Trends in
Ecology & Evolution

CellPress

Spotlight

The most abundant mammals on Earth

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New estimates of global mammal abundance that use relationships between traits, estimates of range size, and International Union for Conservation of Nature's (IUCN's) Red List categories to predict the biomass of thousands of species have been developed by Greenspoon *et al.* This approach and some of the challenges that contribute to these estimates are summarized here.

Conservation managers need to identify species that are in decline. This is harder to know than it sounds. For at least two points in time, how many individuals were there? Most of the planet is not monitored for most species. How many went undetected in surveys? Do counts balance the variation in abundance across habitats, times of day, seasons, human impacts, and population cycles [1–3]? Some of the traits that contribute to the vulnerability of a species also challenge survey efforts (Figure 1). For large mammals, low population densities put them at risk of Allee effects, while also making them hard to monitor [4,5]. Small, nocturnal, and fossorial species are rarely seen and, when they are, few observers can tell them apart. Uncharismatic species are under-reported in crowd-sourced platforms, such as iNaturalist and eBird [6], which are big contributors to the Global Biodiversity Information Facility (GBIF). GBIF is often used to estimate the ranges of species. Information from a host of sources can be cobbled together in meta-analysis, in which the trends in spatially and temporally unbalanced data often do not represent population trends [5,7,8]. Despite the many challenges, contemporary biodiversity loss inspires efforts to synthesize. Over the past century, many (most?) mammal species probably lost most of their ranges, while vertebrates may be disappearing at a rate of two species per year [9].

Greenspoon *et al.* [10] offer an ambitious effort to estimate global mammal abundance. There are two classes of estimate in this paper. The first class comprises 382 species that are extracted from IUCN reports (Figure 2); thus, it builds in the limitations of that effort. The IUCN tables are a brave attempt to turn multiple sources of information into species abundance and trends. Take, for example, the African savanna elephant (*Loxodonta africana*). Surveys come from national parks and game reserves. A fraction of most populations can be monitored, and methods vary widely [11]; as they say in one IUCN report 'identification of individual animals, aerial counts, dung counts, and guesses'. In the IUCN effort, observations become population estimates, which are then extrapolated to the area of a site or reserve. The effective area to which a survey applies is hard to know, due to the wide variation in habitats across a given site.

The IUCN attempts to accommodate heterogeneous observation effort and errors (they can be large) and unknown spatial distributions. There is an ordinal scale for uncertainty. Additional decisions address changes in area over time. Ultimately, the survey information leads to a table with a number for population size at two time points and an area to which those numbers apply. This is used to assign the IUCN threat category. They caution on the use of these estimates: 'Taking these tables' numbers as concrete estimates is not appropriate given the model's structure and objective. Rather the values reflect relative weighting at the site level in our density model. This relative weighting is recommended in the IUCN Red List Guidelines (p. 37 section 4.5.3) and we applied it as requested to maintain methodological consistency across the more than 134,000 species assessed for the IUCN Red List'. Despite this caveat, IUCN is effectively using them, because they are the basis for estimates of decline. Greenspoon *et al.* use them too, and for the same reason: when confronted with so many species, sites, and methods, there are few options.

The second class of estimates is used for species not covered in IUCN. The method of Greenspoon *et al.* is necessarily indirect and sure to invite discussion (Figure 2). The population densities (numbers divided by areas) of the 382 species included in IUCN are the basis for predicting non-IUCN species. The predictors are range size (not used for rodents), body mass, Red List category, taxonomic order, trophic level, and generation time. A regression calibrated to the 382 IUCN species is used to predict density for 4805 non-IUCN species. These estimated (IUCN) and predicted (non-IUCN) densities are then extrapolated to an area that might represent the species range. Thus, we now need a guess for the range of every species, another big source of uncertainty for most species. Finally, translating numbers to biomass entails the assumption that 60% of all populations are adults, and adults weigh twice as much as juveniles.

Errors from this approach will undoubtedly be massive, and they will differ by species and survey method. Aerial counts along flight lines can offer estimates of animals per area; there is a count and an effort in terms of area surveyed, sometimes incorporating distance [4]. Many other monitoring approaches cannot estimate animals per area. Camera traps used for large mammals and live trapping of small mammals provide an index of activity, but typically not reliable

Figure 1. Estimates of density (animals per area) are multiplied by an estimate of species range size to obtain abundance. Both numbers are hard to estimate. Two of the most abundant mammals estimated by Greenspoon *et al.* [10] contrast in terms of detection. Due to size and color, African savanna elephants (*Loxodonta africana*) are readily identified from aerial surveys during dry seasons at Kruger National Park, where they can be tallied with known effort. A survey yields counts per area, or density. The white-tailed deer (*Odocoileus virginianus*), estimated to be most abundant globally, is difficult to monitor, due to coloration and avoidance of locations and times of day frequented by observers. Camera traps, such as the one that obtained this photo, offer insight on 'activity', but they do not give density (animals per area).

estimates of animals per area [12,13]. Estimates of range suffer from limited knowledge of suitable habitat [14].

