





Are we eating the world's megafauna to extinction?

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Abstract

Many of the world's vertebrates have experienced large population and geographic range declines due to anthropogenic threats that put them at risk of extinction. The largest vertebrates, defined as megafauna, are especially vulnerable. We analyzed how human activities are impacting the conservation status of megafauna within six classes: mammals, ray-finned fish, cartilaginous fish, amphibians, birds, and reptiles. We identified a total of 362 extant megafauna species. We found that 70% of megafauna species with sufficient information are decreasing and 59% are threatened with extinction. Surprisingly, direct harvesting of megafauna for human consumption of meat or body parts is the largest individual threat to each of the classes examined, and a threat for 98% (159/162) of threatened species with threat data available. Therefore, minimizing the direct killing of the world's largest vertebrates is a priority conservation strategy that might save many of these iconic species and the functions and services they provide.

KEYWORDS

conservation, endangerment, exploitation, global, vertebrates

1 | INTRODUCTION

Maintaining biodiversity is crucial to ecosystem structure and function, but it is compromised by population declines and geographic range losses that have left roughly one fifth of the world's vertebrate species threatened with extinction

(Ceballos et al., 2015; Dirzo et al., 2014; Hoffmann et al., 2010; McCauley et al., 2015). The main causes of vertebrate biodiversity declines are overexploitation and habitat loss associated with an increasing human population and per capita resource use (Hoffmann et al., 2010; Maxwell, Fuller, Brooks, & Watson, 2016; Ripple et al. 2017a). The effects of these and other drivers such as habitat fragmentation, pollu-

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tion, pathogens, the introduction of nonnative species, and, notably, global climate change provide mounting evidence that humans are poised to cause a sixth mass extinction event (Barnosky et al., 2011). The ongoing biodiversity crisis has prompted researchers to explore how species' life history traits relate to their threat status (Dirzo et al., 2014). Although it is known that the largest species of terrestrial mammals are at a high risk of extinction (Ripple et al., 2015, 2016; Smith, Smith, Lyons, & Payne, 2018), especially from anthropogenic sources, threats to megafauna across all major classes of vertebrates taken together have not been fully considered (Ripple et al., 2017b).

Here, we construct a list of species that qualify as megafauna based on new criteria of body size thresholds for six classes of vertebrates. Specifically, we defined megafauna as vertebrate species that are unusually large compared with other species in the same class. This approach builds on published definitions of megafauna that are based mostly on terrestrial mammals from the Pleistocene (Supporting Information Table S1; Martin & Klein, 1989). In doing so, the megafauna concept becomes context dependent and not fixed on one specific minimum body size or mass for all taxa (Hansen & Galetti, 2009). Motivated by previously published thresholds, which mostly ranged between 40 and 100 kg (Supporting Information Table S1), we define mass thresholds for megafauna separately for each class. Thus, we considered megafauna to be all species ≥ 100 kg for mammals, ray-finned fish, and cartilaginous fish, and all species ≥ 40 kg for amphibians, birds, and reptiles, because they have smaller body sizes, on average, compared with large mammals and fish.

These new megafauna mass thresholds extend the number and diversity of species included as megafauna, thereby allowing for a broader analysis of the status and ecological effects of the world's largest vertebrates. Under this framework, we herein provide an analysis of the status, trends, and key threats to megafauna, and report on the ecological consequences of their decline. We end by outlining priority conservation strategies to help ensure the survival of the Earth's remaining megafauna in marine, freshwater, and terrestrial ecosystems. By considering megafauna across classes, our analysis highlights similarities for the threats faced by species that differ geographically, taxonomically, and in their habitats.

2 | METHODS

We obtained body mass data from the Amniote database for mammals, reptiles, and birds (Myhrvold et al., 2015), and acquired body lengths from FishBase for ray-finned and cartilaginous fish (Froese & Pauly, 2000) and AmphibiaWeb for amphibians (AmphibiaWeb, 2016). Using the 1,735 fish species with known maximum lengths and masses in FishBase, we modeled the relationship between length and

mass (both log transformed) with a generalized additive model, which allows for nonlinearity. We used this model to predict masses for all species in FishBase with known maximum lengths and unknown masses. For amphibians, we used the allometric equations given in Pough (1980) to predict masses from total and snout-to-vent lengths given in AmphibiaWeb species accounts. After determining body masses, we restricted our analysis to only those species that met our megafauna criteria (≥ 100 kg for mammals and fish and ≥ 40 kg for birds, amphibians, and reptiles).

