Current Biology

Report

Rethinking Trade-Driven Extinction Risk in Marine and Terrestrial Megafauna

Highlights

- We identified >100 species of megafauna hunted for international luxury markets
- Economic value overrides biological sensitivity above a threshold value
- Individual marine animals are as valuable as the most valuable terrestrial species
- Large ranges buffer risk for terrestrial species, but not for marine species

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In Brief

For large-bodied animals targeted for international luxury markets, McClenachan et al. identify a threshold above which economic value is the key driver of risk. When value per individual is considered, marine animals are as valuable as the most valuable terrestrial species. Unlike on land, large range size does not buffer extinction risk in the sea.

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Rethinking Trade-Driven Extinction Risk in Marine and Terrestrial Megafauna

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SUMMARY

Large animals hunted for the high value of their parts (e.g., elephant ivory and shark fins) are at risk of extinction due to both intensive international trade pressure and intrinsic biological sensitivity. However, the relative role of trade, particularly in non-perishable products, and biological factors in driving extinction risk is not well understood [1–4]. Here we identify a taxonomically diverse group of >100 marine and terrestrial megafauna targeted for international luxury markets; estimate their value across three points of sale; test relationships among extinction risk, high value, and body size; and quantify the effects of two mitigating factors: poaching fines and geographic range size. We find that body size is the principal driver of risk for lower value species, but that this biological pattern is eliminated above a value threshold, meaning that the most valuable species face a high extinction risk regardless of size. For example, once mean product values exceed US$12,557 kg^{-1}, body size no longer drives risk. Total value scales with size for marine animals more strongly than for terrestrial animals, incentivizing the hunting of large marine individuals and species. Poaching fines currently have little effect on extinction risk; fines would need to be increased 10- to 100-fold to be effective. Large geographic ranges reduce risk for terrestrial, but not marine, species, whose ranges are ten times greater. Our results underscore both the evolutionary and ecosystem consequences of targeting large marine animals and the need to geographically scale up and prioritize conservation of high-value marine species to avoid extinction.

RESULTS

Which Are the Double-Jeopardy Species of Large Body Size Traded for Non-perishable Parts? A Typology of Extinction Risk in Traded Animals

The extinction of large-bodied animals traded in international luxury markets, such as elephants and rhinoceroses, is among the most significant conservation concerns of the past half century [5–8]. Less attention has been paid to marine species, but evidence that trade is increasing extinction risk in large marine fishes has begun to result in international protections, particularly for sharks and rays (subclass Elasmobranchii), heavily traded for dried fins and gill plates [9–11]. Both sharks and rays and large terrestrial and marine mammals exploited for international luxury markets possess two features that drive extreme extinction risk, putting them at double jeopardy of extinction. We therefore conceptualize vulnerability to trade-induced extinction risk along two dimensions: the intrinsic sensitivity of species (represented by body size) and the exposure to international trade [12] (Figure 1).

First, body size is a well-understood proximate correlate of extinction risk, such that larger species tend to have the lowest population growth rates and hence are less able to replace individuals killed by hunting [13–15]. Here, we selected the largest species (>10 kg) targeted for trade as those requiring the most urgent attention because of this intrinsic sensitivity. Although our focus is on these largest species, trade-driven extinction risk is also problematic for small-bodied species, including seahorses, parrots, butterflies, and orchids. In some cases, extinction risk may be compounded by the additional interaction of small geographic range size and habitat degradation, but this is independent of hunting, which is our focus here [13, 14, 16]. These megafaunal species represent only a small, but highly controversial, percentage of protected species; only 4.8% of Convention on International Trade in Endangered Species (CITES)-listed species are mammals, and fewer than 0.1% are elasmobranchs [17].