In the Greenspoon *et al.* estimates, even-toed ungulates come out on top of terrestrial wild mammals, led by the North American white-tailed deer (*Odocoileus virginianus*) (Figure 1). Considering the many sources of uncertainty, the species rank is intriguing: few studies compare American deer with African elephants.

A population biologist would not use an approach like this, thinking instead about the role of observation effort and error and how the samples attempt to cover habitat heterogeneity and fluctuations from year to year and decade to decade. By contrast, the estimates needed to manage a reserve (or interpret demographic rates and population growth) do not translate to continents or the globe.

Greenspoon *et al.* expand the dialog surrounding conservation of the planet's vertebrates in an important direction. Do all of the unmeasured errors wash out in a global extrapolation? This is unlikely. However, the global abundance of an important species group gets a new perspective here. Their study will invigorate the discussion and motivate revisions to the numbers, a dialog that could lead to an expanded understanding of biodiversity trends and threats.

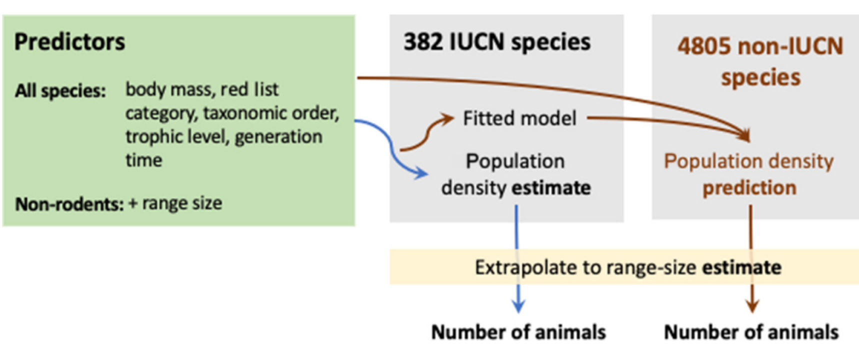

Figure 2. Summary of the method used by Greenspoon *et al.* [10]. Predictors are available for all species (except range size for rodents). Population density estimates come from IUCN and are not available for the non-IUCN species. For the latter, population density is predicted from the model fitted to IUCN species. For both groups, abundance is extrapolated with an estimate of the range size.

Acknowledgments

I thank Ruben Palacio for comments.

Declaration of interests

None declared by the author.

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https://doi.org/10.1016/j.tree.2023.05.001

References

1. Fink, D. *et al.* (2020) Modeling avian full annual cycle distribution and population trends with citizen science data. *Ecol. Appl.* 30, e02056
2. Rosenberg, K.V. *et al.* (2019) Decline of the North American avifauna. *Science* 366, 120–124
3. Tang, B. *et al.* (2021) Modeling spatially biased citizen science effort through the eBird database. *Environ. Ecol. Stat.* 28, 609–630

4. Botha, J. *et al.* (2008) Application of distance sampling to estimate population densities of large herbivores in Kruger National Park. *Wildl. Res.* 35, 371–376
5. Stephens, P.A. *et al.* (2015) Management by proxy? The use of indices in applied ecology. *J. Appl. Ecol.* 52, 1–6
6. Scher, C.L. and Clark, J.S. (2023) Species traits and observer behaviors that bias data assimilation and how to accommodate them. *Ecol. Appl.* 33, e2815
7. Qiu, T. *et al.* (2023) Habitat–trait interactions that control response to climate change: North American ground beetles (Carabidae). *Global Ecol. Biogeogr.* Published online March 23, 2023. https://doi.org/10.1111/geb.13670
8. Robinson, O.J. *et al.* (2022) Extreme uncertainty and unquantifiable bias do not inform population sizes. *Proc. Natl. Acad. Sci. U.S.A.* 119, e2113862119
9. Ceballos, G. *et al.* (2017) Biological annihilation via the ongoing sixth mass extinction signaled by vertebrate population losses and declines. *Proc. Natl. Acad. Sci. U.S.A.* 114, E6089–E6096
10. Greenspoon, L. *et al.* (2023) The global biomass of wild mammals. *Proc. Natl. Acad. Sci. U.S.A.* 120, e2204892120
11. Hayward, M. *et al.* (2015) Ambiguity in guideline definitions introduces assessor bias and influences consistency in IUCN Red List status assessments. *Front. Ecol. Evol.* 3, 87
12. Karanth, K.U. *et al.* (2004) Tigers and their prey: predicting carnivore densities from prey abundance. *Proc. Natl. Acad. Sci. U.S.A.* 101, 4854–4858
13. Gilbert, N.A. *et al.* (2021) Abundance estimation of unmarked animals based on camera-trap data. *Conserv. Biol.* 35, 88–100
14. Börger, L. *et al.* (2006) Effects of sampling regime on the mean and variance of home range size estimates. *J. Anim. Ecol.* 75, 1393–1405