We merged the body mass data with information on species-level extinction risk from the IUCN Red List (ver. 2018.1) using species' scientific names and taxonomic synonyms. Species not found in the IUCN Red List, because they have yet to be assessed, were listed separately but excluded from further analysis. We also excluded extinct (EX), extinct in the wild (EW), and data-deficient (DD) species from most of the analysis, focusing only on those classified as critically endangered (CR), endangered (EN), vulnerable (VU), near threatened (NT), or least concern (LC). We did, however, calculate the percentages of megafauna and all vertebrates that have gone extinct since 1500 CE (the timeframe used in the IUCN Red List). Lastly, we grouped the species by class for the following classes: ray-finned fish (Actinopterygii), cartilaginous fish (Chondrichthyes), birds, mammals, reptiles, and amphibians. Other minor fish classes contained no species with masses ≥ 100 kg and thus were only included in the results for all vertebrates together. We determined the percentages of species threatened and decreasing for both species classified as megafauna and for all vertebrates with available data. We also estimated the percentages of megafauna species by class that are threatened within various ecosystem types as defined by the IUCN Red List (Marine, Freshwater, and Terrestrial).

The threats faced by species were assessed using coded information from the IUCN Red List threats classification scheme (IUCN, 2018). Only threatened species with coded threat information available were included in this portion of the analysis. To separate threats related to livestock/aquaculture and crops, and those related to harvesting and logging, we split two of the top-level threats categories. Specifically, we split the "Agriculture & aquaculture" category (2) into agricultural "cropping" (composed of categories 2.1: "Annual & perennial nontimber crops" and 2.2: "Wood & pulp plantations") and "livestock/aquaculture (categories 2.3: "Livestock farming & ranching" and 2.4: "Marine & freshwater aquaculture") and the "Biological resource use" category (5) into "harvesting" (5.1: "Hunting & collecting terrestrial animals" and 5.4: "Fishing & harvesting aquatic resources") and "logging" (5.2: "Gathering terrestrial plants" and 5.3: "Logging & wood harvesting"). Finally, we manually recorded the reasons for harvesting of each megafauna species based on information in the IUCN Red List fact sheets and Arkive (2018).

3 | RESULTS

A total of 362 extant species qualified as megafauna based on our taxonomy-based size thresholds (Supporting Information Tables S2–S4). We excluded 77 species (38 mammals, 16 ray-finned fish, 6 reptiles, and 17 cartilaginous fish) from subsequent analyses (unless otherwise noted) because they were either extinct in the wild (EW; two species), extinct (EX; seven species), data deficient (DD; 48 species), or not listed in the IUCN Red List (20 species) (Supporting Information Table S3). Close to half of the remaining 292 megafauna species were mammals ($n = 140$), followed by cartilaginous fish ($n = 58$), ray-finned fish ($n = 56$), reptiles ($n = 33$), birds ($n = 4$), and an amphibian ($n = 1$) (Supporting Information Table S2).

Megafauna species are more threatened and have a relatively higher percentage of decreasing populations than all vertebrates together. Of the 39,493 (non-DD/EW/EX) vertebrate species in the IUCN Red List, 21% are catalogued as threatened and 46% have decreasing populations (Figure 1, Supporting Information Table S4). In contrast, of the 292 megafauna species, 70% have decreasing populations and 59% are threatened (Figure 1). Generally, freshwater ecosystems contain the highest proportion of threatened megafauna, while marine systems contain a lower proportion of threatened megafauna (Supporting Information Figure S1).

Notably, the top-ranked threat within each megafauna class was direct harvesting by humans, although there were typically multiple co-occurring threats, mostly related to habitat degradation (Figure 2). Meat consumption was the most common motive for harvesting megafauna for all classes except reptiles where harvesting eggs was ranked on top (Figure 3). Other leading reasons for harvesting megafauna included medicinal use, unintended bycatch in fisheries and trapping, live trade, and various other uses of body parts such as skins and fins (Figure 3). Over half (64%) of the threatened megafauna were listed by the Convention on International Trade in Endangered Species (CITES) because of threats involving global trade in these species (Supporting Information Table S5). Since 1500 CE, 2% of assessed megafauna species have gone extinct compared to 0.8% of all assessed vertebrates (Supporting Information Table S4). Interestingly, within each of the six vertebrate classes, some of the largest individual species were threatened with extinction (Figure 4, Supporting Information Table S2).