Second, non-perishable traded products such as tusks, dried fins, and dried gill plates can be gathered and stockpiled by globally distributed networks of buyers [18]. This has the effect of disconnecting consumer-exploiter feedbacks and stymieing efforts to track source populations and develop effective local conservation [19, 20]. It is generally predicted that as the cost of exploitation exceeds the value of product, reduced exploitation allows recovery of the target species [21]. However, consumer-exploiter feedbacks are decoupled by the globalization of trade in preserved products, which can be aggregated and stored across multiple source populations. Hence, rising prices at the endpoint drive global serial depletion through a diffuse portfolio of traders (e.g., [22]). By comparison, species traded alive or for perishable products have shorter supply chains that are more easily monitored. For example, animals traded for zoos and aquaria tend to be individually identified, subject to

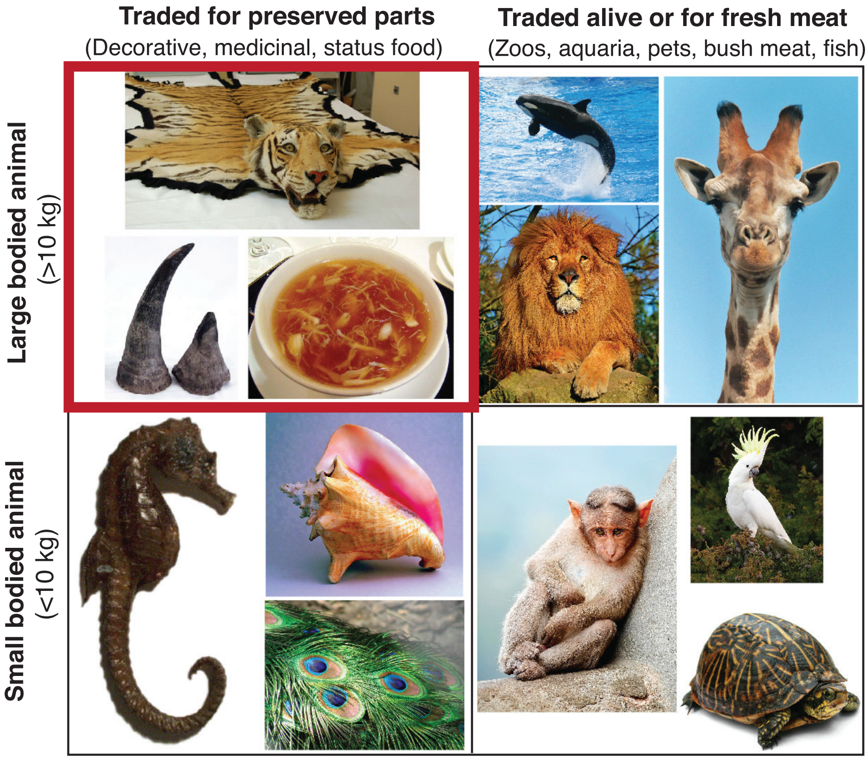

Figure 1. Trade and Double-Jeopardy Species

The large-bodied animals targeted for international trade in preserved parts, represented by those in the upper-left quadrant. (Images are reproduced under Creative Commons license; Wikimedia and freeimages.com.) See also Table S1.

tighter control, and at lower risk of extinction than other species [23].

Using this typology of extinction risk in traded animals, we identified 67 terrestrial and 62 marine species of large-bodied "megafaunal" animals traded in international luxury markets for their non-perishable products (Table S1). Products include those used for decorative purposes (ivory, horn, shell, skins, musk gland extract, rostra, and jaws), traditional medicine (gill plates, gall bladder extract, powdered horn, bone, and body parts), and status food (fins).

What Is Their Value across Three Points of Sale?

Individually, species traded in international luxury markets are often described as worth their weight in gold, with high values signifying incentive to exploit animals, even at low abundances [1–4, 24]. However, trade data have not been compiled and compared across groups. For each product, we identified first sale, mean retail, and maximum retail values in US$ per kilogram. We found that the maximum reported values of preserved animal products spanned three orders of magnitude, from $512 to >$470,000 kg^{-1}, with five products more valuable than gold ($38,900 kg^{-1}, February 2016 [25]; Table S2). Four of these products (tiger penis, bear gall bladder, rhinoceros horn, and deer musk) are used in traditional Asian medicine, and one (Tibetan Antelope fur) is sold primarily in Western markets for decorative products. Marine products (shark fins, sawfish rostra, turtle shells, walrus ivory, and devil and manta gill plates) had maximum values ranging from $512 to $1,697 kg^{-1}.

