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Title: The impact of hunting on tropical mammal and bird populations

A. Benítez-López^{1*}, R. Alkemade^{2,3}, A. M. Schipper², D. J. Ingram⁴, P. A. Verweij⁵, J. A. J. Eikelboom^{2,5,6}, M. A. J. Huijbregts^{1,2}

Affiliations:

¹Department of Environmental Science, Institute for Wetland and Water Research, Radboud University, P.O. Box 9010, NL-6500 GL, Nijmegen, The Netherlands.

²PBL, Netherlands Environmental Assessment Agency, P.O. Box 30314, 2500 GH The Hague, The Netherlands.

³Environmental Systems Analysis Group, Wageningen University, P.O. Box 47, 6700 AA Wageningen, The Netherlands

⁴School of Life Sciences, University of Sussex, UK.

⁵Copernicus Institute of Sustainable Development, Utrecht University, Heidelberglaan 2, 3584 CS Utrecht, The Netherlands.

⁶Resource Ecology Group, Wageningen University & Research, Droevendaalsesteeg 3a, 6708 PB Wageningen, The Netherlands

*Correspondence to: a.benitez@science.ru.nl

Abstract:

Hunting is a major driver of biodiversity loss, but a systematic large-scale estimate of hunting-induced defaunation is lacking. We synthesized 176 studies to quantify hunting-induced declines of mammal and bird populations across the tropics. Bird and mammal abundances declined by 58% (25 – 76 %) and by 83% (72 – 90%) in hunted compared to un hunted areas. Bird and mammal populations were depleted within 7 and 40 km from

hunters' access points (roads and settlements). Additionally, hunting pressure was higher in areas with better accessibility to major towns where wild meat could be traded. Mammal population densities were lower outside protected areas, particularly due to commercial hunting. Strategies to sustainably manage wild meat hunting in both protected and unprotected tropical ecosystems are urgently needed to avoid further defaunation.

One Sentence Summary: Hunting accounts for 58% and 83% declines in bird and mammal populations across the tropics.

Main Text:

Global biodiversity loss is occurring at an unprecedented rate (1). Few undisturbed areas remain in the tropics (2), but these are threatened by escalating road and infrastructure expansion, which promotes human accessibility to otherwise remote areas facilitating illegal colonization and hunting (3-5). Hunting exerts a major pressure on wildlife, causing large declines and local extirpations of wildlife populations in forests that appear structurally undisturbed (6). Overhunted “half-empty” or “empty ecosystems” are becoming common across the tropics (7). Indeed, the abundance of wildlife in natural ecosystems is more closely related to patterns of hunting than to factors such as forest type, habitat area, or habitat protection status (8). A growing body of research is focusing on defaunation and its far-reaching cascading effects, including disruptions in seed dispersal mutualisms and a decline in total biomass (9, 10). However, hunting-induced defaunation is a cryptic phenomenon difficult to monitor, and no large-scale estimates of the impact of hunting on wildlife abundances are available.

Here we analyse the impact of hunting on bird and mammal populations at a pantropical scale, in terms of both magnitude (decline in abundance) and spatial extent (depletion

distances). We collated 176 studies, including 384 and 1938 effect sizes for 97 bird and 254 mammal species, respectively (11) (Fig 1.), and estimated the overall reduction in mammal and bird abundance in hunted compared to unhunted sites with a random effects meta-analysis. As effect size, we calculated response ratios, between the abundance of each species in hunted (X_h) and unhunted sites (X_c) within each study ($RR = \log (X_h / X_c)$, (12)). RR are therefore negative ($RR < 0$) or positive ($RR > 0$) if abundance estimates are lower or higher due to hunting pressure, respectively. Based on the central-place foraging hypothesis, hunting intensity is generally higher in the proximity of hunters' access points (e.g.: settlements, roads (5, 10)), generating gradients of increasing species densities up to a distance where no effect is observed (i.e.: species depletion distances). We used single meta-regression models to estimate species depletion distances and quantify how the impact of hunting varied depending on accessibility to urban markets for trade (travel time to major towns (13), region, type of hunting (commercial vs subsistence vs both), protection status (protected vs non-protected area), species body size and functional guild. Finally, we tested the relative importance of these moderators using an information-theoretic approach of several multiple meta-regression models including first- and second-order interactions.