4 | DISCUSSION

Our results suggest that we are in the process of eating the world's megafauna to extinction. Megafauna are heavily exploited for human consumption (Figure 3) and are, on average, 2.75 times more likely to be threatened by extinction than

other vertebrate species that have been assessed by the IUCN (and are not DD, EW, or EX) (Supporting Information Table S4). This means that seven out of 10 of our largest and most iconic fauna will experience further population declines in the near future, and three out of five could go extinct. Declines of the largest vertebrate species will jeopardize ecosystem services to humans and generate cascading evolutionary and ecological effects on other species and processes (Estes et al., 2011; Estes, Heithaus, McCauley, Rasher, & Worm, 2016; Ripple et al., 2017b).

The Pleistocene extinctions reinforce our findings regarding the elevated extinction risk of extant megafauna. Since the late Pleistocene, humans have emerged as a “super-predator” (Darimont, Fox, Bryan, & Reimchen, 2015), specializing in killing prey larger than their individual body mass, similar to gray wolves (*Canis lupus*) and orcas (*Orcinus orca*). In the wake of growing human populations, their increased geographic range, and improved tool use, many large terrestrial mammals went extinct during the late Pleistocene (Sandom, Faurby, Sandel, & Svenning, 2014). The strong extinction bias toward species of large size is highly unusual and unmatched over the prior 65 million years (Smith et al., 2018). Humans, commonly using projectile weapons, differ from other predators of large prey, such as lions (*Panthera leo*) and wolves, in their ability to cause death at a distance (Worm, 2015). Attacking from a safe distance enables the tackling of very large, dangerous prey with much less risk to the predator, compared with the physical combat required for all non-human predators on land and sea. In addition, the limitation of predator numbers through natural prey availability does not hold for humans, whose global population grows disproportionately to its sustainability because of our ability to produce food.

The impact of the human appetite for large prey was first felt on land with the extinction of the Pleistocene megafauna in terrestrial systems, and more recently extended to marine and freshwater ecosystems as humans enhanced their fishing skills with sophisticated technology (Jackson et al., 2001). Historically, human hunters have preferentially targeted large prey items as a way of signaling their fitness – a pattern that may be continuing today in the form of trophy hunting (Darimont, Coddling, & Hawkes, 2017). Following this habitual (or possibly hard-wired) pattern of humans focusing on the largest size classes in our prey spectrum, direct harvesting for meat or egg consumption is still a dominant threat for all megafauna classes (Figures 2 and 3). The current trend is consistent with optimal foraging theory, which predicts that predators attempt to gain the most benefit (e.g., large vulnerable prey) at the least cost (Stephens & Krebs, 1986). But in today's world, the reasons for continuing such a practice are unclear, because the vast majority of human food is produced by agriculture and aquaculture, and most “wild” meat likely comes from smaller bodied species, which are more plentiful. Despite this

