PNAS COMMENTARY

Wild mammals through the lens of biomass rather than biodiversity

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Human activities have put increasingly severe stress on populations of wild vertebrates throughout the biosphere. Most of the attention to the global status of wildlife has focused on numbers of species, i.e., biodiversity, and this is understandable. It is certainly alarming when a whole species is lost from the biosphere, never to return. We are living through a period of time that has been likened to a concentrated mass extinction, comparable in magnitude to any recorded in the fossil record (1). However, declining numbers of species are not the whole story. The abundances of wild species are also important to take into account if we want to conserve and manage what is left (2). We still have many species, but are their total abundances low or high? What kinds of species are doing the best (or worst) under current circumstances? Do we have a reference point for the global biomass of wild species from which we can assess changes from this point on? In PNAS, Greenspoon et al. (3) provide part of this picture — a baseline global estimate for the biomass of living wild mammals — based on a per-species analysis. What it shows should give us pause, as the data permit a different lens through which to view the plight of wild mammals in the face of anthropogenic activities, and yield some striking results.

Standing crop biomass represents the mass of living tissue that makes up a given species at any moment in time, and is the value that Greenspoon et al. estimated for each species at a global scale. Biomass is an intuitive quantity. It is axiomatic that there must be greater numbers of individuals of small-bodied species in a given area (or globally) than large-bodied ones, so expressing the abundance of all species in terms of their biomass contributes substantially toward correcting for size-related differences in numbers. As an assessment of abundances, it is meaningful to treat the mass of one elephant as equal to that of 35 gazelles or that of 15,000 grass mice. A wild mammal species' biomass is directly relevant to the magnitude of the effects of its physical activities (unrelated to levels of resource consumption per se) on its environment, such as changes in vegetation structure, soil modifications, and other "ecological engineering" by animals (4, 5). Biomass can also be used to compare trophic (food) energy-consumption and productivity rates of species of similar sizes. However, the primary value of this global biomass dataset is in having a baseline, or snapshot, of the current state of wild mammal abundances worldwide.

The calculation of biomass for a species is deceptively simple: Multiply the number of individuals (in a population, community, region, or the globe) times the average body mass of an individual of that species. Body mass is well documented for most mammalian species. However, global population numbers definitely are not. Although we have extensive information on the numbers of many species found in local habitats and nature preserves, Greenspoon et al. found that global population estimates were available for only 392 species, about 6% of wild mammal species. Estimating global population numbers is not easy. It requires knowledge of the total geographical range of the species, as well as the distribution of suitable habitat types within that range, and the species abundance in each. In addition, numerous ecological attributes of a species also affect its abundance. To fill out their dataset, Greenspoon et al. used the data from the 392 well-documented species to build a machine-learning model that could predict global biomass for the remaining 4,413 species. The predicted values for individual species may be subject to considerable uncertainty, but the figure for total biomass of all wild terrestrial mammals (≈22 Mt wet weight) is likely to be realistic.

Greenspoon et al. report a number of striking results. One is that over 40% of wild land mammal biomass is made up of just 10 species (wild boar, warthog, five deer species, two kangaroos, and the African bush elephant). Not surprisingly, high contributors to biomass are species that are relatively large-bodied, and both maintain large local populations and have extremely large ranges (e.g., white-tailed deer). However, many of the larger species that we do monitor are highly endangered anyway (6). Furthermore, Greenspoon et al. infer that slightly over half of the estimated total wild mammalian biomass is contributed by those 392 species for which we have global data, suggesting that we really know less than we should about most wild mammals, especially small ones, other than that they account for relatively little biomass overall. In spite of the appearance of large existing areas of wildlands and preserves, most wild mammals are represented by fairly small or restricted populations. We may think we already know this, but the actual numbers still make an impact.

Second, humanity's efforts to stock the globe with mammals that are of value to us (630 Mt of biomass) dwarf the remaining biomass of wild land mammals (22 Mt). We are used to thinking of animals used in agriculture as a major human impact on the globe, and this is true, but less often discussed is the fact that the biomass of domestic dogs on earth is approximately the same as the total biomass of all

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wild land mammals. We should be acutely aware of the potential for small, seemingly insignificant changes in our collective behavior to exert large effects on natural environments.

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Where do we go from here? The database of Greenspoon et al. is fundamentally based on numbers of individuals and body mass. The total number of individuals (in a community, region, or globally) is a basic component of most models of extinction risk for individual species (7), but these values alone are difficult to compare among species of greatly differing body size. Ten elephants, or 10 whales, mean something quite different ecologically than do 10 mice. Biomass has been discussed above. There is a third ecological measure by which species may be compared: the trophic energy flux through each species. Trophic energy requirements and rates of production of new biomass are the best measures of the direct impact that species have on each other, as consumers or as resources, and also represent the trophic energy "cost" (to the community, region, or biosphere) of supporting a particular species. In general, species energy-use and productivity do not scale proportionally to biomass. The same volume of biomass metabolizes, and turns over, at a slower rate if that biomass is in a large species as opposed to a small one. If one tries to compare the energetic impact of species of significantly different sizes using biomass values alone, one will overestimate the energetic impact of the large species (8). So, can we take the same approach that Greenspoon et al. have done with biomass and apply it to energy-use? That seems unlikely; reliable, direct estimates of energy-use in natural conditions are available for very few mammal species, so there is no "training set" for a machine-learning model to work with. Instead, the best we can do for the foreseeable future is to use numbers of individuals and make assumptions about energy-use and body size to estimate energy-relations. The details of those assumptions are still under considerable debate (9).

So all of these measures have their uses. However, at the global scale, the biomass-based dataset of Greenspoon et al. — or a future incarnation of it — is likely to remain a fundamental resource for all of them.

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