Opportunistic exploitation: an overlooked pathway to extinction

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How can species be exploited economically to extinction? Past single-species hypotheses examining the economic plausibility of exploiting rare species have argued that the escalating value of rarity allows extinction to be profitable. We describe an alternative pathway toward extinction in multispecies exploitation systems, termed ‘opportunistic exploitation’. In this mode, highly valued species that are targeted first by fishing, hunting, and logging become rare, but their populations can decline further through opportunistic exploitation while more common but less desirable species are targeted. Effectively, expanding exploitation to more species subsidizes the eventual extinction of valuable species at low densities. Managers need to recognize conditions that permit opportunistic depletion and pass regulations to protect highly desirable species when exploitation can expand to other species.

Pathways to extinction by exploitation

Humans are by far the biggest drivers of extinction, both directly and indirectly [1]. Yet extinction through exploitation seems paradoxical: how can this be profitable given the exorbitant costs of targeting rare species? Two previous hypotheses suggest ways in which this could be profitable, but here we expand on another exploitation mode termed opportunistic exploitation (see Glossary) that arguably offers a much more widespread pathway to extinction.

One previous hypothesis, the ‘economics of overexploitation’ [2], contends that when population growth rates are low relative to monetary returns on investments, exploiters could maximize their net present value by catching the entire population, banking the money, and living off the comparatively high interest. The applicability of this hypothesis has recently been challenged: even for very unproductive species, catching the last individual would be too costly to maximize net present value [3].

An alternative hypothesis is the ‘anthropogenic Allee effect’, which notes that humans place exaggerated value on species as they become rare, allowing profitable exploitation at very low population sizes [4,5]. For example, the traditional Chinese medicine market generates intense demand for products from rare fauna such as rhinoceroses and tigers [6]. One instance of this demand is for the Chinese bahaba, Bahaba taipingensis, which possesses a swimbladder that is highly coveted by Asian consumers of tonic soups for its supposed medicinal properties [7]. A single 60.5 kg Chinese bahaba caught in the Fujian and Guangdong Provinces was once sold for the same price (US$23,895) as a three-bedroom house [7]. However, the 100–200 Taiping boats seeking this species must make their living off other species, because only a handful of Chinese bahaba are caught each year [7].

Glossary

Accidental exploitation: this mode occurs when the exploited species has no economic value but is killed while a target species is exploited. Cases include the deaths of sea snakes caught and discarded in trawl fisheries in Australia [47] and accidental snare captures in Newfoundland of endangered marten (Martes americana) while snowshoe hares (Lepus americanus) are targeted [48].

Incidental exploitation: this mode involves the exploitation of less desirable species when commingled with the target species (e.g., Figure 5 in [4]). In fisheries, it has long been recognized that, in such a situation, maximizing catches from all species combined will result in the depletion or extirpation of less-resistant species [49-52]. Specific examples include the incidental bycatch of shark species in longline fisheries for tuna and swordfish [53] and the near extinguition of common skate (Diapterus batis) in the Irish Sea when caught by trawlers targeting more valuable and abundant species such as cod [42,54].

Opportunistic exploitation: the exploitation of a scarce but desirable species, when encountered while targeting other less desirable but more common species. Exploitation is only profitable because of the presence of the less desirable species. The term was originally coined as ‘opportunistic depletion’ [8]. Opportunistic exploitation allows for continued exploitation at densities below the bioeconomic equilibrium [55], when profit (income minus expenses) is the same as from available alternatives. In the single-species case, humans should logically cease exploitation at this point. However, where multiple species can be exploited in the same habitat, humans will often first deplete the most desirable species, depleting it to the point of bioeconomic equilibrium, before switching to less desirable species. The crux of opportunistic exploitation is that at this point the sparse but desirable species can continue to be taken opportunistically whenever it is encountered, providing an unexpected bonus to the exploiter. The definition of ‘opportunistic’ involves ‘exploiting circumstances or opportunities to gain immediate advantage, rather than following a predetermined plan ... especially with the implication of cynicism or a lack of regard to principles’ (Oxford English Dictionary, http://www.oed.com). Thus, opportunistic exploitation carries the dual connotations of being both unplanned and selfishly targeting an already depleted species.