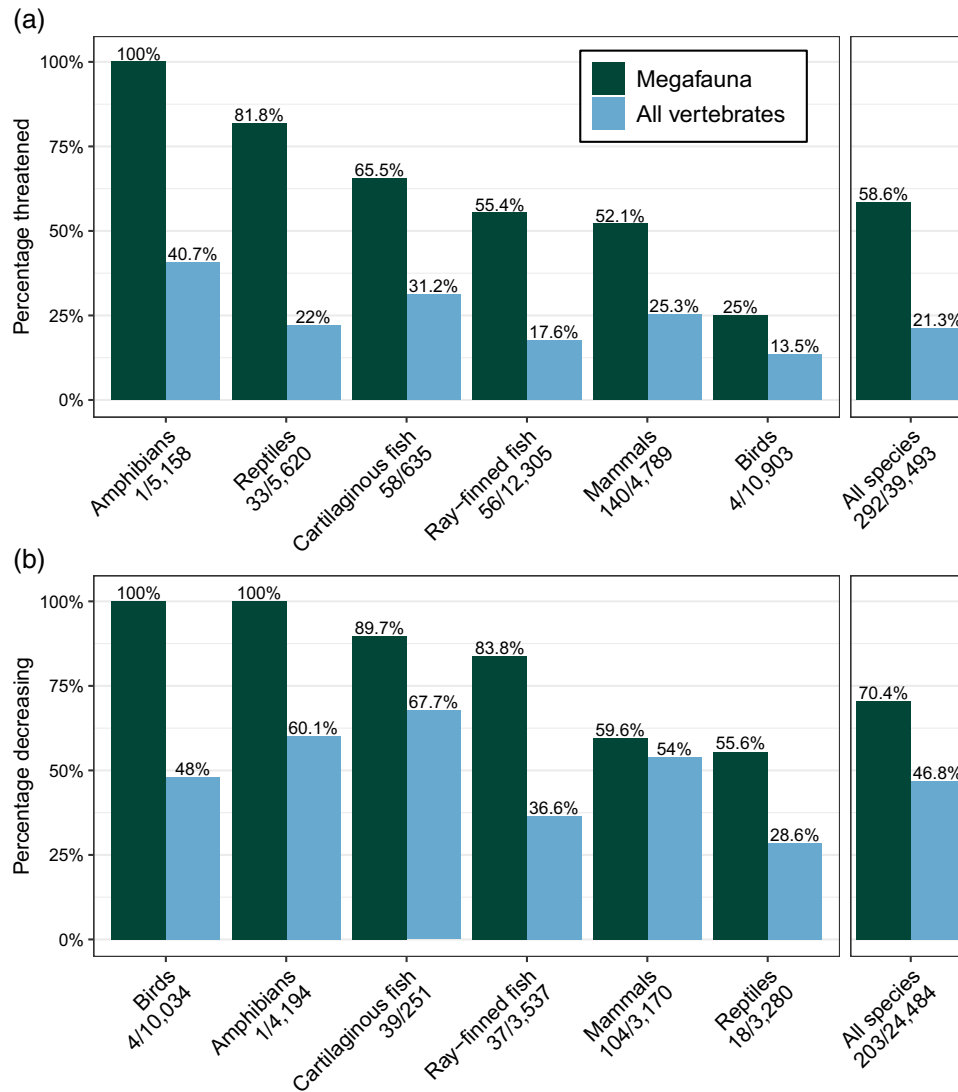


FIGURE 1 Megafauna extinction risk and trends. Shown are percentages of species classified as (a) threatened (IUCN Red List Category Vulnerable, Endangered, or Critically Endangered) and (b) with decreasing population trend. Data are separated by megafauna (dark green) versus all vertebrate species (blue) in each class, and for all vertebrates combined (IUCN, 2018). Numbers of megafauna species in each class followed by numbers of all IUCN-assessed species in each class are indicated at the bottom of each panel. Only species with IUCN Red List category and population trend data are counted for panels (a) and (b), respectively. Megafauna are defined here as species with ≥ 100 kg body mass for mammals, ray-finned fish, and cartilaginous fish, and ≥ 40 kg for amphibians, birds, and reptiles

pattern, humanity's predatory behavior can cause declines in megafauna because a given rate of exploitation will reduce populations of large animals more quickly, because on average, they tend to be less abundant and productive, than smaller species. Although consideration should be given to the fact that megafauna can be an important food source for some people in developing countries, bushmeat hunting for food and medicinal products may harvest millions of tonnes of animal biomass per year in the southern hemisphere (Cawthorn & Hoffman, 2015), and worldwide, threatens over 300 terrestrial mammal species with extinction, some of which are large size (Ripple et al., 2016). In certain cases, if people no longer eat wild meat for subsistence, they may need to obtain suf-

ficient nutrients from agricultural sources that could result in other impacts to habitats. The surge in demand for Asian traditional medicinal products also exert heavy tolls on the largest species, which are often the most appealing, for various reasons (Ellis, 2013).

There is good reason to raise further awareness of the declining status of large vertebrates. Nine megafauna species went extinct or became extinct in the wild between the 1760s and 2012, and in each case this was due to excessive hunting or a combination of hunting and habitat degradation (Supporting Information Table S6). The reasons for hunting these species to extinction were for the acquisition of meat for consumption or for body parts such as skins, horns, organs, and antlers

