites represent more than one settlement. Hunter offtake data were deemed suitable if (1) the number of individual wild animals hunted per taxonomic group was reported (or estimated, as in one study<sup>72</sup>); (2) the hunters monitored were deemed representative of hunters at a given site (that is, the source or the data owner did not mention monitoring a specified minority group of hunters—however, we could not determine from studies whether the communities that were monitored were chosen randomly); (3) the survey method was reported; (4) the coordinates of the site(s), or a map from which the coordinates could be acquired by georeferencing against Google Earth, were available; (5) the source included information on the number of days that hunting was surveyed and the number of hunters whose offtakes were monitored; (6) the settlement at which the hunting was monitored was a permanent dwelling (that is, not a hunting camp); and (7) the hunting method and the use of the hunted animals (that is, sold, eaten or other) were reported. We either extracted hunter offtakes directly from the sources or contacted the authors for their raw data.

### Wild meat data curation

Species names were extracted directly from the sources when reported. When animals were not identified to the species level, we allocated them to the most resolved taxonomic level possible—for example, if an animal was identified as a ‘genet’, it was allocated to *Genetta*. Taxonomic identity was spell-checked across all sources and harmonized against the IUCN Red List ([www.iucnredlist.org](http://www.iucnredlist.org)), and each unique taxonomic identity

was then given a unique numeric identifier. So that we could convert the number of animals hunted into the total biomass extracted (see below), we also allocated each species a body mass. Given that sources rarely contained data on the mass of each carcass, we instead matched the average adult body mass for each species from Myhrvold et al.<sup>73</sup>. For *Dendroaspis*, *Naja* and *Python*, we matched animals to adult body mass data reported in Abugiche<sup>74</sup>. When animals were identified to a lower taxonomic resolution than species (for example, genus), we calculated and allocated the mean body mass of those species within that taxonomic unit present in our dataset. On rare occasions when an animal was identified to a taxonomic unit for which no other animals had been identified to species level within that unit in our dataset, we allocated the mean body mass of all species in that unit from Myhrvold et al.<sup>73</sup>.

Individual hunter offtakes typically vary considerably within a settlement<sup>75</sup>. To compare offtakes across time, space and study, we calculated a standardized mean hunter offtake rate (per day) for each study–site combination. Offtake rates were standardized by first multiplying the number of animals caught per species by their respective body mass and then summing the species biomasses within each study–site. As many studies did not have offtake data available for each hunter separately, we calculated the offtake variable used in our analyses—that is, mean hunter offtake per day (kg per hunter per day)—by dividing the total study–site biomasses by both the number of hunters that were continuously monitored and the number of days they were surveyed in each study. Elephants (Elephantidae) rarely appeared in hunting records given that elephant hunting is usually a specialist, illegal activity typically requiring expensive high-velocity rifles and as such is not conducted by most wild meat hunters<sup>76</sup>. Additionally, their enormous size means that elephant records disproportionately affect mean offtakes. To avoid overestimating typical hunter offtakes, we removed all elephants before calculating mean hunter offtake per day<sup>64</sup>.

The studies varied in the types of hunters monitored. While most studies solely monitored village hunters from typically agricultural rural communities (63 studies; most commonly Bantu peoples), 17 studies included or solely monitored traditional forest hunter-gatherers—that is, those whose subsistence depends on a forager and hunter-gatherer lifestyle (for example, Aka and Baka). For each study, we calculated the proportion of hunters monitored that were village hunters: a study that monitored only forest hunter-gatherers would have a proportion of 0, while a study that monitored only village hunters would have a proportion of 1. This proportion was then used directly as a variable in the analyses. For three studies located in the same area, it was unclear whether any forest hunter-gatherers were monitored, so we assigned these the mean proportion across all other studies.

The composition of offtake has been shown to reflect the diversity and relative abundance of hunted wild animals in an area<sup>55,62–65,70</sup>. We calculated four taxonomic composition metrics of the offtake as proxies for wild animal depletion. First, for each study, we calculated the minimum species richness in the hunter offtake, measured as the count of unique species hunted. In several studies, not all animals could be identified at the species level, but they could be identified to other taxonomic resolutions. Animals not identified to the species level often belonged to groups that are hunted relatively infrequently and were less likely to be already represented in a count of species richness based solely on animals identified to the species level. Therefore, to reduce the underestimation of species richness, we manually checked through all studies and added one to the richness count each time it was clear that individuals identified to a lower resolution were not already represented in the count of a given study. For example, if five animals were identified only as *Genetta* in a study, and no animals were identified to a specific species of *Genetta*, we added one to the study richness count.

Second, as a measure of possible depletion of larger-bodied ungulates, which are preferentially hunted in West and Central Africa and are potentially more sensitive to hunting (at least in the case

of some species), we adapted a regional indicator called the “B/M ratio”<sup>58</sup>. Using this indicator, we explored the suggestion that the ratio of small, fast-breeding blue duikers (*Philantomba monticola*; B) to slower-breeding, medium-sized red duikers (*Cephalophus* spp., not including the larger-bodied *C. silvicultor*; M) in the offtake is indicative of the status of the fauna in a given area<sup>58</sup>. The ratio is based on the observation that larger, slower-reproducing duiker species are depleted first as hunting pressure increases, while smaller, faster-reproducing duikers increase in density under the same regime until hunting pressure becomes too high and they are too depleted<sup>58,70,77</sup>. This was supported in another study, which found that the proportion of red duikers was greater in more intact forests in Central Africa<sup>59</sup>. We adapted the B/M ratio in the following ways: (1) as our studies encompassed both West and Central Africa and blue duikers are not present in most of West Africa, we expanded the ratio to the genus level to include the highly similar *Philantomba* species from West Africa (*P. maxwellii*); and (2) so that a high ratio may be indicative of better faunal status of large-bodied animals sensitive to hunting pressure, we expressed our results as the M/B ratio (including both medium- and large-bodied duikers (that is, *C. silvicultor*) in the *Cephalophus* genus), with a larger value thus indicating greater relative abundance of larger-bodied duikers.

Third, we calculated the ratio of ungulates (here even-toed ungulates including deer, antelopes and pigs; hereafter ‘ungulates’) to rodents among all animals hunted, which has often been considered a metric of wild animal depletion in the tropics<sup>32,70</sup>, as increases in rodent offtake can coincide with the depletion of preferred larger-bodied animals<sup>65,78</sup>. The ungulate:rodent ratio was calculated as the number of ungulates divided by the number of rodents caught. A larger value of this indicator represents a greater relative abundance of ungulates than rodents.

Finally, we calculated the relative proportion of primates in the total number of animals caught to investigate the impact of gun hunting on a preferred group of species.