Targeted exploitation: this is the most common mode, which occurs when one or a few species are the primary subjects of resource extraction. Examples include trophy hunting for wild goats (subfamily Caprinae) [5] and diving for black-lip abalone (Haliotis rubra) in Australia [56].

Key differences between exploitation modes

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<tr>
<th>Exploitation mode</th>
<th>Value of species</th>
<th>Primary target?</th>
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<tbody>
<tr>
<td>Opportunistic</td>
<td>Higher than target</td>
<td>No</td>
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<tr>
<td>Targeted</td>
<td>Profitable</td>
<td>Yes</td>
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<td>Incidental</td>
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Both the economics of overexploitation and the anthropogenic Allee effect hypotheses offer explanations of how exploitation focused on a single species (target exploitation) can lead to extinction. However, it is much more common for multiple species to be exploited together, offering more pathways to extinction. These pathways include accidental exploitation of species with no value and incidental exploitation of species with lower value while pursuing target species. We contend that a further pathway occurs when rare, high-value species are encountered during the exploitation of more common target species. We term this largely unrecognized mode opportunistic exploitation [8]. This pathway allows critically sparse but valuable species to be profitably exploited when they are encountered while targeting abundant but lower-value species in the same habitat (Figure 1). Note that opportunistic exploitation is more pernicious than incidental or accidental exploitation, because the depleted species has high value, which results in stronger economic incentives for further exploitation. Opportunistic exploitation examples from disparate habitats, scales of exploitation, and trophic levels now provide compelling support for this extinction pathway.

Marine examples of opportunistic exploitation
Antarctic blue whales were used as the key example exemplifying the economics of overexploitation by Colin Clark [2], but ironically exemplify opportunistic exploitation. As quoted within the original article [2]: ‘Gulland [pers. comm.] has pointed out to me that fishing for the Antarctic blue whale probably would have become un economical several years earlier had it not been for the simultaneous occurrence of finback whales in the same area.’ This view is even held by Clark himself in a recent book, where he writes that targeting Antarctic blue whales was effectively a zero-cost activity subsidized by the exploitation of fin whales [9]. The underlying story is that Antarctic blue whales were heavily depleted by pelagic whalers, who caught 28,000 in 1930 but only 7000 in 1950 and fewer than 200 in 1963 as the population size plummeted [10]. However, this was not due to targeted exploitation, which would never have been profitable at such low population sizes. By the 1950s, profits flowed from less sought-after but more abundant species, particularly fin whales (Balaenoptera physalus) and sperm whales (Physeter macrocephalus). Although Antarctic blue whales were too scarce to support a target whaling industry, they were targeted opportunistically whenever they were encountered, resulted in depletion to near-extinction. Small catches of other species have been excluded. The comparative scale of the whale drawings is indicative. Whale drawings reproduced with permission from Greenpeace.

Multispecies trawl fisheries are also prone to opportunistic exploitation. For example, in India, trawl fisheries began by targeting valuable shrimp, cephalopods, and large fishes such as snapper and grouper in the 1950s, primarily for export. After these were depleted, trawlers shifted focus to lower-value fish such as croakers and sardines for domestic markets, including the traditionally discarded bycatch comprising small-bodied animals with lower consumer preference, called ‘trash fish’. In India and many other parts of South and Southeast Asia, trash fish are now processed to fishmeal and used as a protein supplement in the poultry and aquaculture industry. The extra subsidy received from these former discards (Figure 3) has allowed trawlers to further deplete high-value species whenever they are encountered [11].