Hunters don't kill kilograms; instead they are driven to kill whole animals because of the *total value* of each kill. To understand the local economic incentive to kill rather than conserve, we calculated the value of product per animal killed (Figure 2). We used product values and the mass of product (kilogram) per individual to calculate values per individual. Although products derived from marine species are less valuable per kilogram, our key finding is that individual marine animals yield nearly as much potential value as the most valuable terrestrial species. This is because of comparatively large body sizes and strong allometric size dependency of product values, particularly for shark fins, suggesting a high incentive to target the largest individuals and species of marine megafauna (Figure 2). The most valuable marine species, the whale shark (*Rhincodon typus*), have a maximum potential value of $341,140 in traded parts, nearly equivalent to that of the white rhinoceros (*Ceratotherium simum*) and tiger (*Panthera tigris*), the most valuable individual animals ($368,000 and $350,193, respectively). Nearly half (13/29) of the species whose maximum potential value exceeded $10,000 are elasmobranchs (Figure 2; Table S3). Marine species also had high first sale value, which implies incentive to participate in the development of new markets and to poach protected species.

How Do High Value and Body Size Interact to Drive Extinction Risk?

High value is a known correlate of extinction risk, particularly within heavily exploited groups, such as mammals [2] tunas and billfishes [3], sea cucumbers [4], and sharks and rays [24, 26]. However, the relationship between value and extinction risk has not been generalized across taxonomic groups or biomes, compared across multiple types of values, or investigated in relation to large body size. We identified a significant interaction between size and value in driving risk (McFadden's R^2 = 0.64; Figure 3; Table S4). Specifically, low-value species demonstrated a strong size dependency of risk, with probability of risk increasing with size, across all three types of value (Figure 3A). In contrast, the size dependency of risk was not apparent for more valuable species (Figure 3B). Additionally, we identified a threshold past which biological drivers are overwhelmed by high product values (Figure 3C). For example, once mean product values exceed $12,557 kg^{-1}, the size-risk relationship is eliminated. This threshold was lower and higher for first sale values ($774 kg^{-1}) and maximum potential values ($28,158 kg^{-1}), respectively (Figure 3C). This negative interaction between maximum size and price holds across all values,

