argue that trophy hunting can be an important conservation tool, provided it can be done in a controlled manner to benefit biodiversity conservation and local people. Where political and governance structures are adequate, trophy hunting can help address the ongoing loss of species.

International Outrage over Trophy Hunting in Africa

An American hunter killed a charismatic male lion (Panthera leo) called Cecil in Zimbabwe in July 2015. This sparked international outrage, mainly via a storm of social and other media. Several alleged aspects of the hunt itself, such as baiting close to national park boundaries, were done illegally and apparently against the spirit and ethical norms of well-managed trophy hunts. Online outrage had also been sparked earlier in 2015 by the legal hunt of a Critically Endangered male black rhino (Diceros bicornis). This hunt was sanctioned by the Namibian Government via an auctioned permit that cost the hunter US$350,000 for the privilege. This outrage arose even though the male was considered ‘surplus’ to the national black rhino management plan, and the revenue generated from the hunt was to be reinvested into a conservation trust fund to the wider good of conservation in Namibia. These two high-profile hunts and the ensuing public backlash against the ethics and conduct of trophy hunting in general have led to proposals to ban the practice throughout Africa. Furthermore, some commercial passenger and cargo airlines have decided to stop, or may soon stop, the transport of trophies of hunted animals shot legally and sustainably by foreign tourists, irrespective of international conventions, such as the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) and national laws that allow trophy hunting.

Hunting Industry in Sub-Saharan Africa

Trophy hunting strongly contributes to the conservation enterprise in sub-Saharan Africa, where large areas support important terrestrial biodiversity that is currently allocated to trophy hunting use (Table 1). While most of the hunted individuals (e.g., 96% in South Africa in 2012) [1] are often from more common and less valuable species (Table 1), most of the trophy hunting revenue is generated from a few species carrying valuable trophies, particularly the charismatic ‘Big Five’ (lion leopard Panthera pardus; elephant Loxodonta africana; buffalo Syncerus caffer; and black or white rhinoceros Ceratotherium simum) [2]. Out of the US$68 million of gross revenue generated from trophy hunting in South Africa in 2012, over US$28 million (at least 41%) was generated from the Big Five alone (i.e., $5,635,625 from 635 buffaloes; $1,914,600 from 33 elephants; $647,500 from 37 leopards; $15,270,750 from 617 lions, $300,000 from one black rhinoceros; and $5,355,000 from 63 white rhinoes) [1]. Southern African countries and Tanzania exported most of the Big Five trophies between 2009 and 2013 (Figure 1). At the same time, two countries that do not typically attract many tourists (the Central African Republic, currently undergoing a conflict, and Cameroon, where poaching pressure is high) allowed trophy hunting of big cats and elephants, respectively, over the same period (Figure 1).
individuals are not often implemented [5]. In addition, the contribution of some forms of trophy hunting to conservation is debatable. This is particularly the case for ‘canned lion hunting’, where future targets are bred and raised in captivity and kept in confined enclosures until shot, to ensure that hunters are guaranteed a kill. In South Africa, which is by far the largest exporter of lion trophies across sub-Saharan Africa (Figure 1), 80% of the trophies between 2009 and 2013 were from lions raised in captivity or ranched. The ethics of canned hunting are dubious, and this abhorrent practice requires reform before it brings down ethically practiced hunting.

The profitability of their respective hunting industries is hard to compare across sub-Saharan countries [5]. Nevertheless, it is known that the gross annual revenue generated by the hunting industry comprises tens of millions of US$ in countries such as South Africa, Tanzania, and Botswana (Table 1). Despite this, the amount of accrued revenue allocated to conservation authorities that could in principle be reinvested in improved management appears to be limited. In Tanzania, for example, the accrued revenue allocated to the Wildlife Division in 2008 amounted to 22% (US$12,353,180) of the gross revenue generated by hunting in that year [5]. The remainder of the revenue went to the private sector.

Another limitation is that revenue generated from trophy hunting currently provides few benefits to local communities sharing habitats with biodiversity [6,7]. In Namibia, however, revenue generated from trophy hunting has encouraged local community participation in conservation, which in turn has resulted in substantial increases in the abundance of many wildlife species and in the total area of land falling under community protection through conservancies [6]. It is less clear in other African countries what proportions of hunting-permit revenue are directed to community-development projects, whether they are payments to community-based organizations, or payments to communities for concession fees, resource fees, or payments for welfare and education. Finally, legal controls over biological, ethical, and financial aspects of the hunting industry can be more easily circumvented in many sub-Saharan countries where management capacity and governance structures are ineffective [8].

**Why Blanket Bans Could Exacerbate Biodiversity Loss**

One currently promoted solution to address such concerns is to ban trophy hunting altogether. However, a blanket ban on trophy hunting could lead to worse conservation outcomes for three main reasons. First, financial resources for conservation are limited, particularly in developing countries. Hence, both nonconsumptive and consumptive uses of wildlife are necessary to generate enough funding to support meaningful conservation success over large areas [9]. While ecotourism can help reduce poverty in communities coexisting with biodiversity [3], ecotourists generally prefer travelling to more accessible areas [10], greatly limiting the opportunities for conservation in more remote regions. Instead, sustainable hunting can create important incentives for biodiversity conservation in areas where ecotourism is not economically viable [11]. At a time when greater proportions of conservation budgets are being spent on enforcement, the revenue from trophy hunting can empower