Opportunistic exploitation also occurs in small-scale sea cucumber fisheries where multiple species are targeted [8]. Sea cucumbers feature prominently in Asian medicinal markets and banquet dishes [12]. In sea cucumber fisheries, one or two high-value species are often fished to low levels before fishers shift to lower-value species in the same grounds and then the high-value species continue to be fished while lower-valued species are targeted. In unfished
areas, high-value sea cucumber species (Figure 3) are naturally common and widely distributed, but in areas subject to multispecies sea cucumber fisheries they are often critically overfished [13]. Conversely, in single-species sea cucumber fisheries in Alaska, Iceland, New Zealand, British Columbia, Newfoundland and Labrador, Washington, and eastern Russia, where there are no other sea cucumber species to support opportunistic exploitation, even high-value sea cucumber species have not been heavily depleted [8]. In other words, economic value must be coupled with the presence of more abundant but less desirable species to subsidize the chronic depletion of sea cucumber stocks.

Given these examples, we argue that this switch from targeted exploitation to opportunistic exploitation [14] is probably widespread in marine and freshwater environments. For example, overfishing of Napoleon wrasse (Cheilinus undulatus) [15], white abalone (Haliotis sorenseni) [16], and freshwater populations of lake trout (Salvelinus namaycush) and walleye (Stizostedion vitreum) [17] were all likely to have been exacerbated because fishing could continue on other species in the same habitat. We also speculate that examples of opportunistic exploitation might include the extinctions of Steller’s sea cow (Hydrodamalis gigas) [18] and the Caribbean monk seal (Monachus tropicalis) [19].

Terrestrial case studies
Terrestrial systems also provide examples of opportunistic exploitation. For instance, black rhinoceroses (Figure 3) were illegally poached in the Luangwa Valley, Zambia in the 1980s, despite an economic analysis showing this was unprofitable due to their rarity [20]. However, poachers could make a living by targeting elephants, which were ten times more abundant, while poaching black rhinoceroses when they were encountered [20]. By the end of the 20th century, black rhinoceroses were extinct not just in the Luangwa Valley, but in all of Zambia [21].

Similarly, hunters in the Indonesian island of Sulawesi use snares to trap abundant Sulawesi wild pigs (Sus celebensis), but this allows them simultaneously to poach another wild pig, the rare babiru (Babyrousa celebensis) (Figure 3) [22], which would otherwise not be profitable to hunt. Although the babiru are legally protected, they are caught more easily by the snares and thus even a small amount of trapping of Sulawesi wild pigs can eliminate babiru from an area. Rowcliffe et al. make use of wordplay to describe this example as ‘piggyback extinction’ [23]. Bushmeat hunting in Equatorial Guinea and Ghana also displays classic signs of opportunistic exploitation, with more abundant smaller animals maintaining profitable hunting while larger, rare, and more valuable animals are still hunted whenever they are encountered [24,25].

Selective logging of big-leaf mahogany (Swietenia macrophylla) also exemplifies opportunistic exploitation. In the Brazilian Amazon, these highly valued lumber trees are found at low densities, but logging removes 93–95% of commercial-sized trees [26]. Further waves of logging for low-value species ensures that big-leaf mahogany missed during the first wave are eradicated [27], leading to simplified forests containing only low-value species.
There are likely to be many more terrestrial examples of opportunistic exploitation, from both the past and the present. Possible candidates include the present-day depletion of Madagascar rosewood (Dalbergia spp.) [28], the near-extinction of American bison (Bison bison) [29], and the extinctions of South African blue antelope (Hippotragus leucophaeus) [30] and New Zealand moa species (Aves, Dinornithiformes) [31].

Parallels in ecological theory
Opportunistic exploitation might thus be a widespread but overlooked phenomenon wherever humans exploit multiple species together, with some ecological parallels in the general field of ‘apparent competition’ where the abundance of two prey species becomes linked through shared predators, affecting predator functional responses [32]. Multispecies models invoking apparent competition can explain how early hunters caused the mass extinction of large mammals in North America, whereas models based on a single prey species cannot [33,34]. For instance, common forms of functional response in predators can act to keep one prey species in a low-abundance ‘predator pit’ [35,36] whereby, if they increase, predators will start targeting them and keep their numbers depressed, but at low densities predators no longer maintain a search image for that species and switch to other prey species [37]. Unlike most natural predators, however, humans maintain and even increase their desire to target high-value species when they are encountered at low densities [5], so there is no refuge in rarity.