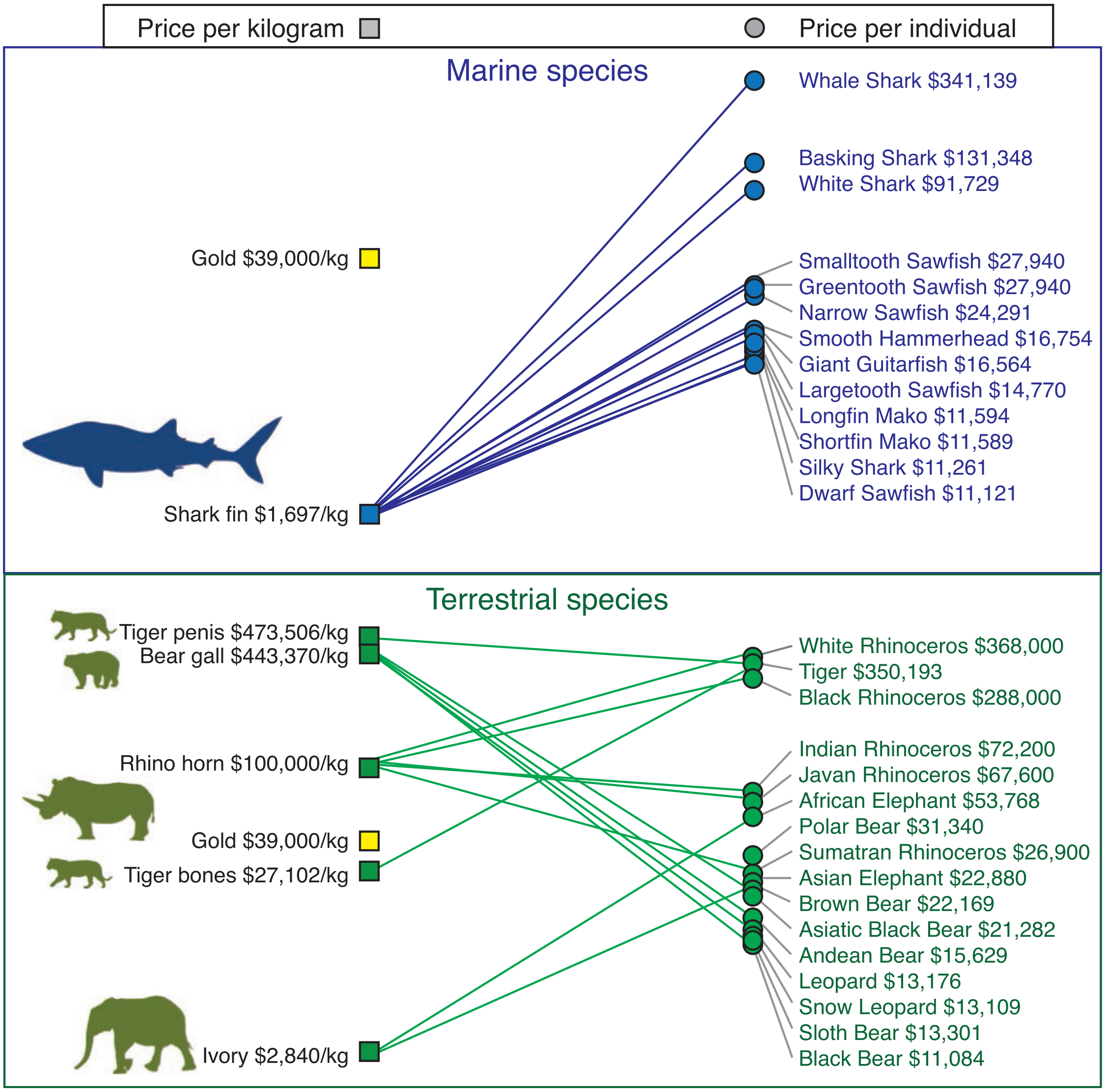

Figure 2. The Species That Are Worth Their Weight in Gold

Maximum reported price per kilogram for the highest-value products (left) and individuals (right). Marine species (top) are as valuable as the most valuable terrestrial species (bottom) when considering individual values. (Images are from PhyloPic.org, reproduced under public-domain dedication [ray, tiger, rhinoceros, and bear] and Creative Commons license [whale shark and elephant], vectorized by T. Michael Keesey.) Additional product values are presented in Table S2, and individual species values for all species shown here are presented in Table S3.

suggesting that the most valuable species face a high risk of extinction across all sizes (Figure 3B). However, in reality, there are very few large-bodied species left with very high values. Given the interaction between size and value per kilogram, in all further analyses we consider a composite of the two: US$ per individual (Figure 4; Table S4).

Is Trade Risk Mitigated by Higher Poaching Fines or Larger Geographic Ranges?