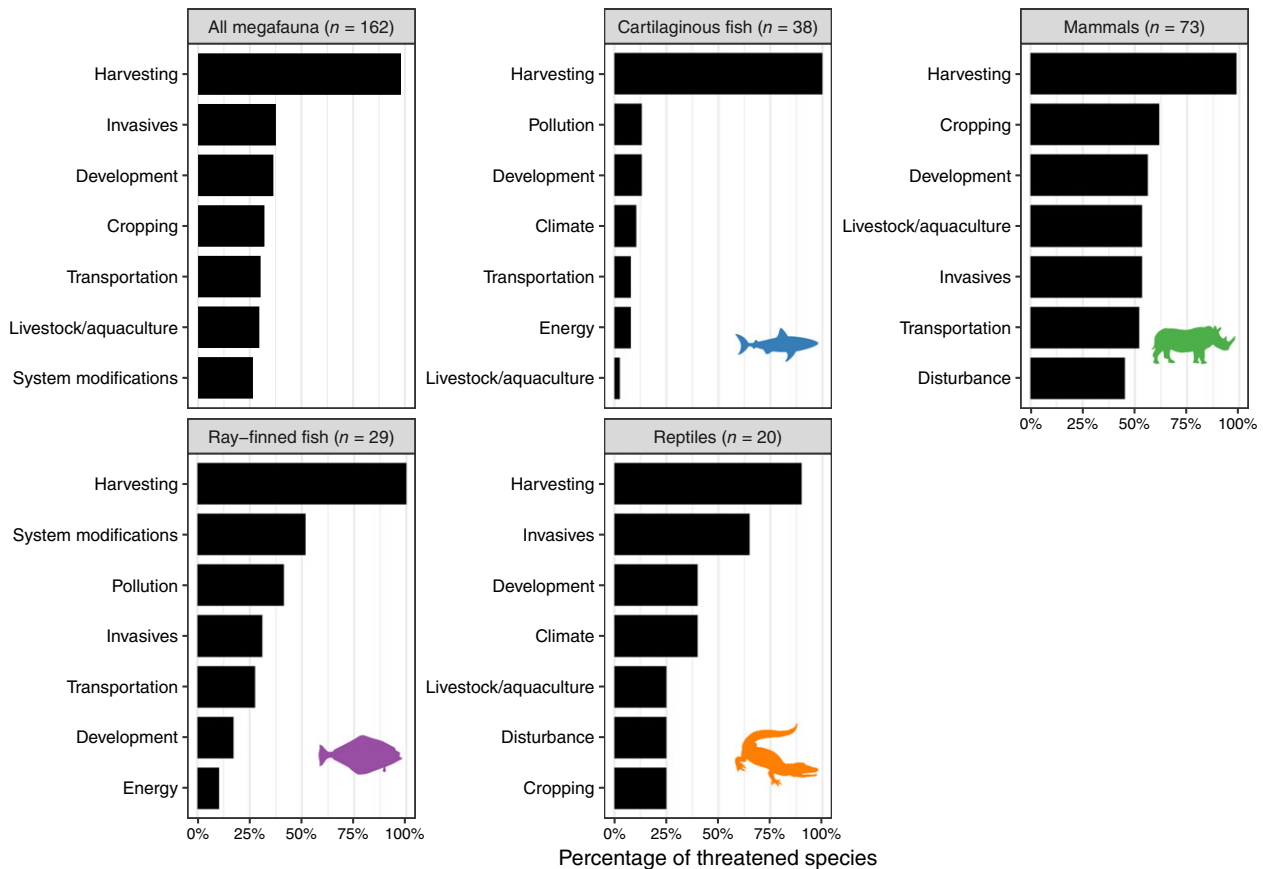


FIGURE 2 Current threats to megafauna. Shown are percentages of threatened megafauna species in each class facing different types of threats. We used the top-level coded threat data on species Red List fact sheet pages, grouping threats 5.1/5.4 together as “Harvesting,” 5.2/5.3 as “Logging,” 2.1/2.2 as “Cropping,” and 2.3/2.4 as “Livestock/aquaculture.” Only threatened species with coded threat information available (145/155) were used for this plot. Only the seven most common threats for each group are shown. No panel is shown for the single threatened amphibian species, the Chinese giant salamander. It was threatened by harvesting, system modifications, pollution, logging, energy, and cropping. Similarly, no panel is shown for the single threatened bird species, the Somali Ostrich, which was threatened by harvesting, livestock, and cropping