### Processing and extraction of spatial layers

Several spatial layers were acquired or calculated for use as variables in our analyses (Supplementary Table 2). For some layers, we were able to directly download appropriate spatial layers, including the SHDI v.5.0 (ref. 79) and the estimated travel time to the nearest town<sup>80</sup>. The SHDI is an index constructed to represent the dimensions of education, health and standard of living and is created from expected years of schooling, mean years of schooling, life expectancy and gross national income per capita<sup>79</sup>. For the SHDI, we extracted the identity of each subregion from the SHDI layer for each site and then matched the index value to the same year as the study. For travel time to the nearest town, we used the 2015 layer<sup>80</sup> to calculate the travel time from each grid cell to the nearest settlement with 10,000+ people<sup>81</sup>. Travel time estimates consider movement by foot, roads, railways, rivers, water bodies, land cover class, slope, elevation and national borders<sup>80</sup>. We then extracted travel times for each of our sites by conducting value point extractions from the recalculated spatial layer. The cut-off point of 10,000 people was selected to represent settlements from small towns upwards, where wild meat markets may be present<sup>82</sup>. While we recognize that travel times will have varied across the period for which we have data (1991–2020), we did not have access to contextual data allowing us to adjust travel times to the year of data collection.

To calculate the distance to the nearest PA for each site, we downloaded PA polygons and point locations from the World Database of Protected Areas v.1.6 (<https://www.protectedplanet.net/en>). We excluded Ramsar and UNESCO Man and Biosphere sites because they do not necessarily have protective legislation (apart from any portions in overlapping nationally protected areas, which would be retained in our dataset). Then for each site, we calculated the Euclidean distance from the site to the nearest PA boundary. This underestimates the actual distance for a hunter or trader travelling on paths or roads<sup>83</sup>, but for



analysis at a regional scale, we deemed this an adequate approximation given the lack of site-level information on the most direct paths/routes. Mean distance from a PA was estimated on the basis of the Euclidean distance of randomly selected points within a 1 km<sup>2</sup> grid overlaid in the study area ( $N = 1 \times 10^6$ ). As all sites were in forested areas, we included a measure of forest condition in our models. We used the forest integrity index ('forest condition')<sup>84</sup>, which is constructed as an index (ranging from 0 to 10) based on observed human pressures (infrastructure, agriculture and tree cover loss), proximity to observed human pressures (inferred) and change in forest connectivity<sup>84</sup>. For each site, we calculated the mean forest condition within a 20 km radius; this radius was chosen to represent the furthest distance subsistence hunters are likely to travel<sup>24</sup> and to include the area probably able to act as the source of most hunted species. To estimate the human population density around each site, we first downloaded all human population density layers from WorldPop v.2.0, available every five years between 2000 and 2020. For each site, we then allocated the human population density layer for the year nearest to the study and calculated the mean human population density within 20 km, to match the forest layers.

All spatial layers were reprojected into an Albers equal-area conic projection to conserve distance, and if not already at a 1 km grid-cell resolution, we resampled layers to a 1 km × 1 km grid-cell size so that all layers had the same projection, extent and cell size (see Supplementary Table 2 for the native resolution). For each study site, we extracted the point-level estimates of spatial variables. Sites that represented more than one settlement (where data could not be separated per settlement) were all located close to each other, so for spatial extractions for these sites, we used the coordinates of the settlement that had the highest offtake where possible or the centre point of the surveyed settlements. All spatial extractions and manipulations were conducted in R version 4.1.1 (ref. 85).

### Modelling offtake and composition

To examine the variables associated with hunter offtake, use and hunting methods, and taxonomic composition, we constructed a series of Bayesian generalized linear multilevel models. We first checked for correlations between possible variables and did not include variables in the same models where Pearson's  $r \geq 0.7$  (ref. 86). We used variance inflation factors to check the extent to which variables were influenced by their correlation with the other independent variables and found all to have limited influence (variance inflation factor < 2). All of the following models included two measures of survey effort as variables: the number of hunters surveyed and the number of monitoring days. For hunter offtake, we constructed a core Bayesian generalized linear multilevel structural equation model<sup>87</sup>, which included three primary response variables: offtake as mean hunter offtake per day (kg per hunter per day; see above for how this was derived), the proportion of the total number of animals hunted that were sold and the proportion of the total number of animals that were hunted by gun. Different combinations of variables were selected for different responses on the basis of their a priori hypothesized relationships (Supplementary Tables 3 and 4): the travel time to town, the forest condition within 20 km, the distance to the nearest PA, the year of study, the SHDI, the proportion of hunters monitored that were village hunters, the proportion of animals hunted by gun and the proportion of animals hunted that were sold. For the proportion-hunted-by-gun model, we included an interaction term between the year of study and the proportion of hunters monitored that were village hunters. Four further response variables were included as a multivariate response with offtake: species richness, the duiker ratio, the ungulate-to-rodent ratio and the proportion of hunted animals that were primates. All four taxonomic composition metric models included the same variables: the travel time to town, the forest condition within 20 km, the distance to the nearest PA and the proportion of animals hunted by gun. To standardize the comparison of the effects of variables, all values of continuous

variables were centred by subtracting the mean and scaled by dividing by the standard deviation.

Offtake, duiker ratio and ungulate-to-rodent ratio were modelled with gamma distributions (log link), while species richness was modelled with a negative binomial distribution (log link). Prior to modelling, we added 1 to the number of rodents in one study where the original value was 0 so that we could calculate and subsequently model the ungulate-to-rodent ratio. The number of animals that were primates was modelled using a beta binomial distribution (logit link), accounting for overdispersion and the differences in study sample sizes through the response variable structure in the model (coded as successes/trials)<sup>88</sup>. The proportions of animals hunted by gun and the proportions that were sold were extracted from studies and modelled with beta distributions (logit link). Before modelling, we added 0.001 to the proportion-of-gun-hunting variable for one study where the original value was 0, which a beta regression could not model<sup>88</sup>. For all models, we included varying intercepts (but not slopes) for each unique reference ID (modelled as correlated across formulas), within which studies and sites are linked to account for variation due to differences in the methods employed by researchers. Given that multisite studies were often conducted in the same area, this varying intercept may partially account for possible spatial autocorrelation within studies; however, we conducted further distance-based autocorrelation checks (see below). We did not include varying intercepts for each country due to the low number of studies in some countries, which meant that country accounted for the same variation as the study reference in some cases. The weak explanatory power of countries in the data was further shown in preliminary analyses, in which including country caused convergence issues.

We fitted the models in the Stan probabilistic programming language<sup>89</sup> through the R statistical environment (v.4.1.1)<sup>85</sup> using the package brms<sup>90,91</sup>. The models ran four chains, each with 6,000 iterations, of which the first 1,500 were used to calibrate the sampler, leading to a total of 18,000 posterior samples. We used weakly informative normal (0,5) priors for all population-level parameters estimated. We assessed model convergence by visually assessing trace plots for sufficient mixing and by checking the Gelman–Rubin convergence diagnostic,  $\hat{R}$  (ref. 92); in all our models,  $\hat{R}$  values for the estimated parameters were 1.0, indicating adequate model convergence. Residual checks and distance-based autocorrelation using Moran's  $I$  were assessed using the DHARMA and DHARMA.helpers packages (Supplementary Table 4)<sup>93–95</sup>. To calculate Moran's  $I$ , the residuals were first aggregated at the level of each unique site. Model performance and fit were checked through graphical diagnostic checks of the predictive distribution in the R package bayesplot using standardized protocols<sup>96,97</sup> (Supplementary Table 5), and we observed a close correspondence between the posterior predictive distributions and the observed data. The posterior means and UIs were used to interpret the strength and uncertainty of the estimated effects<sup>91</sup>. We considered variables to be meaningful when the 89% UI of their effect sizes did not overlap zero (marginal support) and strongly supported when their 95% UI did not overlap zero<sup>98,99</sup>. To further check the model effects, we also estimated the probability of direction using the bayestestR package, which represents "the certainty with which an effect goes in a particular direction"<sup>100</sup>. All graphs of model predictions were produced using the expected values, holding other variables at means or medians depending on the variable. Several R packages were used for spatial mapping, extraction and analysis (raster, rgdal, sf, gdalUtils and mapproj<sup>101–105</sup>); correlations (GGally<sup>106</sup>); data manipulation (reshape2, stringr, broom.mixed, tidyr, dplyr, tidyverse and tidybayes<sup>107–113</sup>); and plotting (ggplot2, patchwork, cowplot, gridExtra and rphylopic<sup>114–118</sup>).