While high value and large body size interact to drive risk, the size of poaching fines may be sufficient to dissuade hunting. We found that maximum reported penalties relative to the value of individuals ranged five orders of magnitude, from 2% to 12,789% of maximum potential value. Penalties that were notably less than the individual's potential value include the Indian rhinoceros (2%), Tibetan antelope (3%), and tiger (5%). Across all species, there was little effect of increased poaching fines on threat; the paucity of marine poaching fines diluted the strong poaching fine effect identified for terrestrial species (Figures 4A, 4B, and S2; Table S4). Species subject to small poaching fines (in the lowest total value quartile, <$1,722 for all species and <$1,510 for terrestrial species) had the highest probability of being threatened across three types of value. However, we found the effect of increasing penalties—within the current range—to be inadequate to meaningfully reduce risk. For example, a species with a total value of $10,000, subject to the median poaching fine of $10,000 has a 93% probability of being threatened; doubling the fine will only reduce risk to 91% (Figure 4A). Hence, poaching

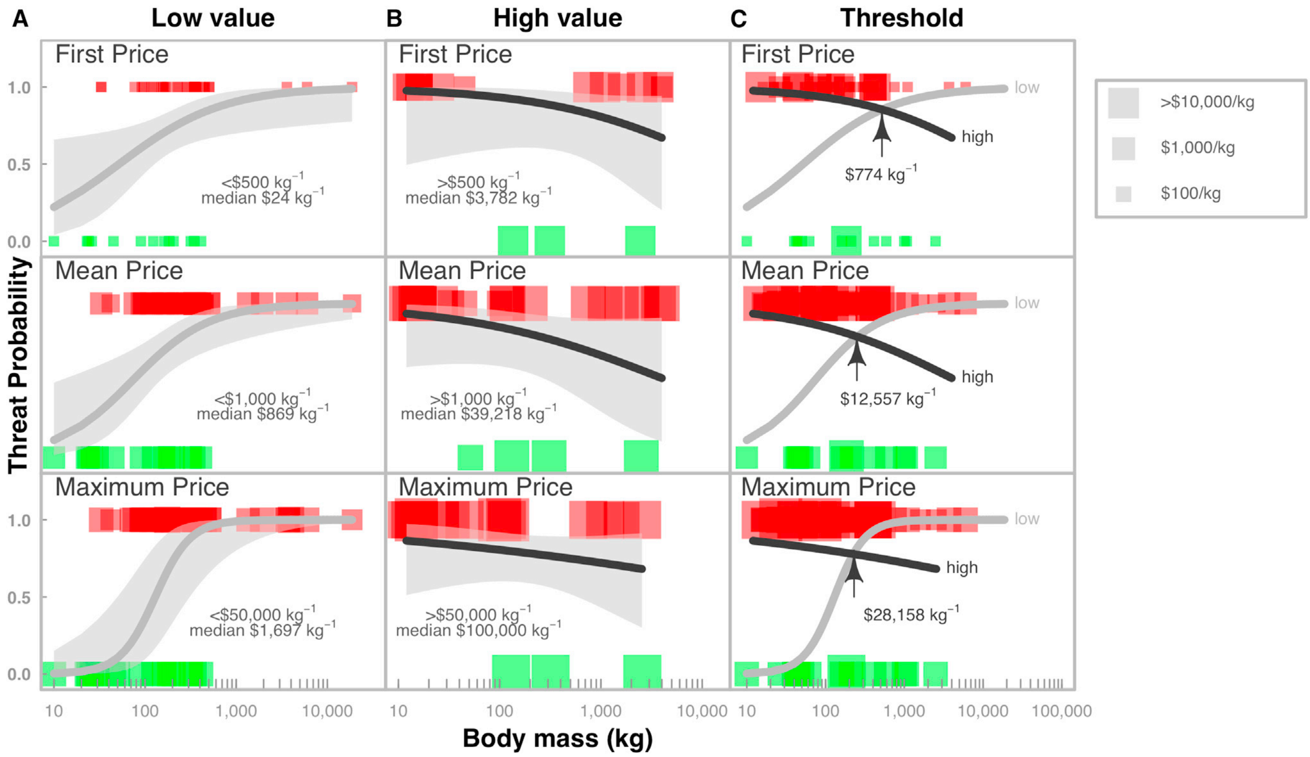

Figure 3. Threshold in the Size-Value Extinction Risk Relationship for Traded Megafauna