<table>
<thead>
<tr>
<th>Country</th>
<th>Area Covered by Game Ranches (% of Total Land Area)</th>
<th>Terrestrial Protected Areas (% of Total Land Area)</th>
<th>Top 3 Most Exported Trophies in 2012</th>
<th>Annual Revenue (US$ million)</th>
</tr>
</thead>
<tbody>
<tr>
<td>South Africa</td>
<td>13.1</td>
<td>6.2</td>
<td>impala, warthog, kudu</td>
<td>68.0</td>
</tr>
<tr>
<td>Tanzania</td>
<td>26.4</td>
<td>32.2</td>
<td>leopard, hippopotamus, elephant</td>
<td>58.3</td>
</tr>
<tr>
<td>Botswana</td>
<td>23.0</td>
<td>37.2</td>
<td>elephant, leopard, lechwe</td>
<td>40.0</td>
</tr>
<tr>
<td>Namibia</td>
<td>11.4</td>
<td>43.2</td>
<td>zebra, chacma baboon, leopard</td>
<td>28.5</td>
</tr>
<tr>
<td>Zimbabwe</td>
<td>16.6</td>
<td>27.2</td>
<td>elephant, leopard, chacma baboon</td>
<td>15.8</td>
</tr>
<tr>
<td>Mozambique</td>
<td>10.5</td>
<td>17.6</td>
<td>Nile crocodile, elephant, hippopotamus</td>
<td>5.0</td>
</tr>
<tr>
<td>Zambia</td>
<td>21.3</td>
<td>37.8</td>
<td>lechwe, hippopotamus</td>
<td>3.6</td>
</tr>
<tr>
<td>Total</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>217.2</td>
</tr>
</tbody>
</table>

[a][13].
[c]CITES trade database ([http://trade.cites.org](http://trade.cites.org)).
[d]Chacma baboon (Papio ursinus), elephant (Loxodonta africana), hippopotamus (Hippopotamus amphibius), impala (Aepyceros melampus), greater kudu (Tragelaphus strepsiceros), lechwe (Kobus leche), leopard (Panthera pardus), Nile crocodile (Crocodylus niloticus), warthog (Phacochoerus africanus), zebra (Equus quagga).
[e]Data not adjusted for inflation.

Table 1. Hunting Contribution to Biodiversity Conservation and National Economies in Sub-Saharan Countries
Second, trophy hunting can have a smaller footprint than ecotourism in terms of carbon emissions, infrastructure development, and personnel, and can generate more revenue from a lower volume of tourist hunters. An often-neglected relation exists between ecotourism and aviation with regard to energy use and greenhouse gas emissions. Compared with ecotourism, the trophy-hunting industry relies on fewer tourist hunters, because the income generated per hunter is higher [13]. Additionally, hunters are interested in maintaining good-quality habitat for the simple reason that the quality of the individuals harvested therein is also high [14]. Finally, hunters are prepared to hunt in areas lacking attractive scenery, and require less infrastructure, therefore minimizing habitat degradation.

Third, management for hunting places emphasis on maintaining large wildlife populations for offtake, as opposed to ecotourism, where the presence of only a few individual animals is sufficient to maximize profits [2]. Both the consumptive and nonconsumptive uses of biodiversity can generate important revenue, so allowing local stakeholders, such as private landowners and communities, to retain property rights over these species is a necessary precursor for them to justify offsetting the direct and opportunity costs of conservation. Thus, the economic models underlying ecotourism and trophy hunting may lead to diverging management strategies. Empirical evidence shows that the strategy of artificially managing small populations within electrified fences to maximize economic return from communities to protect their resources by the employment of more antipoaching rangers or the construction of disincentive infrastructure [12]. If revenue cannot be generated from trophy hunting, natural habitats will be transformed to other forms of land use that provide higher return on investments compared with conservation [3], but have negative impacts on biodiversity.

Figure 1. Number of Trophies Exported from 2009 to 2013 (Red Bars) for Six Charismatic African Species Subject to Trophy Hunting. Gray-shaded areas correspond to the range maps of species obtained from www.iucnredlist.org/technical-documents/spatial-data. Each species is listed under the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES). Net export data for each species retrieved from the CITES Trade Database (http://trade.cites.org) by searching for ‘trophy’ under the ‘trade terms’ bar. Information about the conservation status, population trend, and CITES listing retrieved from www.iucnredlist.org and www.cites.org. Numbers next to the external bar in each panel indicate the scale to interpret bar charts of annual trophies taken per species and per country.
ecotourism and minimize management costs might be the most appropriate to enhance tourist experiences [2]. By contrast, wildlife populations potentially have higher hunting value when their sizes are larger (i.e., are more viable) and populations are better connected to enhance gene flow, because the latter can affect the fitness and quality of the individuals harvested.

**Concluding Remarks**

Inadequate political, legal, and governance structures are currently preventing trophy hunting from being an effective tool for creating conservation incentives in sub-Saharan Africa. At the same time, banning trophy hunting might not be the best solution because biodiversity loss could even be worse in its absence. Therefore, we propose a set of prescriptions that could enhance the contribution of trophy hunting to conservation and to the equitable sharing of the benefits with local people (Box 1).

To make these prescriptions more relevant for decision-makers, we have summarized them according to the guiding principles on trophy hunting promoted by the International Union for the Conservation of Nature [15]. In particular, we make suggestions on how net biodiversity benefits and stakeholder returns can be achieved simultaneously, and highlight how the hunting industry and governance structures can be made more transparent to avoid unethical or illegal practices. Finally, we provide additional guidelines to account for animal welfare concerns. Promoting these and other prescriptions could enhance the role of trophy hunting in addressing the ongoing loss of species.

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**References**

15. IUCN (2013) Guiding Principles on Trophy Hunting as a Tool for Creating Conservation Incentives, IUCN