While the appropriateness of weighting models is subject to academic debate, we tested the influence of a version of the models that was weighted by one metric of survey effort, the number of hunters surveyed. The weighted model further accounted for differences in

survey effort in our models by weighting the likelihood contributions of each observation by a scaled version of the number of hunters surveyed. To avoid over- or underweighting each observation, we rescaled the number of hunters surveyed so that all values fell between 1 and 5, given that weights in the *brms* package are taken literally—that is, an observation with weight 2 receives 2 times more weight than an observation with weight 1, essentially allowing one to put more importance on some data points. The weighting was not applied to the models where the response was the proportion of animals that were primates because these were already adjusted through their model structure (successes/trials). The scaled weighting variable was calculated as follows:

$$x_{\text{normalized}} = (b - a) \frac{x - \min(x)}{\max(x) - \min(x)} + a$$

where *a* and *b* are the range of the scaled variable (here 1 and 5), respectively, and *x* is the survey effort (the number of hunters surveyed). The weighted model results and comparison are presented in Supplementary Table 6.

### Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

### Data availability

No new data were generated as part of this study. For details on the spatial datasets, see Supplementary Table 2. The spatial datasets are available at <https://www.protectedplanet.net/en/> (PAs), <https://glad.earthengine.app/> (forest cover), <https://hub.worldpop.org/> (human population density), <https://malariaatlas.org/> (travel time to town), <https://www.forestintegrity.com/> (forest condition) and <https://globaldatalab.org/> (SHDI). Hunting data were extracted directly from published papers and from multiple original sources. Individual datasets from different sources (before processing) are being made available to download with restrictions through the WILDMEAT Data Portal (<https://explorer.wildmeat.org/>), which is stored in the CIFOR Dataverse. WILDMEAT is a new data sharing platform designed to house data on the hunting, consumption and trade of wildlife. Due to the highly sensitive nature of the data (locations of potentially vulnerable communities conducting illegal activities in some cases; locations of endangered species), each dataset is available under different data sharing conditions as determined by the original data owner through a Data User Agreement. This is to allow individual data providers to assess the use of the data against their ethical assessments and agreements. Information on wild meat indicators is freely available via the new toolkit at <https://www.wildmeat.org/toolkit/indicators/>.

### Code availability

All of our analyses were conducted using the R statistical environment (v.4.1.1) through the open-access integrated development environment for R, R Studio (freely available at <https://posit.co/download/rstudio-desktop/>). The code used to develop the models is available via GitHub at <https://github.com/DJIngram/regional-hunting>.

### References

1. *Living Planet Report 2022—Building a Nature-Positive Society* (WWF, 2022).
2. Benítez-López, A. et al. The impact of hunting on tropical mammal and bird populations. *Science* **356**, 180–183 (2017).
3. He, F. et al. Disappearing giants: a review of threats to freshwater megafauna. *WIREs Water* **4**, e1208 (2017).
4. Bogoni, J. A., Peres, C. A. & Ferraz, K. M. P. M. B. Extent, intensity and drivers of mammal defaunation: a continental-scale analysis across the Neotropics. *Sci. Rep.* **10**, 14750 (2020).
5. Ingram, D. J. et al. Widespread use of migratory megafauna for aquatic wild meat in the tropics and subtropics. *Front. Mar. Sci.* **9**, 837447 (2022).
6. Dirzo, R. et al. Defaunation in the Anthropocene. *Science* **345**, 401–406 (2014).
7. Redford, K. H. The empty forest. *Bioscience* **42**, 412–422 (1992).
8. Lindsey, P. A. et al. The bushmeat trade in African savannas: impacts, drivers, and possible solutions. *Biol. Conserv.* **160**, 80–96 (2013).
9. Benítez-López, A., Santini, L., Schipper, A. M., Busana, M. & Huijbregts, M. A. J. Intact but empty forests? Patterns of hunting induced mammal defaunation in the tropics. *PLoS Biol.* **17**, e3000247 (2019).
10. Young, H. S., McCauley, D. J., Galetti, M. & Dirzo, R. Patterns, causes, and consequences of Anthropocene defaunation. *Annu. Rev. Ecol. Evol. Syst.* **47**, 333–358 (2016).
11. Nielsen, M. R., Meilby, H., Smith-Hall, C., Pouliot, M. & Treue, T. The importance of wild meat in the Global South. *Ecol. Econ.* **146**, 696–705 (2018).
12. Ingram, D. J. et al. Wild meat is still on the menu: progress in wild meat research, policy, and practice from 2002 to 2020. *Annu. Rev. Environ. Resour.* **46**, 221–254 (2021).
13. Brown, D. in *Bushmeat and Livelihoods: Wildlife Management and Poverty Reduction* (eds Davies, G. & Brown, D.) 111–124 (Wiley-Blackwell, 2007).
14. Nasi, R., Taber, A. & Van Vliet, N. Empty forests, empty stomachs? Bushmeat and livelihoods in the Congo and Amazon Basins. *Int. For. Rev.* **13**, 355–368 (2011).
15. Lindsey, P. A. et al. The Zambian wildlife ranching industry: scale, associated benefits, and limitations affecting its development. *PLoS ONE* **8**, e81761 (2013).
16. Dounias, E. & Ichikawa, M. Seasonal bushmeat hunger in the Congo Basin. *Ecohealth* **14**, 575–590 (2017).
17. van Vliet, N. ‘Bushmeat crisis’ and ‘cultural imperialism’ in wildlife management? Taking value orientations into account for a more sustainable and culturally acceptable wildmeat sector. *Front. Ecol. Evol.* **6**, 112 (2018).
18. Ingram, D. J. Wild meat in changing times. *J. Ethnobiol.* **40**, 117–130 (2020).
19. *The Thematic Assessment Report on the Sustainable Use of Wild Species of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services* (IPBES Secretariat, 2022).
20. Obura, D. et al. Prioritizing sustainable use in the Kunming-Montreal Global Biodiversity Framework. *PLoS Sustain. Transform.* **2**, e0000041 (2023).
21. Mace, G. M. et al. Aiming higher to bend the curve of biodiversity loss. *Nat. Sustain.* **1**, 448–451 (2018).
22. Coad, L. et al. *Towards a Sustainable, Participatory and Inclusive Wild Meat Sector* (CIFOR, 2019).
23. UNPD *World Population Prospects 2024: Summary of Results* UN DESA/POP/2024/TR/No. 9 (Population Division of the Department of Economic and Social Affairs of the United Nations Secretariat, 2024); <http://esa.un.org/unpd/wpp/>
24. Abernethy, K. A., Coad, L., Taylor, G., Lee, M. E. & Maisels, F. Extent and ecological consequences of hunting in Central African rainforests in the twenty-first century. *Phil. Trans. R. Soc. B* **368**, 20120303 (2013).
25. Dounias, E. From subsistence to commercial hunting: technical shift in cynegetic practices among southern Cameroon forest dwellers during the 20th century. *Ecol. Soc.* **21**, 23 (2016).
26. Dobson, A. D. M., Milner-Gulland, E. J., Ingram, D. J. & Keane, A. A framework for assessing impacts of wild meat hunting practices in the tropics. *Hum. Ecol.* **47**, 449–464 (2019).

