REPORT

DEFAUNATION

The impact of hunting on tropical mammal and bird populations

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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 to 76%) and by 83% (72 to 90%) in hunted compared with unhunted areas. Bird and mammal populations were depleted within 7 and 40 kilometers 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 because of commercial hunting. Strategies to sustainably manage wild meat hunting in both protected and unprotected tropical ecosystems are urgently needed to avoid further defaunation.

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 and facilitates illegal colonization and hunting (*3*–*5*). Hunting exerts a major pressure on wildlife, which can result in large population 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 that is difficult to monitor and, to date, no large-scale estimates of the impact of hunting on wildlife abundances are available.

Here, we analyze 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 with unhunted sites with a mixed effects meta-analysis. As an effect size, we calculated response ratios (*RR*) 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, respectively, because of hunting pressure. Based on the central-place foraging hypothesis, hunting intensity is generally higher in the proximity of hunters' access points (e.g., settlements and 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 to 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 versus subsistence versus both), protection status (protected versus unprotected area), species body size, and feeding guild. Finally, we tested the relative importance of these moderators using an information-theoretic

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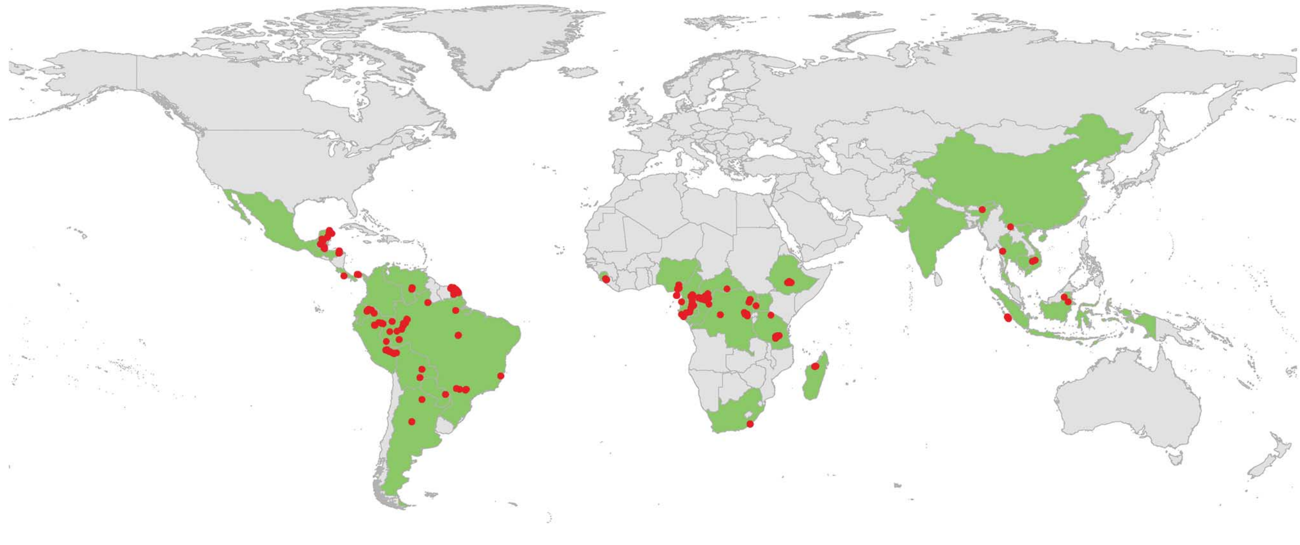

Fig. 1. Geographical location of the 176 studies included in the meta-analysis. Locations as red dots. Countries that contain at least one study are in green color. Red dots may represent multiple effect sizes.

approach of several multiple meta-regression models including first- and second-order interactions.

Overall, bird and mammal abundances were reduced by 58% [95% confidence interval (CI): 25, 76%] and 83% (95% CI: 72, 90%), respectively, in hunted areas (Fig. 2). Hunting pressure had a larger effect on mammals than on birds, probably because hunters preferentially 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 (figs. S3 and 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 (Figs. 3 and 4 and table S5). For birds, effect sizes were the lowest in proximity to hunters' access points (RR_b = −3.17, 95% CI = −2.62, −3.71, ~95% loss at 500 m) and approximated 0 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 (~90% loss), and then increased steadily up to 0 at ~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 (tables S6 and S7). Smaller mammals were consistently more abundant at higher hunting pressure than larger species (fig. S5), probably owing 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 because of hunting-induced losses of prey species (*16*).

Bird and mammal population abundances were lower in hunted areas with higher accessibility to urban markets (Fig. 3, C and D). Effect sizes approached 0 within 1 to 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, whereas birds are generally killed for a hunter's 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 the Amazon, 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 unhunted control areas left for pairwise comparisons.

The most important terms retained in our multiple meta-regression models were distance for both groups (tables S6 and 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

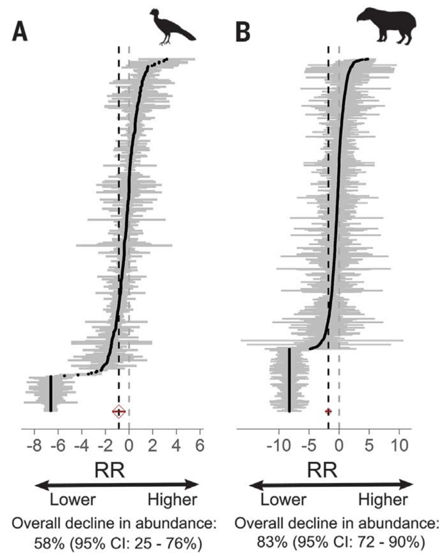

Fig. 2. Forest plots of 384 and 1938 effect size estimates for birds and mammals, respectively. (**A**) Birds and (**B**) mammals. *RR*, response ratios (effect sizes), black dots with 95% confidence intervals (CI) as gray lines. Overall weighted mean effect size estimate, black dashed line and red diamond. 95% CI of weighted mean effect size, red line. *RR* = 0, dashed gray line. Extremely negative effect sizes indicate local extirpations.