for traditional medicine or trophies (Supporting Information Table S6). Persecution is a major cause of mortality for many of the large carnivores in terrestrial systems (Ripple et al., 2014). Due to their slow life history traits, involving delayed reproduction and few offspring, megafauna are extremely vulnerable to fishing, trapping, and hunting pressures (Johnson, 2002). In addition to intentional harvesting, much of this mortality is due to bycatch in snares and traps in terrestrial systems or gillnets, trawls, and longlines in aquatic systems. Many of the megafauna species are simultaneously affected by various types of habitat degradation (Figure 2). When taken together, these threats to habitats can have major negative cumulative effects on vertebrate species (Betts et al., 2017; Shackelford, Standish, Ripple, & Starzomski, 2018). Consistent with our results, overexploitation and habitat loss (mainly from agriculture) are considered major twin threats to biodiversity in general (Maxwell et al., 2016).

The world's terrestrial mammalian megafauna are more prone to elevated extinction risk than all terrestrial mammal species considered as a group (59% vs. 21% threatened,

Supporting Information Table S4). Megafaunal mammals in marine systems are faring relatively better, with only nine of 33 species (27%) currently assessed as threatened, although 28 more species are data deficient (Supporting Information Tables S2–S4). Indeed, many of the largest marine mammals are in the process of recovering after the global cessation of industrial whaling in 1986 (Magera, Flemming, Kaschner, Christensen, & Lotze, 2013). This bold action required global cooperation and enforcement and has been successful in halting and reversing extinction threats for most of the great whales, with some notable exceptions such as the North Atlantic right whale (*Eubalaena glacialis*) (Taylor & Walker, 2017). Efforts to rebuild depleted fish populations worldwide have been more limited, but with some regional successes (Neubauer, Jensen, Hutchings, & Baum, 2013; Worm et al., 2009). The situation appears particularly dire for cartilaginous fish; sharks, skates, and rays include the highest proportion (9%) of species ≥ 100 kg of any of the classes examined here, and are more threatened, on average than any other marine group (Figure 1; Dulvy et al., 2014; Worm et al., 2013). The