‘Hyperpredation’ in natural systems is also somewhat analogous to opportunistic exploitation. Hyperpredation occurs when one prey source increases, subsidizing higher predator populations, which in turn cause declines in alternative prey populations [38]. This is typified by declines and extinctions of native Australian rodents, where feral cats and other predators subsidize their diets with introduced rabbits and mice [38], and by the declines of island foxes in the California Channel Islands due to introduced pigs providing a steady food source for predatory golden eagles [39]. However, whereas hyperpredation requires an increase in alternative prey, opportunistic exploitation can happen even when the abundance of alternative prey is constant or declining.

Implications for conservation and policy
Management and conservation policies need to identify species at risk of opportunistic exploitation and take steps to avoid their potential depletion and extinction. Past studies have focused on attributes of each species in isolation to predict their risk of extinction: factors such as life-history traits, overexploitation, loss of habitat, disease, rates of decline, abundance, and geographic range [4,40]. We argue that multispecies attributes are also important; the risk of opportunistic exploitation not only depends on the value of the species in question, but is also linked to the presence of co-occurring lower-value species that could subsidize continued exploitation.

There are several specific management actions that can be taken to overcome opportunistic exploitation. One key realization is that private ownership of multispecies resources can lead to economically rational overexploitation. Managers should pay special attention to rare species that are highly valuable and institute protocols to limit and monitor trade. For example, Papua New Guinea has an export ban on seven species of birdwings, the largest butterflies in the world, due to their rarity and the global demand from collectors [41]. Another useful policy is to develop shortlists of allowed species [8], instead of imposing species bans that inevitably are developed too late to avoid depletion from opportunistic exploitation. The shortlists could include common exploitable species but exclude threatened high-value species and others that are not targeted to preserve ecosystem functioning. Used in this manner, shortlists would prevent the future expansion of exploitation to new species before they can be assessed. Naturally, trade restrictions and shortlists should be based on sound taxonomy, to ensure that the diagnosis of extinction risk is not clouded by cryptic species that are part of undetected species complexes [42]. Another pitfall to avoid is a group quota for the exploitation of multiple similar species. The International Whaling Commission initially set an annual quota on the weighted catch of all species of large whales combined, which contributed greatly to the decline of individual species, including Antarctic blue whales. Instead, sustainable individual-species quotas should be set wherever quotas can be practically established, monitored, and enforced.

Related to the idea of individual quotas for species is the proposal for balanced fisheries exploitation, where catches are spread broadly across a range of species while care is taken to ensure that exploitation rates for individual species remain in proportion to their productivity [43,44]. Fishers are capable of applying this approach in multispecies fisheries, provided there are sufficient incentives to target and avoid particular species, but this requires near-100% enforcement and monitoring [45]. The danger of the balanced-exploitation approach is that expanding catches to new species acts as a subsidy for the continued exploitation of current species, as seen in our example of multispecies trawl fisheries in India.

In addition to these specific policy ideas to mitigate opportunistic exploitation, there are a number of familiar policies that are also needed. For instance, ideally, species should be regulated by limiting the amount exploited and not the amount of effort expended (a surprisingly common regulation in fisheries). Terrestrial and marine reserves should be set aside where no extractive exploitation is allowed, to serve as a refuge against opportunistic exploitation. Finally, all regulations are moot without effective monitoring and enforcement to deter illegal exploitation.

Concluding remarks
Examples from fishing, hunting, and logging demonstrate that opportunistic exploitation is a pervasive pathway to depletion and extinction wherever multiple species are exploited. We anticipate that further examples of opportunistic exploitation, both historically and in the present, will come to light wherever humans exploit natural resources. For example, opportunistic exploitation might arise in spearfishing, in trapping, and in the process of collecting bird eggs, orchids, mushrooms, insects, shells, and ornamental corals.
Policy efforts should focus on conserving rare, high-value species exploited within multispecies systems, to avoid scenarios where subsidy by lower-value species allows a profitable pathway that drives species toward extinction.

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References

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