27. Akani, G. C., Petrozzi, F. & Dendi, D. Correlates of indigenous hunting techniques with wildlife trade in bushmeat markets of the Niger delta (Nigeria). *Vie Milieu* **65**, 169–174 (2015).
28. Bowler, M. et al. LED flashlight technology facilitates wild meat extraction across the tropics. *Front. Ecol. Environ.* **18**, 489–495 (2020).
29. Halpern, B. S. et al. Putting all foods on the same table: achieving sustainable food systems requires full accounting. *Proc. Natl Acad. Sci. USA* **116**, 18152–18156 (2019).
30. Taylor, G. et al. Synthesising bushmeat research effort in West and Central Africa: a new regional database. *Biol. Conserv.* **181**, 199–205 (2015).
31. Ingram, D. J. *Quantifying the Exploitation of Terrestrial Wildlife in Africa* (Univ. Sussex, 2017).
32. Wilkie, D. S. & Carpenter, J. F. Bushmeat hunting in the Congo Basin: an assessment of impacts and options for mitigation. *Biodivers. Conserv.* **8**, 927–955 (1999).
33. Fa, J. E. & Peres, C. A. in *Conservation of Exploited Species* (eds Reynolds, J. D. et al.) 203–241 (Cambridge Univ. Press, 2001).
34. Fa, J. E. et al. Differences between pygmy and non-pygmy hunting in Congo Basin forests. *PLoS ONE* **11**, e0161703 (2016).
35. Ziegler, S. et al. Mapping bushmeat hunting pressure in Central Africa. *Biotropica* **48**, 405–412 (2016).
36. Gill, D. J. C., Fa, J. E., Rowcliffe, J. M. & Kumpel, N. F. Drivers of change in hunter offtake and hunting strategies in Sendje, Equatorial Guinea. *Conserv. Biol.* **26**, 1052–1060 (2012).
37. Coad, L. et al. Social and ecological change over a decade in a village hunting system, Central Gabon. *Conserv. Biol.* **27**, 270–280 (2013).
38. Godoy, R., Reyes-García, V., Byron, E., Leonard, W. R. & Vadez, V. The effect of market economies on the well-being of indigenous peoples and on their use of renewable natural resources. *Annu. Rev. Anthropol.* **34**, 121–138 (2005).
39. Duda, R., Gallois, S. & Reyes-García, V. Ethnozoology of bushmeat: importance of wildlife in diet, food avoidances and perception of health among the Baka (Cameroon). *Rev. Ethnoécol.* <https://doi.org/10.4000/ethnoecologie.3976> (2018).
40. Lee, T. M., Sigouin, A., Pinedo-Vasquez, M. & Nasi, R. *The Harvest of Wildlife for Bushmeat and Traditional Medicine in East, South and Southeast Asia* Occasional Paper No. 115 (CIFOR, 2014).
41. Chaves, W. A. et al. Changing wild meat consumption: an experiment in the central Amazon, Brazil. *Conserv. Lett.* <https://doi.org/10.1111/conl.12391> (2018).
42. Wieland, M., Frost Yocum, L., Vanegas, L., Wright, J. & Mwinyihali, R. From the forest to the fork: a conceptual framework of the wild meat supply–demand system to guide interventions in tackling unsustainable trafficking and consumption in the Congo Basin. *Afr. J. Ecol.* **60**, 193–196 (2022).
43. Johnson, T. F., Isaac, N. J. B., Paviolo, A. & González-Suárez, M. Socioeconomic factors predict population changes of large carnivores better than climate change or habitat loss. *Nat. Commun.* **14**, 74 (2023).
44. Nasi, R. et al. *Conservation and Use of Wildlife-Based Resources: The Bushmeat Crisis* CBD Technical Series No. 33 (Secretariat of the Convention on Biological Diversity and Center for International Forestry Research, 2008).
45. Manyama, F. F., Nielsen, M. R., Roskaft, E. & Nyahongo, J. W. The importance of bushmeat in household income as a function of distance from protected areas in the Western Serengeti Ecosystem, Tanzania. *Environ. Nat. Resour. Res.* **9**, 49–62 (2019).
46. Ceppi, S. L. & Nielsen, M. R. A comparative study on bushmeat consumption patterns in ten tribes in Tanzania. *Trop. Conserv. Sci.* **7**, 272–287 (2014).
47. Lhoest, S. et al. Conservation value of tropical forests: distance to human settlements matters more than management in Central Africa. *Biol. Conserv.* **241**, 108351 (2020).
48. Ichikawa, M., Hattori, S. & Yasuoka, H. in *Hunter-Gatherers in a Changing World* (eds Reyes-García, V. & Pyhälä, A.) 59–76 (Springer International, 2017).
49. Lupo, K. D. & Schmitt, D. N. How do meat scarcity and bushmeat commodification influence sharing and giving among forest foragers? A view from the Central African Republic. *Hum. Ecol.* **45**, 627–641 (2017).
50. Bennett Hennessey, A. & Rogers, J. A study of the bushmeat trade in Ouesso, Republic of Congo. *Conserv. Soc.* **6**, 179–184 (2008).
51. Mbete, R. A. et al. Profil des vendeurs de viande de chasse et évaluation de la biomasse commercialisée dans les marchés municipaux de Brazzaville, Congo. *Trop. Conserv. Sci.* **4**, 203–217 (2011).
52. Cronin, D. T. et al. Long-term urban market dynamics reveal increased bushmeat carcass volume despite economic growth and proactive environmental legislation on Bioko Island, Equatorial Guinea. *PLoS ONE* **10**, e0134464 (2015).
53. Doughty, H. L., Karpanty, S. M. & Wilbur, H. M. Local hunting of carnivores in forested Africa: a meta-analysis. *Oryx* **49**, 88–95 (2014).
54. Kumpel, N. F. *Incentives for Sustainable Hunting of Bushmeat in Rio Muni, Equatorial Guinea*. PhD thesis, Imperial College London, University of London/Institute of Zoology, Zoological Society of London (2006).
55. Kumpel, N. F., Milner-Gulland, E. J., Rowcliffe, J. M. & Cowlshaw, G. Impact of gun-hunting on diurnal primates in continental Equatorial Guinea. *Int. J. Primatol.* **29**, 1065–1082 (2008).
56. Koné, I., Refisch, J., Jost Robinson, C. A. & Ayoola, A. O. in *Primates in Anthropogenic Landscapes* (eds McKinney, T., Waters, S. & Rodrigues, M. A.) 45–59 (Springer, 2023).
57. Nana, E. D. et al. Putting conservation efforts in Central Africa on the right track for interventions that last. *Conserv. Lett.* **15**, e12913 (2022).
58. Yasuoka, H. et al. Changes in the composition of hunting catches in southeastern Cameroon: a promising approach for collaborative wildlife management between ecologists and local hunters. *Ecol. Soc.* **20**, 25 (2015).
59. Breuer, T., Breuer-Ndoundou Hockemba, M., Opepa, C. K., Yoga, S. & Mavinga, F. B. High abundance and large proportion of medium and large duikers in an intact and un hunted afro-tropical protected area: insights into monitoring methods. *Afr. J. Ecol.* **59**, 399–411 (2021).
60. Cowlshaw, G., Mendelson, S. & Rowcliffe, J. M. Evidence for post-depletion sustainability in a mature bushmeat market. *J. Appl. Ecol.* **42**, 460–468 (2005).
61. Kumpel, N. F., Milner-Gulland, E. J., Cowlshaw, G. & Marcus Rowcliffe, J. Assessing sustainability at multiple scales in a rotational bushmeat hunting system. *Conserv. Biol.* **24**, 861–871 (2010).
62. Rao, M., Myint, T., Zaw, T. & Htun, S. Hunting patterns in tropical forests adjoining the Hkakaborazi National Park, north Myanmar. *Oryx* **39**, 292–300 (2005).
63. Remis, M. J. & Jost Robinson, C. A. Reductions in primate abundance and diversity in a multi-use protected area: synergistic impacts of hunting and logging in a Congo Basin forest. *Am. J. Primatol.* **74**, 602–612 (2012).
64. Marrocoli, S. et al. Using wildlife indicators to facilitate wildlife monitoring in hunter-self monitoring schemes. *Ecol. Indic.* **105**, 254–263 (2019).
65. Fonteyn, D. et al. Hunting indicators for community-led wildlife management in tropical Africa. *NPJ Biodivers.* **3**, 15 (2024).