Size and price are positive drivers of risk, but a negative interaction exists for these two variables, resulting in a turning point at which the importance of size disappears. Individual species are represented by squares along the value axis; green squares indicate species with a threat probability of 0 (species listed by the International Union for Conservation of Nature [IUCN] Red List as Least Concern and Near Threatened), and red squares indicates species with a threat probability of 1 (species listed as Vulnerable, Endangered, and Critically Endangered). The size of the squares represents values in US$ per kilogram. Lines indicate threat probability as a function of body mass and value per kilogram, for each of the three prices: first sale price, mean sale price, and maximum sale price. Shown are specific size-value relationships for low-value species, with 95% confidence intervals (A); specific size-value relationships for high-value species, with 95% confidence intervals (B); and thresholds in the size-value extinction risk relationship, with the price beyond which the value-risk relationship is inverted indicated (C). Comparisons of model fit and coefficient estimates are reported in Figure S1, and model values are reported in Table S4.

fines need to be far greater than the value per animal to disincentivize hunting.

Likewise, large ranges are typically thought to spare species from extinction, with an inverse relationship between range size and risk and demonstrated for terrestrial carnivores, primates [27], birds [16], and amphibians [28]. In the ocean, large range sizes are similarly believed to confer protection for otherwise vulnerable species [29], but this may not be true for exploited species that migrate through the waters of multiple countries [26]. We found that high-value species with larger ranges do have a lower risk of extinction, but only on land (Figures 4C, 4D, and S3A–S3F; Table S4). This pattern is most apparent when range size is measured as the number of countries in which the species is present (Figure 4D), rather than as the extent of occurrence in square kilometers (Figure 4C). By comparison, there is little variation in risk with range size in marine species (Figures 4E, 4F, and S3G–S3I; Table S4), suggesting a failure of large geographic ranges to mitigate extinction risk in the sea. This result contradicts the idea that species with small geographic ranges are more extinction prone across all biomes and lends support to the hypothesis that managing wide-ranging marine species across many jurisdictions may present challenges that override the biological benefit of large range sizes [26].

Compounding this result, we found that marine species span a significantly greater geographic area than terrestrial species and are found in significantly more countries, demonstrating a substantial jurisdictional challenge for coordinated management. The average range size for marine megafauna hunted for internationally luxury markets is 48 million square kilometers, an order of magnitude greater than terrestrial species, whose average range size was 4 million square kilometers (t_{111} = 3.94, $p < 0.0001$). Perhaps more relevant to the ability of national environmental policy to affect conservation outcomes, marine species are found in four times more countries than terrestrial animals (39 versus 11; $t_{127} = 5.91$, $p < 0.0001$). Hence, national legislation has to be developed for almost four times more jurisdictions to ensure effective protection of traded marine species. That is, for marine species' protection, four times more governments need to be persuaded to enact and defend trade protections, develop federal conservation protections, and ensure legislation is adequate and consistent with that of multiple other responsible national agencies.

DISCUSSION

High values drive risk across national boundaries, globalizing the conservation challenge for animals traded in luxury markets.