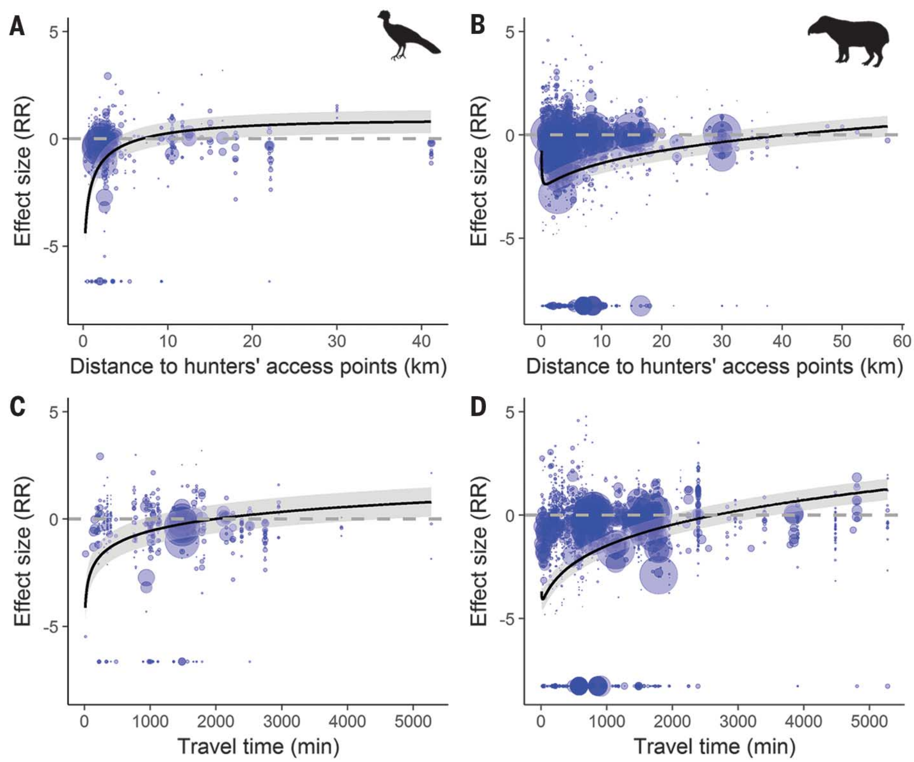

Fig. 3. Change in species abundance with distance to hunters' access points and travel time to major towns. (**A** and **B**) Distance to hunter's access points and (**C** and **D**) travel time to major towns; for birds (A and C) and mammals (B and D). RR, response ratios. *RR* = 0, dashed gray line; predicted mean effect size (with 95% CI in gray), black lines. Size of data points (in blue) is proportional to the sampling variance. Results obtained with single meta-regressions.

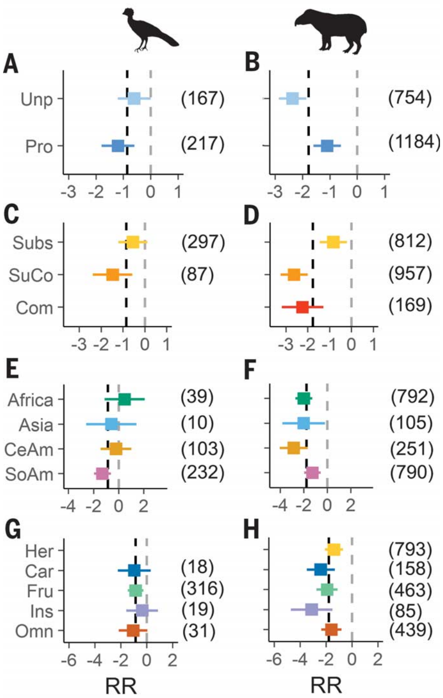

Fig. 4. Change in species abundance for different levels of protection, type of hunting, regions, and feeding guilds. (**A** to **H**) Parameters as labeled for birds (left) and mammals (right). Number of effect sizes is shown between brackets. RR, response ratios. Mean weighted effect size, dashed black line; *RR* = 0, dashed gray line; 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; and Omn, omnivores. Results obtained with single meta-regressions. None of the studies reported on bird hunting for commercial purposes solely.

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 (~1 million km^2) is affected by hunting on the basis of 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 protected areas, limit human encroachment around them, monitor hunting activities, and control overexploitation via law enforcement, if needed, while implementing alternative livelihood programs for wild meat–dependent communities.

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SUPPLEMENTARY MATERIALS

www.sciencemag.org/content/356/6334/180/suppl/DC1
Materials and Methods
Figs. S1 to S6
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References (*27–159*)

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Editor's Summary

Quantifying hunting-induced defaunation

As the human population grows and increasingly encroaches on remaining wildlife habitat, hunting threatens many species. Benítez-López *et al.* conducted a large-scale meta-analysis of hunting trends and impacts across the tropics (see the Perspective by Brashares and Gaynor). Bird and mammal populations were considerably lower in areas where hunting occurred. Although commercial hunting and proximity to roads and urban centers were the most damaging factors, all hunting had worrying impacts, even in protected areas. Protection and alternative approaches for sustainable subsistence hunting must be implemented soon if we are to prevent further, rapid defaunation.

Science, this issue p. 180; see also p. 136