66. Zwerts, J. A. et al. FSC-certified forest management benefits large mammals compared to non-FSC. *Nature* **628**, 563–568 (2024).
67. Kleinschroth, F., Laporte, N., Laurance, W. F., Goetz, S. J. & Ghazoul, J. Road expansion and persistence in forests of the Congo Basin. *Nat. Sustain.* **2**, 628–634 (2019).
68. Ingram, D. J. et al. Indicators for wild animal offtake: methods and case study for African mammals and birds. *Ecol. Soc.* **20**, 40 (2015).
69. Salo, M., Sirén, A. & Kalliola, R. *Diagnosing Wild Species Harvest: Resource Use and Conservation* (Academic Press, Elsevier, 2014).
70. Hongo, S. et al. Predicting bushmeat biomass from species composition captured by camera traps: implications for locally based wildlife monitoring. *J. Appl. Ecol.* **59**, 2567–2580 (2022).
71. Johnson, T. P. Snowball sampling: introduction. in *Wiley StatsRef: Statistics Reference Online* (eds Balakrishnan, N. et al.) <https://doi.org/10.1002/9781118445112.stat05720> (Wiley, 2014).
72. Froese, G. Z. L. et al. Coupling paraecology and hunter GPS self-follows to quantify village bushmeat hunting dynamics across the landscape scale. *Afr. J. Ecol.* **60**, 229–249 (2022).
73. Myhrvold, N. P. et al. An amniote life-history database to perform comparative analyses with birds, mammals, and reptiles. *Ecology* **96**, 3109 (2015).
74. Abugiche, S. A. *Impact of Hunting and Bushmeat Trade on Biodiversity Loss in Cameroon: A Case Study of the Banyang-Mbo Wildlife Sanctuary* (Brandenburg Univ. Technology, 2008).
75. Coad, L. et al. Distribution and use of income from bushmeat in a rural village, Central Gabon. *Conserv. Biol.* **24**, 1510–1518 (2010).
76. Willcox, A. S. & Nambu, D. M. Wildlife hunting practices and bushmeat dynamics of the Banyangi and Mbo people of southwestern Cameroon. *Biol. Conserv.* **134**, 251–261 (2007).
77. Lahm, S. A. in *L'Alimentation en Forêt Tropicale Interactions Bioculturelles et Perspectives de Développement* (eds Hladik, C. M. et al.) 383–400 (UNESCO, 1996).
78. Effiom, E. O., Nuñez-Iturri, G., Smith, H. G., Ottosson, U. & Olsson, O. Bushmeat hunting changes regeneration of African rainforests. *Proc. R. Soc. B* **280**, 20130246 (2013).
79. Smits, J. & Permanyer, I. Data descriptor: the Subnational Human Development Database. *Sci. Data* **6**, 190038 (2019).
80. Weiss, D. J. et al. A global map of travel time to cities to assess inequalities in accessibility in 2015. *Nature* **553**, 333–336 (2018).
81. Nelson, A. et al. A suite of global accessibility indicators. *Sci. Data* **6**, 266 (2019).
82. Abernethy, K. & Ndong Obiang, A. M. *Bushmeat in Gabon* (Eaux et Forêts, 2010).
83. Deith, M. C. M. & Brodie, J. F. Predicting defaunation: accurately mapping bushmeat hunting pressure over large areas. *Proc. R. Soc. B* **287**, 20192677 (2020).
84. Grantham, H. S. et al. Anthropogenic modification of forests means only 40% of remaining forests have high ecosystem integrity. *Nat. Commun.* **11**, 5978 (2020).
85. R Core Team. *R: A Language and Environment for Statistical Computing* <http://www.r-project.org/> (R Foundation for Statistical Computing, 2021).
86. Dormann, C. F. et al. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography* **36**, 27–46 (2013).
87. Froese, G. Z. L. et al. Fluid hunter motivation in Central Africa: effects on behaviour, bushmeat and income. *People Nat.* **5**, 1480–1496 (2023).
88. Douma, J. C. & Weedon, J. T. Analysing continuous proportions in ecology and evolution: a practical introduction to beta and Dirichlet regression. *Methods Ecol. Evol.* **10**, 1412–1430 (2019).
89. Stan Development Team. *Stan Modeling Language Users Guide and Reference Manual* v. 4.1.1 <https://mc-stan.org> complete (2021).
90. Bürkner, P. brms: an R package for Bayesian multilevel models using Stan. *J. Stat. Softw.* **80**, 1–28 (2017).
91. Bürkner, P. Advanced Bayesian multilevel modeling with the R package brms. *R J.* **10**, 395–411 (2018).
92. Gelman, A. & Hill, J. *Data Analysis Using Regression and Multilevel/Hierarchical Models* (Cambridge Univ. Press, 2006).
93. Moran, P. A. P. Notes on continuous stochastic phenomena. *Biometrika* **37**, 17–23 (1950).
94. Hartig, F. DHARMA: Residual diagnostics for hierarchical (multi-level/mixed) regression models. R package version 0.4.5 <https://cran.r-project.org/package=DHARMA> (2022).
95. Rodríguez-Sánchez, F. DHARMA.helpers v.0.0.2. *GitHub* <https://pakillo.github.io/DHARMA.helpers/index.html> (2024).
96. Gabry, J., Simpson, D., Vehtari, A., Betancourt, M. & Gelman, A. Visualization in Bayesian workflow. *J. R. Stat. Soc. A* **182**, 389–402 (2019).
97. Gabry, J. & Mahr, T. bayesplot: Plotting for Bayesian models. R package version 1.10.0 <https://mc-stan.org/bayesplot/> (2022).
98. McElreath, R. *Statistical Rethinking: A Bayesian Course with Examples in R and Stan* (CRC, 2018).
99. Zhang, Z., Liu, Y., Yuan, L., Weber, E. & van Kleunen, M. Effect of allelopathy on plant performance: a meta-analysis. *Ecol. Lett.* **24**, 348–362 (2021).
100. Makowski, D., Ben-Shachar, M. & Lüdtke, D. bayestestR: describing effects and their uncertainty, existence and significance within the Bayesian framework. *J. Open Source Softw.* **4**, 1541 (2019).
101. Hijmans, R. J. raster: Geographic data analysis and modeling. R package version 3.6-3 <https://cran.r-project.org/package=raster> (2022).
102. Bivand, R., Keitt, T. & Rowlingson, B. rgdal: Bindings for the 'geospatial' data abstraction library. R package version 1.5-27 <https://cran.r-project.org/package=rgdal> (2021).
103. Pebesma, E. Simple features for R: standardized support for spatial vector data. *R J.* **10**, 439–446 (2018).
104. Greenberg, J. A. & Mattiuzzi, M. gdalUtils: Wrappers for the Geospatial Data Abstraction Library (GDAL) utilities. R package version 2.0.3.2 <https://cran.r-project.org/package=gdalUtils> (2020).
105. Bivand, R. & Lewin-Koh, N. mapproj: Tools for handling spatial objects. R package version 1.1-2 <https://cran.r-project.org/package=mapproj> (2021).
106. Schloerke, B. et al. GGally: Extension to 'ggplot2'. R package version 2.1.2 (2021).
107. Wickham, H. Reshaping data with the reshape package. *J. Stat. Softw.* **21**, 1–20 (2007).
108. Wickham, H. stringr: Simple, consistent wrappers for common string operations. R package version 1.4.0 <https://cran.r-project.org/package=stringr> (2019).
109. Bolker, B. & Robinson, D. broom.mixed: Tidying methods for mixed models. R package version 0.2.7 <https://cran.r-project.org/package=broom.mixed> (2021).
110. Wickham, H. tidyr: Tidy messy data. R package version 1.1.4 <https://cran.r-project.org/package=tidyr> (2021).
111. Wickham, H., Francois, R., Henry, L. & Müller, K. dplyr: A grammar of data manipulation. R package version 1.0.7 <https://cran.r-project.org/package=dplyr> (2021).
112. Wickham, H. et al. Welcome to the tidyverse. *J. Open Source Softw.* **4**, 1686 (2019).
113. Kay, M. tidybayes: Tidy data and geoms for Bayesian models. R package version 3.0.1 <http://mjskay.github.io/tidybayes/> (2021).
114. Wickham, H. *ggplot2: Elegant Graphics for Data Analysis* (Springer, 2016).
115. Pedersen, T. L. patchwork: The composer of plots. R package version 1.1.1 <https://cran.r-project.org/package=patchwork> (2020).