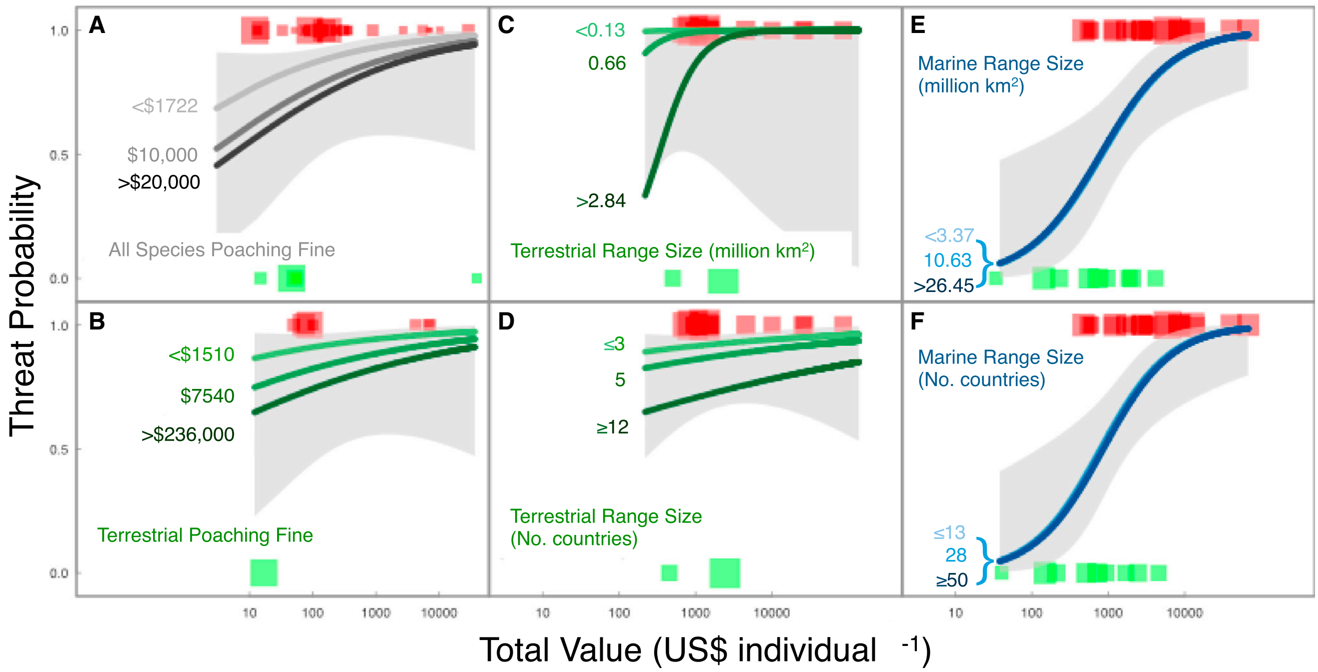

Figure 4. The Role of Mitigating Factors in Reducing Extinction Risk

Poaching fines for all species (A); poaching fines for terrestrial species (B); range size for terrestrial species (C and D); and range size for marine species (E and F). Individual species are represented by squares along the value axis; green squares indicate species with a threat probability of 0 (species listed by the IUCN Red List as Least Concern and Near Threatened), and red squares indicate species with a threat probability of 1 (species listed as Vulnerable, Endangered, and Critically Endangered). The size of the squares represents values in US$ per kilogram (see the legend for Figure 3). Lines indicate threat probability as a function of total value and each of the mitigating factors; the middle line represents the median value for each mitigating factor, the upper and lower lines indicate quartiles, and the shaded polygon is the 95% confidence interval of the median range model. Divergent lines demonstrate an effect of the mitigating factor on threat probability. Therefore, the three overlapping lines in (E) and (F) indicate no effect of range size on threat probability of marine species. Values represent mean individual values. First sale and maximum values are reported in Figures S2 and S3, comparison of model fit and coefficient estimates are reported in Figure S4, and model values are reported in Table S4.

Additionally, diffuse trade networks mean that sequential depletion by roving bandits can overwhelm any local conservation ethic [30]. Our results suggest that both marine and terrestrial species targeted for international luxury markets face risk, with the high value of preserved parts overwhelming biological patterns. That is, all high-value species are at risk, regardless of body size. Therefore, lessons from land will be necessary to avoid large-scale extinction in global oceans [31].

However, we also identified two fundamental differences between marine and terrestrial species that require specific attention. First, larger marine animals have higher potential values due to the stronger allometric relationship between body size and the size of their preserved parts. The resultant incentivized hunting of the largest species and individuals has evolutionary and ecological consequences [32]. From a policy perspective, reports on trade in high-value products typically emphasize the value of *products* as a driver of extinction risk. This focus deemphasizes the more important driver of hunting—total individual value—and potentially deprioritizes marine species, whose individual values far exceed the value in of their products by weight. We recommend that trade regulation and conservation priorities instead focus on total individual value.