Overall, bird and mammal abundances were reduced by 58% (95% CI: 25, 76 %) and 83% (95% CI: 72, 90%) in hunted areas (Fig. 2). Hunting pressure had a larger effect on mammals than on birds, probably because hunters preferably target larger species (6). Results were robust to potential publication bias for mammals, and to Geary diagnostic tests and differences in study quality for both groups (fig. S3, S4)). Hunting-induced abundance reductions varied with distance to hunters' access points (distance, hereafter), accessibility to urban markets, protected area status and type of hunting, with distance being the most important moderator (Fig. 3, Fig. 4, Table S5). For birds, effect sizes were the lowest in the proximity of hunters' access points ($RR_b = -3.17$, 95% CI = -2.62, -3.71, ca. 95% loss at 500

m) and approximated zero at a distance of 7 km (Fig. 3a). For mammals, effect sizes first decreased from -0.76 (-1.30, -0.23) to -2.38 (-2.84,-1.78) within the first 700 m (ca. 90% loss), and then increased steadily up to zero ca. 40 km from hunters' access points (Fig. 3b). This initial higher *RR* may reflect the replacement of large-bodied mammals by smaller ones. Indeed, we found evidence of size-differential mammal defaunation for frugivores, carnivores, herbivores and insectivores (Table S6, S7). Smaller mammals were consistently more abundant at higher hunting pressure than larger species (fig. S5), probably due to release from predation pressure and competition as a result of (near) extirpation of medium- and large-sized mammals (14). Large-bodied frugivores, herbivores and insectivores, including chimpanzees (*Pan troglodytes*), Western gorillas (*Gorilla gorilla*) and Giant armadillos (*Priodontes maximus*), are largely hunted for wild meat consumption and trade (15). In turn, large carnivores such as leopards (*Panthera pardus*) and jaguars (*Panthera onca*) are often persecuted because of livestock-wildlife conflicts, or their populations are reduced due to hunting-induced losses of prey species (16).

Bird and mammal population densities were lower in hunted areas with higher accessibility to urban markets (Fig. 3c, d). Effect sizes approached zero within 1-2 days of travel time from the nearest major town. For mammals, this effect remained after controlling for other factors (Table S6). Across the tropics, the majority of consumed and traded wild meat and body parts comes from mammals, while birds are generally hunted for own consumption (6, 17). However, for both species groups, the transition from subsistence to commercial hunting is having a massive impact on population densities (Fig. 4). Current prospects of infrastructure expansion in the Amazon, Africa and Asia will facilitate accessibility to remote areas (3, 18, 19), boosting wild meat harvest and trade to meet urban demands (7), and thus increasing pressure on wildlife populations.

Mammal population densities were higher inside than outside protected areas (Fig. 4). However, hunting pressure reduced mammal abundances even within protected areas (Fig. 4). Overhunting within protected areas is ubiquitous across Amazonia, Africa and Asia (8, 20). Although our results suggest that the effects within are less detrimental than outside reserves, gazettement of protected areas seems insufficient to safeguard wildlife populations if not accompanied with improved reserve management, effective law enforcement and on-ground protection efforts (20).

Effect sizes were similar across regions for both taxa, although slightly lower in South America for birds (Fig. 4). This indicates that overhunting is affecting mammal and bird populations similarly across the tropics. However, we found more studies in South America and Africa than Asia or Central America (Fig. 1), which implies that our findings are more generalizable for the former two regions. It also points out an urgent need to focus research efforts in less studied areas before wildlife populations are completely extirpated. Unfortunately, overhunting has already emptied most Asian forests (7), leaving few un hunted control areas left for pairwise comparisons.