116. Wilke, C. O. cowplot: Streamlined plot theme and plot annotations for 'ggplot2'. R package version 1.1.1 <https://cran.r-project.org/package=cowplot> (2020).
117. Auguie, B. gridExtra: Miscellaneous functions for 'grid' graphics. R package version 2.3 <https://cran.r-project.org/package=gridExtra> (2017).
118. Chamberlain, S. rphylopic: Get 'silhouettes' of 'organisms' from 'phylopic'. R package version 0.3.0 <https://cran.r-project.org/package=rphylopic> (2020).
119. Hansen, M. C. et al. High-resolution global maps of 21st-century forest cover change. *Science* **342**, 850–853 (2013).

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## Author contributions

D.J.I., L.C., J.P.W.S. and K.A. conceptualized the study and are the senior authors. D.J.I., L.C. and K.A. designed the study, with early input from J.P.W.S. D.J.I., G.Z.L.F., A.S.A., S.A.-W., D. Cornelis, M.D., E.D., H.G.E., J.E.F., D.F., A.G., E.G., K.L., J.M., G.N., G.D.N., F.S., J.S., D.N.S., L.V., H.P.A.V., N.v.V., A.S.W., R.N., L.C. and K.A. collected the data. D.J.I. collated and curated the data, with input from F.M., D.K., L.C., U.M., Y.S., K.A. and J.W. D.J.I. conducted the data processing and statistical analysis, with input from G.Z.L.F., P.C.B., D. Carroll, L.C. and K.A. D.J.I. wrote the manuscript draft, with input from L.C., G.Z.L.F. and K.A. All authors contributed to review and editing.

## Competing interests

The authors declare the following competing interests. Non-financial competing interests: D.J.I. is an unpaid trustee of the Pangolin Project, a UK registered charity; an unpaid scientific advisor for the African Aquatic Conservation Fund, Senegal; an unpaid member of the Conservation Advisory Group, Bristol Zoological Society, UK; an unpaid scientific councillor of the Aquatic Wild Meat Working Group of the Convention on Migratory Species; and an unpaid member of