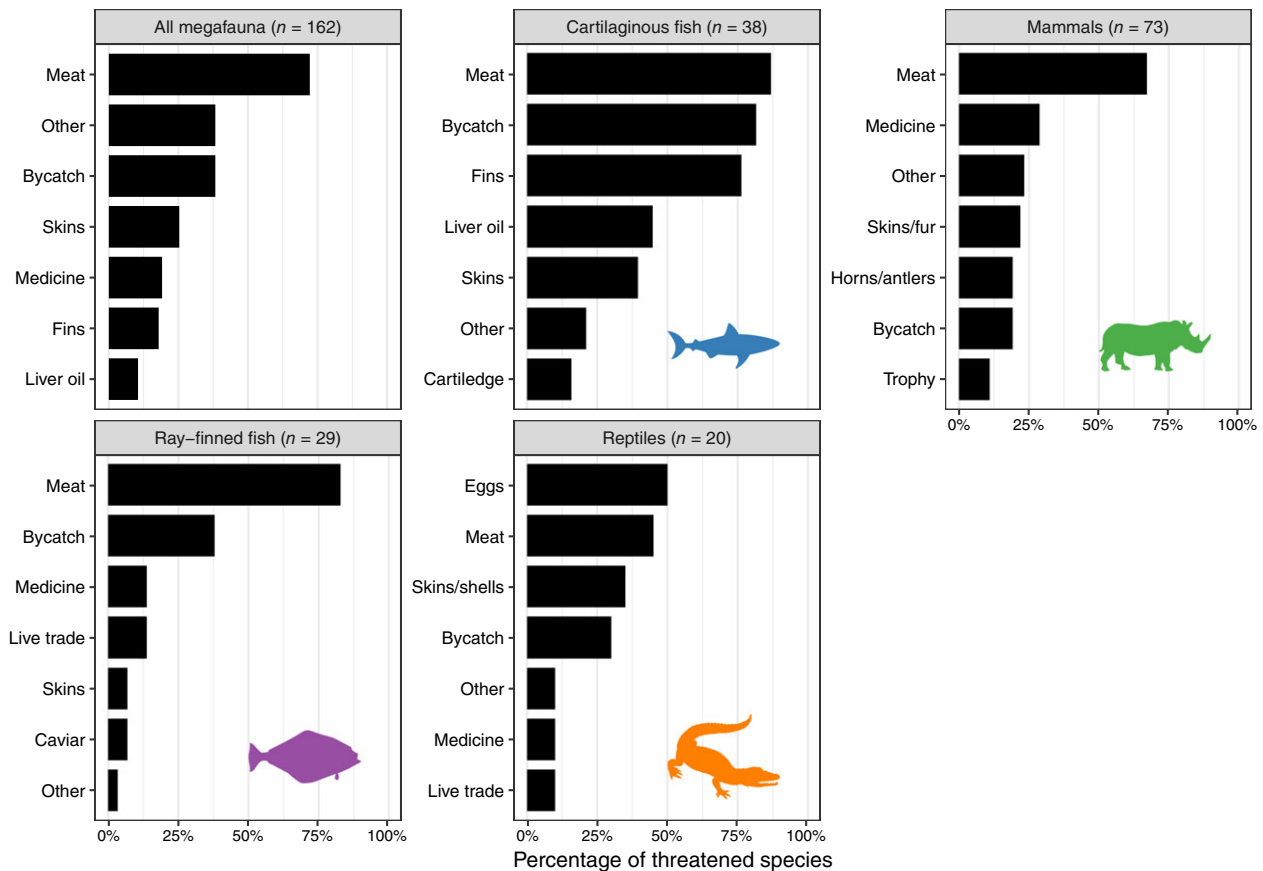


FIGURE 3 Reasons for harvesting threatened megafauna. Numbers of threatened megafauna species are shown in the panel titles. Reasons for harvesting were determined using species Red List fact sheet pages as well as Arkive.org species accounts (Arkive, 2018). Only the six most common reasons for each group are shown (other reasons are grouped under “Other”). No panel is shown for the single threatened amphibian species, the Chinese giant salamander. It is hunted for meat and live trade. Similarly, no panel is shown for the single threatened bird species, the Somali Ostrich, which is hunted for meat, eggs, skins, and feathers

large ray-finned fish are highly threatened in both marine and freshwater systems (Supporting Information Table S2).

The single threatened megafauna bird species, the Somali ostrich (*Struthio molybdophanes*) (Figure 4), is killed for its meat, feathers, and leather. Egg collection is also a major concern. Other threats include logging, livestock, and cropping. Of the amphibians, only one species ≥ 40 kg exists, the Chinese Giant Salamander (*Andrias davidianus*) (Figure 4), and it is critically endangered. This salamander, which can grow to 1.8 m long, is considered a living fossil and is one of only three living species in a family that dates back 170 million years (Chen et al., 2018). However, it is considered a delicacy in Asia, and consequently is threatened by hunting. Other threats include development, pollution, and cropping. Since the 1980s, 14 nature reserves have been created to conserve the Chinese Giant Salamander (Arkive, 2018), but population numbers are still declining (Supporting Information Table S1), and its imminent extinction in the wild has now been predicted (Turvey et al., 2018). We also identified 33 (assessed non-DD/EW/EX) reptile megafauna species, of which 27 (82%) are threatened (Figure 1). Even with this

extraordinary level of threat, reptiles have often been less prominent in global conservation efforts. This is at least partially due to the paucity of available information on their extinction risk and threats reflecting a lack of attention (Böhm et al., 2013). All of the 20 threatened reptile species with coded threat data are at risk due to harvesting (Figure 2). The top reasons for harvesting reptiles include egg collection and meat acquisition (Figure 3). An additional seven reptile megafauna are listed as threatened but lack coded threat data, a situation that should be remedied by the IUCN as soon as possible (Tingley, Meiri, & Chapple, 2016).

The ecosystem impacts that the loss of megafauna may entail are likely out of proportion to their dwindling numbers and small collective biomass. The ongoing loss of megafauna alters the structure and function of their ecosystems, often in ways that are surprising and disruptive (Estes et al., 2011, 2016). Known examples include impacts on seed dispersal, nutrient cycling, fire, and small animals when large terrestrial herbivores decline (Ripple et al., 2015), or the destabilization of fish communities that experienced a loss of sharks and other large predators (Britten et al., 2014). Interestingly, these