A second important difference between marine and terrestrial species is the lack of protection afforded by large range sizes for megafauna in the sea. Notably, our results provide empirical evidence that marine species have relatively larger ranges than terrestrial species; although this has been a common assumption, comparative analyses have been largely lacking [33, 34]. However, our results counter the parallel assumption that these large ranges buffer against extinction risk in the sea [29]. Instead, they imply that a combination of conservation shortfalls and biological sensitivities increase risk for wide-ranging marine species. In particular, the widespread and little-policed hunting in the ocean contrasts with stricter controls on land. Whereas large terrestrial ranges confer a greater likelihood of protection of individuals in some countries, this protection is almost non-existent in the oceans due to widespread deliberate, illegal, and indirect killing, such as bycatch, which affects species irrespective of trade protections that may be in place [35, 36]. Additionally, large marine vertebrates have behaviors that most likely intensify risk. Although many marine species are wide ranging, seasonal aggregative behavior (e.g., for spawning) concentrates individuals in discrete locations. This behavior may override the benefit of a large overall range size, especially if the aggregations coincide spatially with regions of high anthropogenic pressures or poor enforcement of regulations [37]. Similarly, highly migratory behavior common to many large marine vertebrates increases risk; local protections are ineffective at protecting migratory individuals. These biological, regulatory, and policing challenges in the oceans mean that increased attention is required to successfully protect marine species hunted for international luxury markets.

Specifically, we suggest a three-pronged strategy for conserving marine species: (1) international trade control, (2) national and regional protection, and (3) demand reduction. First, the most widely used policy tool to control international trade, CITES, has been effective at reducing pressure on extinction-prone terrestrial species [38]. Thus, recent CITES listings of marine species are promising [11]. However, the high individual values that we identified incentivize black market trade [39], so that strong local and regional conservation efforts are also necessary. Poaching fines are promising, but we show that they are currently too low relative to the individual value on these megafauna to disincentivize illegal hunting. Although diffuse markets make traceability a key concern, particularly for marine species, in which single products can be sourced from dozens of species (Figure 2), molecular approaches to wildlife forensics hold promise to increase the capacity to fine sellers, thereby tightening the feedback between source population and market driven exploitation [19, 40]. Second, local and regional protected areas have demonstrated significant benefits for terrestrial species [41, 42], but the marine environment lags behind terrestrial ecosystems in area protected (3.4% versus 15.4%) [43], small median marine protected area (MPA) size (5 km^2) relative to their geographic range size [44], and the low strength of protection [45–47]. Indeed, 94% of marine protected areas allow fishing, such that <1% of the ocean is effectively protected [48]. Furthermore, the current MPA portfolio is not fit for species conservation, as without exception they are not yet designed to avert the extinction risk of individual species [49]. Finally, the relatively undeveloped trade networks and concentration of demand in a few luxury markets provides strong opportunity for meaningful intervention in a few Southeast Asian countries. Campaigns to reduce demand in shark fins and other luxury products have begun to shift perceptions and consumption patterns [18]. Thus, efforts to understand and reduce consumer demand for unsustainable product should be supported as an essential third prong of conservation for high-value marine species traded in international luxury markets.

SUPPLEMENTAL INFORMATION

Supplemental Information includes Supplemental Experimental Procedures, four figures, and four tables and can be found with this article online at http://dx.doi.org/10.1016/j.cub.2016.05.026.

AUTHOR CONTRIBUTIONS

Conceptualization, L.M., A.B.C., and N.K.D.; Methodology, L.M., A.B.C., and N.K.D.; Investigation, L.M.; Formal Analysis, N.K.D.; Visualization, L.M. and N.K.D.; Writing – Original Draft, L.M. and N.K.D.; Writing – Review & Editing, L.M., A.B.C., and N.K.D.

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