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## Additional information

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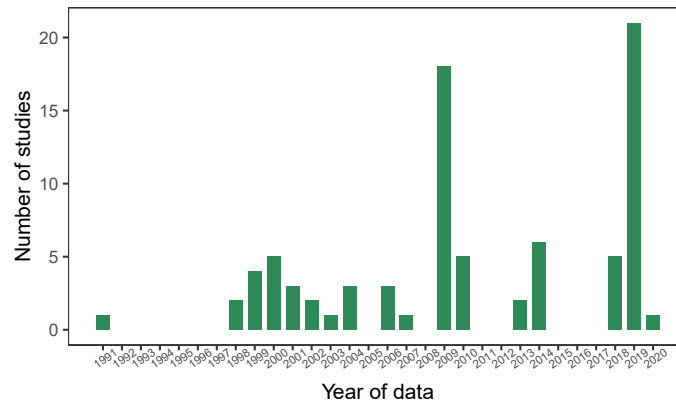
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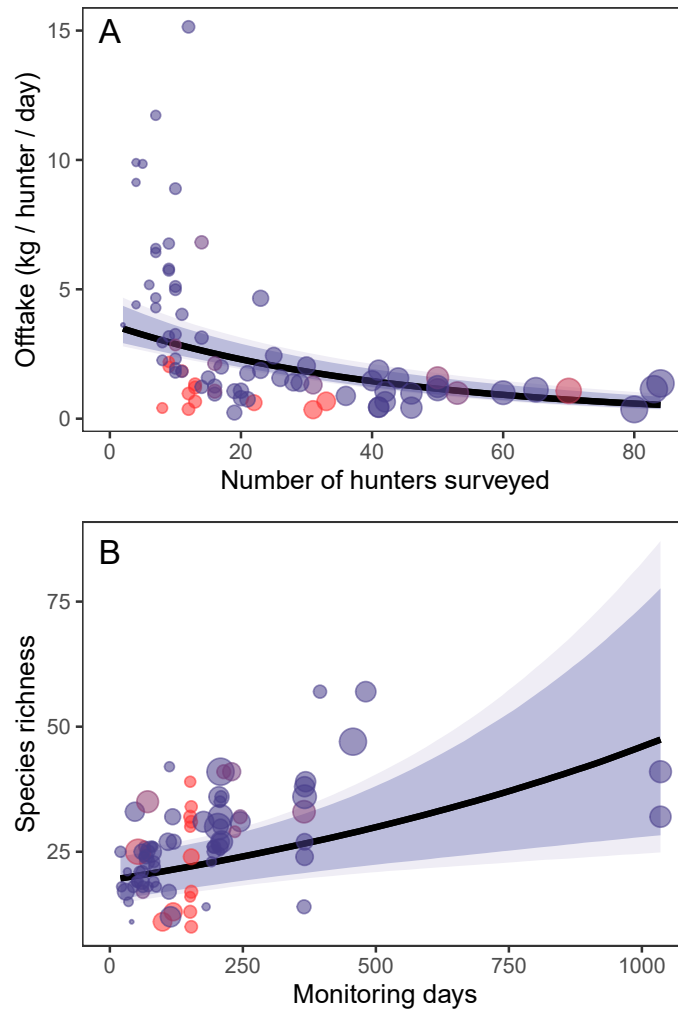
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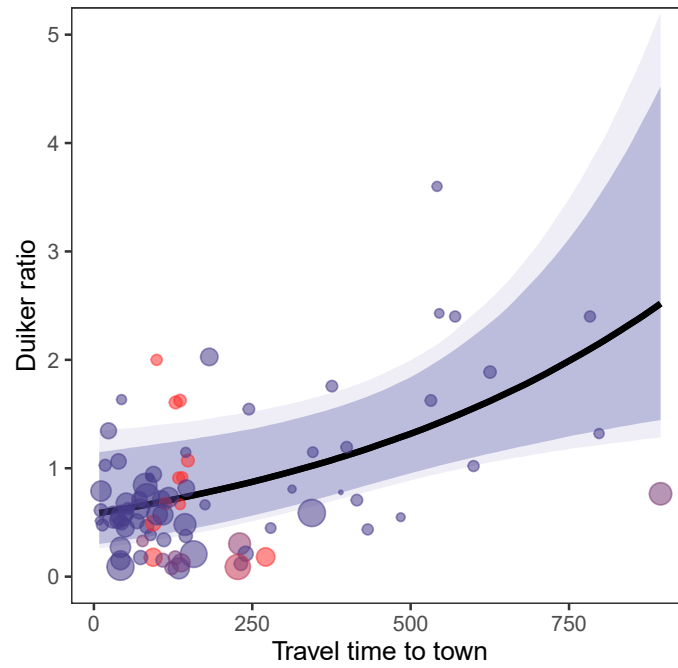
**Extended Data Fig. 1 | The number of studies included in our analyses, plotted by year of data collection.** Note: 1) each study may represent >1 site, and 2) peaks in 2009 and 2019 are from two sources that collected data at multiple sites. The year data was collected in was not correlated with survey effort, as measured by the number of days hunters were monitored (Pearson's  $r = -0.2$ ) or the number of hunters surveyed ( $r = -0.2$ ).



**Extended Data Fig. 2 | Effect of survey effort.** Bayesian generalised linear multilevel model predicted relationship between the number of hunters surveyed and estimates of mean daily hunter offtake (A), and between the number of monitoring days and species richness (B). Purple ribbons show the 89% (dark purple) and 95% uncertainty intervals (light purple), while the black

line shows the global average marginal effect. Points show individual studies (scaled by the number of hunters surveyed) and are coloured by the proportion of hunters monitored that were village hunters (a gradient from orange to purple representing only forest hunter-gatherers to only village hunters). Points are semi-transparent to show point density.





**Extended Data Fig. 3 | Variables associated with duiker ratio.** Bayesian generalised linear multilevel model predicted conditional relationship between the ratio of *Cephalophus* to *Philantomba* cetartiodactyls (duiker ratio) and the travel time of a site to the nearest town with a population >10,000 people. Purple ribbons show the 89% (dark purple) and 95% uncertainty intervals (light

purple), while the black line shows the global average marginal effect. Points show individual studies (scaled by number of hunters surveyed) and are coloured by the proportion of hunters monitored that were village hunters (a gradient from orange to purple representing only forest hunter-gatherers to only village hunters). Points are semi-transparent to show point density.

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### Software and code

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**Data collection** All of our analyses were conducted using the R statistical environment (v. 4.1.1) through the open-access integrated development environment for R, R Studio (freely available at: <https://posit.co/download/rstudio-desktop/>). The code used to develop the models are available via GitHub at: <https://github.com/DJIngram/regional-hunting>

**Data analysis** All of our analyses were conducted using the R statistical environment (v. 4.1.1) through the open-access integrated development environment for R, R Studio (freely available at: <https://posit.co/download/rstudio-desktop/>). All data was analyzed in R version 4.1.1. The following R packages were used: brms (2.21.0), DHARMA (0.4.5), DHARMA.helpers (0.0.2), bayesplot (1.8.1), bayestestR (0.12.1), raster (3.6-3), rgdal (1.5-27), sf (1.0-3), gdalUtils (2.0.3.2), mapproj (1.1-2), GGally (2.1.2), reshape2 (1.4.4), stringr (1.4.0), broom.mixed (0.2.7), tidyr (1.1.4), dplyr (1.0.7), tidyverse (1.3.1), tidybayes (3.0.1), ggplot2 (3.4.2), patchwork (1.1.1), cowplot (1.1.1), gridExtra (2.3), and rphylopic (0.3.0).

For manuscripts utilizing custom algorithms or software that are central to the research but not yet described in published literature, software must be made available to editors and reviewers. We strongly encourage code deposition in a community repository (e.g. GitHub). See the Nature Portfolio [guidelines for submitting code & software](#) for further information.

## Data

Policy information about [availability of data](#)

All manuscripts must include a [data availability statement](#). This statement should provide the following information, where applicable:

- Accession codes, unique identifiers, or web links for publicly available datasets
- A description of any restrictions on data availability
- For clinical datasets or third party data, please ensure that the statement adheres to our [policy](#)

No new data were generated as part of this study. For details of spatial datasets, see Supplementary Table 2. Spatial datasets are available from:

Protected areas: <https://www.protectedplanet.net/en/>

Forest cover: <https://glad.earthengine.app/>

Human population density: <https://hub.worldpop.org/>

Travel time to town: <https://malariaatlas.org/>

Forest condition: <https://www.forestintegrity.com/>

Subnational human development index: <https://globaldatalab.org/>

Hunting data were extracted directly from published papers and from multiple original sources. Individual datasets from different sources (before processing) will also be made available to download with restrictions through the WILDMEAT Data Portal (<https://explorer.wildmeat.org/>) which is stored in the CIFOR Dataverse. WILDMEAT is a new data sharing platform designed to house data on the hunting, consumption, and trade of wildlife. Due to the highly sensitive nature of the data (locations of potentially vulnerable communities conducting illegal activities in some cases; locations of endangered species), each dataset is available under different data sharing conditions as determined by the original data owner through a Data User Agreement. This is to allow individual data providers to assess the use of the data against their ethical assessments and agreements. Information on wild meat indicators is freely available on the new toolkit <https://www.wildmeat.org/toolkit/indicators/>.