FIGURE 4 Largest megafauna species in each major vertebrate group. All of the species shown are threatened with extinction and are threatened by human harvesters seeking their meat, body parts, or eggs. Whale shark (*Rhincodon typus*; upper left) by Christian Jensen (CC BY 2.0), leatherback (*Dermochelys coriacea*; top right) by U.S. Fish and Wildlife Service Southeast Region (CC BY 2.0), Beluga (*Huso huso*; middle left) by Jeff Whitlock (CC BY-NC-SA 3.0), African Elephant (*Loxodonta Africana*; middle right) by Jude (CC BY 2.0), Chinese Giant Salamander (*Andrias davidianus*; bottom left) by James Joel (CC BY-ND 2.0), and Somali Ostrich (*Struthio molybdophanes*; bottom right) by Julian Mason (CC BY 2.0). Whale shark (EN) flesh is highly valued in some Asian markets and the demand for shark-fin soup threatens this species. Leatherbacks (VU) are threatened by fisheries bycatch as well as human consumption of eggs and meat. Belugas (CR) are threatened by overfishing for meat and caviar, which will soon cause global extinction of the remaining natural wild populations. Elephant (VU) poaching is critically elevated due to an increased demand for ivory. The Chinese Giant Salamander (CR) is threatened by hunting, as its flesh is considered a delicacy in Asia. Somali ostriches (VU) are shot for food, leather, and feathers. The largest marine mammal, the blue whale (*Balaenoptera musculus*), is not shown

effects are transmitted both through consumptive and nonconsumptive mechanisms, whereas the presence of megafauna predators fundamentally alters the behavior and distribution of prey species even in the absence of direct predation events (Heithaus, Frid, Wirsing, & Worm, 2008). Megafauna are also of critical importance for conservation because the largest species are often flagship species, umbrella species, keystone, and engineer species or highly charismatic species (Courchamp et al., 2018; Ripple et al., 2015).

Preserving the remaining megafauna is likely going to be a difficult and complex task, as megafauna are represented by a diversity of taxa using assorted (terrestrial, freshwater, marine) habitats, and scattered across jurisdictions around the world. Based on the research presented here, we argue that any successful conservation strategy must consider minimizing the direct killing of megafauna as a priority solution, because it appears to be a major driver of extinction threat. Given the low abundances of most threatened megafauna (abundance is one of the IUCN's criteria for listing species as threatened), the impacts of such a strategy on food supply would likely be minimal, but economic values, cultural practices, and social norms might complicate the picture. We believe creating an informed public is an important first step as educational campaigns can reduce demand for highly valuable megafauna species. For example, shark fin commerce has declined following effective media campaigns involving Chinese celebrities (Dell'Apa, Smith, & Kaneshiro-Pineiro, 2014). For charismatic megafauna species threatened by human harvesting, additional well-organized pleas by celebrities might be very effective, but this is not enough on its own. Where possible, it is also essential to use legal means to lower the harvesting of the concerned species, as these can be more effective than campaigns based on ethical and moral grounds. Legal tools limiting collection and trade would help raise awareness and implicate major economic actors responsible for the overexploitation of many of these species. Ensuring that scientifically established harvesting quotas or bans are established and respected is a key step toward maintaining robust megafauna populations.

In order to achieve effective megafauna conservation, a large group of nations needs to take coordinated action soon. Wealthier countries must stop exacerbating the problem by inflating demand and prices for meat, medicinal, and ornamental products from megafauna. For example, governments could sponsor public awareness campaigns or fund organizations that provide information about the plights of specific megafauna species, ecosystem services of megafauna, as well as health concerns and the lack of proven benefits for some types of wildlife-based medicinal products (Still, 2003; Weiss & Tschirhart, 1994).

The success of the International Whaling Commission suggests that a multinational initiative for saving the full diversity of vertebrate megafauna has merit. New international agree-

ments should include conventions to share the financial burden of responsibility among nations, especially the developed ones. This might help to facilitate accomplishments under existing conventions that are already trying to preserve biodiversity such as CITES, the Convention on Biological Diversity, and for marine areas, the United Nations Convention on the Law of the Sea. At the local scale, it is important that nations that harbor megafauna within their jurisdictions, limit through harvesting laws and informational campaigns, the exploitation of megafauna while at the same time, protect critical habitat.

In conclusion, our heightened abilities as hunters must be matched by a sober ability to consider, critique, and adjust our behaviors to avoid consuming the last of the Earth's megafauna (Darimont et al., 2015; Worm, 2015). As direct mortality is a dominant threat to megafauna and live megafauna entails larger economic benefits (e.g., ecotourism and ecosystem services) than dead megafauna, it appears that conservation dollars may be best spent on addressing direct mortality threats head-on, wherever possible.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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