The most important terms retained in our multiple meta- regression models were distance for both groups (Table S6, S7), and the interactions between guild, body size and distance for mammals (see fig. S5 and explanations above). Our best models were significant according to omnibus tests (birds: $Q_M = 3157.5$, $P < 0.001$, McFadden pseudo- R^2 : 0.29; mammals: $Q_M = 19207.3$, $P < 0.001$, McFadden pseudo- R^2 : 0.18), however residual heterogeneity was large (Table S7), indicating that hunting is a multifaceted phenomenon influenced by additional factors, some of which were not included in our models (e.g.: food security). Additionally,

confounding variables such as small-scale habitat clearing and road disturbance are correlated with distance to settlements and roads (21). However, we minimized their influence as much as possible by avoiding pairwise comparisons where disturbances other than hunting were apparent.

Overexploitation is a long-established major driver of wildlife population declines and extinctions in terrestrial ecosystems which, to date, has not been successfully mitigated and rather shows an increasing trajectory in recent decades (22). Pleistocene extinctions were triggered in part by human hunters (23), and ongoing wildlife population declines and (near) extinctions of large-bodied species seem to share similar pathways. Consequently, defaunation is rendering tropical forests, savannahs and grasslands ‘empty’ (16), with populations so sparse that the strength of species interactions is declining dramatically. The subtle nature of this process makes it undetectable by remote-sensing techniques, which are key to monitor deforestation, but prove futile to track on-ground changes in biodiversity and ecological functioning (24). Matching the findings of many regionally-specific studies (5, 10), our meta-analysis shows that large vertebrates of various functional groups are depleted in the vicinity of settlements and roads. Our estimated hunting depletion distances can be used to assess ecosystem degradation as a result of current and future road developments and settlement establishment. Recently, Peres et al. (25) estimated that 32.4% of the remaining forest across the Brazilian Amazon (ca. 1 mil. km²) is affected by hunting based on hunting distances of 6 km from settlements. Our results however indicate that the Amazon forest area affected by hunting-induced defaunation might be much larger. By 2050, with millions of kilometers of roads planned in developing countries (26), and human population and associated demand for wild meat increasing steadily, it is likely that the term “remoteness” will be a ghost of the past, with the last remnant half-depleted mammal and bird populations

persisting in few protected areas. This can be ameliorated if we undertake coordinated strategies to expand the current network of reserves, limit human encroachment around them and control overexploitation via law enforcement, while providing alternative livelihoods for wild meat-dependent communities.

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Fig. 1. Geographical location of the 176 studies included in the meta-analysis (red dots).

Countries that contain at least one study are in green colour. Red dots may represent multiple effect sizes.

Fig. 2. Forest plots of 384 and 1938 effect size estimates (RR , black dots) with 95% confidence intervals (CI ; grey lines) for a) birds and b) mammals. Black dashed line and red diamond: overall weighted mean effect size estimate with 95% CI (red line); dashed grey line: $RR = 0$. Extremely negative effect sizes indicate local extirpations.

Fig. 3. Change in species abundance (RR) with distance to hunters' access points (a,b) and travel time (minutes) to major towns (c, d) for birds (a, c) and mammals (b, d).

Dashed grey line: $RR = 0$. Black line: predicted lines with 95% CI in grey. Size of data points (in blue) is proportional to the sampling variance. Results obtained with single meta-regressions.

Fig. 4. Change in species abundance (RR) for different levels of protection (a, b), type of hunting (c, d), regions (e, f) and feeding guilds (g, h), for birds (a, c, e, g) and mammals (b, d, f, h). Number of effect sizes is shown between brackets. Dashed black line: mean weighted effect size. Dashed grey line: $RR = 0$. Unp: Unprotected areas, Prot: Protected areas, Subs: Subsistence hunting, SuCo: Subsistence and commercial hunting, Com: Commercial hunting, CeAm: Central America, SoAm: South America, Her: Herbivores, Car: Carnivores, Fru: Frugivores, Ins: Insectivores, Omn: Omnivores. Results obtained with single meta-regressions. None of the studies reported on bird hunting for commercial purposes solely.

Supplementary Materials:

Materials and Methods

Figures S1-S6

Tables S1-S7

References (27 - 159)