## Human research participants

Policy information about [studies involving human research participants and Sex and Gender in Research](#).

### Reporting on sex and gender

*Use the terms sex (biological attribute) and gender (shaped by social and cultural circumstances) carefully in order to avoid confusing both terms. Indicate if findings apply to only one sex or gender; describe whether sex and gender were considered in study design whether sex and/or gender was determined based on self-reporting or assigned and methods used. Provide in the source data disaggregated sex and gender data where this information has been collected, and consent has been obtained for sharing of individual-level data; provide overall numbers in this Reporting Summary. Please state if this information has not been collected. Report sex- and gender-based analyses where performed, justify reasons for lack of sex- and gender-based analysis.*

### Population characteristics

*Describe the covariate-relevant population characteristics of the human research participants (e.g. age, genotypic information, past and current diagnosis and treatment categories). If you filled out the behavioural & social sciences study design questions and have nothing to add here, write "See above."*

### Recruitment

*Describe how participants were recruited. Outline any potential self-selection bias or other biases that may be present and how these are likely to impact results.*

### Ethics oversight

Data was extracted directly from other sources, and meta-analysed together. Overall ethics not necessary for meta-analyses of secondary data.

Note that full information on the approval of the study protocol must also be provided in the manuscript.

## Field-specific reporting

Please select the one below that is the best fit for your research. If you are not sure, read the appropriate sections before making your selection.

Life sciences  Behavioural & social sciences  Ecological, evolutionary & environmental sciences

For a reference copy of the document with all sections, see [nature.com/documents/nr-reporting-summary-flat.pdf](https://www.nature.com/documents/nr-reporting-summary-flat.pdf)

## Ecological, evolutionary & environmental sciences study design

All studies must disclose on these points even when the disclosure is negative.

### Study description

We collate and analyse data from 83 studies, representing 115 settlements, to investigate the socio-cultural, economic, and landscape variables associated with key components of wild meat offtake, using a Bayesian modelling approach that accounts for differences among studies. We investigate factors associated with variation in a) wild meat offtake rate per hunter (mean kg hunter<sup>-1</sup> day<sup>-1</sup>); b) the proportion of hunted animals that are sold (as a proxy for the use of wild meat for income vs food within hunter

households); c) the proportion of all hunted animals killed by gun hunting (a measure of hunting technology use); and, d) four taxonomic composition metrics of the offtake (as proxies for wild animal depletion).

**Research sample**  
In total, we collated data from 83 hunter offtake studies conducted in 78 sites across seven countries in West and Central Africa between 1991 and 2020 (Fig. 1; Extended Data Fig. 1; Supplementary Information). The sites accounted for data from 115 settlements, whereby the number of settlements per site, including single villages, grouped villages, and towns, ranged from 1 to 14. Studies monitored a mean of 23 ± 20 hunters for a mean of 178 ± 173 days (mean ± SD). Across all studies, 85,214 individual animals from 143 unique species and 33 orders were reported to be captured, accounting for a total wild animal mass of > 837,900 kilograms hunted over 462,435 hunter-days (including elephants).

**Sampling strategy**  
Data on the number of animals hunted by hunters in a given location (hereafter 'hunter offtakes') across West and Central Africa were extracted from sources that include published journal articles, grey literature (e.g., NGO reports, university degree theses), and unpublished data (deemed suitable when it had been collected using published methods). We searched for potential data sources between 1st August 2019 and 17th December 2021 using the following methods. Suitable sources were first identified from lists provided in two studies where systematic searching techniques were used. We then conducted regular additional literature searches using search engines and bibliographic databases (Google Scholar [including using alerts], and the ISI Web of Knowledge [All Databases]). We performed searches using Boolean logic with the following words: (bushmeat, game, gibier, hunt\*, offtake, poach\*, viande de brousse, wild meat, wildmeat) AND (Africa, Afrique centrale, Afrique de l'Ouest, Afrique occidentale, Bassin du Congo, Central Africa, Congo Basin, West Africa). Whilst this method was effective at finding sources, we were able to find further sources mostly through subsequent searching of reference lists and contacting wild meat researchers (both akin to chain-referral sampling).

**Data collection**  
Data on the number of animals hunted by hunters in a given location (hereafter 'hunter offtakes') across West and Central Africa were extracted from sources that include published journal articles, grey literature (e.g., NGO reports, university degree theses), and unpublished data (deemed suitable when it had been collected using published methods). We searched for potential data sources between 1st August 2019 and 17th December 2021 using the following methods. Suitable sources were first identified from lists provided in two studies where systematic searching techniques were used. We then conducted regular additional literature searches using search engines and bibliographic databases (Google Scholar [including using alerts], and the ISI Web of Knowledge [All Databases]). We performed searches using Boolean logic with the following words: (bushmeat, game, gibier, hunt\*, offtake, poach\*, viande de brousse, wild meat, wildmeat) AND (Africa, Afrique centrale, Afrique de l'Ouest, Afrique occidentale, Bassin du Congo, Central Africa, Congo Basin, West Africa). Whilst this method was effective at finding sources, we were able to find further sources mostly through subsequent searching of reference lists and contacting wild meat researchers (both akin to chain-referral sampling). The first author collated the data.

**Timing and spatial scale**  
Data were not collected directly for this study, but we used data collected in other studies between 1991 and 2022.

**Data exclusions**  
No data were excluded.

**Reproducibility**  
Repeat data collection and reproducibility of results is not relevant - data were extracted from openly-available sources directly.

**Randomization**  
Randomization is not relevant - data were extracted from openly-available sources directly.

**Blinding**  
Blinding is not relevant - data were extracted from openly-available sources directly.

Did the study involve field work?  Yes  No

## Reporting for specific materials, systems and methods

We require information from authors about some types of materials, experimental systems and methods used in many studies. Here, indicate whether each material, system or method listed is relevant to your study. If you are not sure if a list item applies to your research, read the appropriate section before selecting a response.

### Materials & experimental systems

- |                                     |  |
|-------------------------------------|--|
| n/a                                 | Involvement in the study                               |
| <input checked="" type="checkbox"/> | <input type="checkbox"/> Antibodies                    |
| <input checked="" type="checkbox"/> | <input type="checkbox"/> Eukaryotic cell lines         |
| <input checked="" type="checkbox"/> | <input type="checkbox"/> Palaeontology and archaeology |
| <input checked="" type="checkbox"/> | <input type="checkbox"/> Animals and other organisms   |
| <input checked="" type="checkbox"/> | <input type="checkbox"/> Clinical data                 |
| <input checked="" type="checkbox"/> | <input type="checkbox"/> Dual use research of concern  |

### Methods

- |                                     |   |
|-------------------------------------|---|
| n/a                                 | Involvement in the study                        |
| <input checked="" type="checkbox"/> | <input type="checkbox"/> ChIP-seq               |
| <input checked="" type="checkbox"/> | <input type="checkbox"/> Flow cytometry         |
| <input checked="" type="checkbox"/> | <input type="checkbox"/> MRI-based neuroimaging |