LETTER

Endangering the endangered: The effects of perceived rarity on species exploitation

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Abstract

Classifying species by threat status can result in conservation benefits such as increased protection, but can also be an incentive to hunters responding to increased consumer demand for goods perceived to be rare, and therefore valuable. Bioeconomic theory provides a framework for examining the population consequences of differing responses of consumers (demand) and hunters (supply) to perceived rarity. We present a series of illustrative case studies of how perceived rarity affects consumer behavior and hunting pressure, and use a model to explore the scenario of most conservation concern (where rarity itself fuels increased exploitation). Rarity-fuelled demand can have two undesirable outcomes: the species may become trapped at a low population size, or escalating hunting effort may drive the species to extinction. Understanding the response of consumers and hunters to perceived rarity is vital for predicting the impact of intervention strategies that seek to minimize extinction risk.

Introduction

The world is facing an extinction crisis (Ceballos & Ehrlich 2002; Thomas *et al.* 2004). Organizations such as IUCN produce lists of species ranked by threat status, which are used to prioritize conservation interventions such as regulation of human activities which impact on these species' survival. In spite of local enforcement and international trade restrictions, hunting (here referring broadly to killing or the collection of live specimens from wild populations) continues to threaten many endangered animal and plant species (Bulte & Van Kooten 1999; Seidensticker *et al.* 1999; Davenport & Ndangalasi 2003; Gonzalez 2003; Haitao *et al.* 2007). To design effective strategies to deter hunting of threatened species, there is a pressing need to identify the social and economic forces that maintain its profitability, and the consequences for the exploited population.

It is a well-established economic principle that people value objects for their rarity—the rarer an item is, the more desirable it becomes (Ekelund & Herbert 1997). Owning rare goods increases a consumer's social status, since their acquisition may require such perceived attributes such as money, power, skill, and endurance. This value in rarity extends to products derived from species perceived to be rare, and there are thriving markets—legal and illegal—in exotic pets (Slone *et al.* 1997), hunting trophies (Baldus & Cauldwell 2004), and luxury goods such as caviar (Raymakers 2002) to name but a few. Worryingly, there is increasing evidence that traders use the threat status of certain species, as indicated by their listing in appendices of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES; Rivalan *et al.* 2007), or the description of species new to science (Stuart *et al.* 2006) to capitalize on increased consumer interest in rare items. Courchamp *et al.* (2006) hypothesized that if consumers place disproportionate value on rare species, this could result in a cycle in which increased exploitation further reduces the population size, which in turn increases its value and ultimately leads to its extinction in the wild—a process they termed the "anthropogenic Allee effect."

Supply and demand curves provide a means of formalizing consumer and hunter behavior within an economic context, by representing the quantity hunters are prepared to provide to the market at a given price (supply) and the quantity consumers are willing to buy at a given price (demand). Here we investigate how these curves may shift in relation to changes in a species' perceived rarity, and outline a number of illustrative case studies. We then focus on the case of highest conservation concern, that is, where rarity-fuelled demand sustains hunting targeted at a single, vulnerable species. We investigate possible consequences for a population subject to open-access exploitation, when the price per unit catch and the cost per unit hunting effort depend on the species' perceived rarity. If increased demand for rare species causes a jump in their market price, increased hunting pressure may trap the species at a dangerously low population size. If demand continues to climb as the species declines, an ever-increasing market price can offset rising hunter costs and result in species extinction through an anthropogenic Allee effect. We conclude with a discussion of the relative merits of possible intervention strategies designed to avoid such outcomes, and highlight some "warning signals" to enable conservationists to detect rarity-fuelled exploitation.

Perceived rarity, supply, and demand

While a species' "true" rarity suggests a low population size, human perception of rarity is skewed and scale-dependent: a species may be considered to be rare if it is widespread but at low densities throughout its range (e.g., large carnivores), found only in few locations (e.g., island endemics), locally scarce but more numerous elsewhere (e.g., brown bear in western Europe versus Alaska), or rarely encountered due to secretive behavior or inaccessible habitat. Additional cues for a species' rarity arise indirectly through threat listing by a conservation organization, and the associated publicity (wildlife documentaries, fundraising campaigns) and management actions (trade restrictions, antipoaching patrols). Here we discuss how different aspects of perceived rarity affect the supply of wild specimens to the market by hunters and consumer demand.

The supply curve describes the relationship between the quantity of a good provided to the market and its price. For an exploited population, this curve is typically backward bending (Figure 1), reflecting the fact that increasing hunting effort increases the quantity provided to the market, up to a point (the maximum sustainable yield), after which further increases in effort actually reduce the quantity provided in the long term (overexploitation). The upper branch of the supply curve accounts for the effect of "real" rarity (i.e., a small population size) on exploitation: rising hunter costs per unit catch through increased search times result in higher prices and lower offtake (Clark 1990). In general, the slope (elasticity) of this part of the curve will be steep because most species become harder to find at low population sizes; however, animal behavioral responses can result in local increases in catchability with rarity (see examples in Table 1), resulting in a shallower slope and an increased risk of extinction via exploitation.

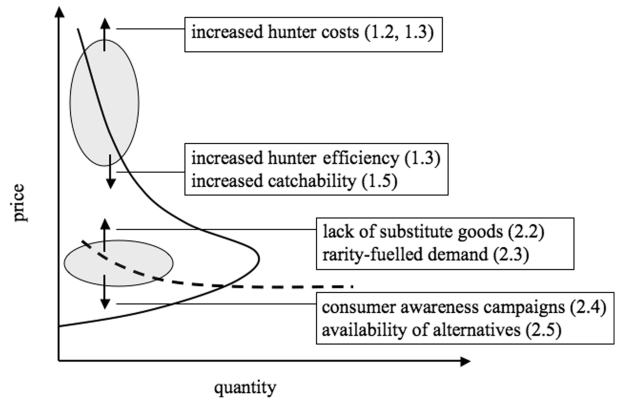

Figure 1 Supply (bold) and demand (dashed) curves for an exploited population. The shaded sections of the curves are those that are most affected by perceived rarity, when the quantity provided to the market is necessarily limited. The arrows represent the direction of a shift and/or change in elasticity for each curve, and the adjacent numbers refer to the analogous economic processes described in Tables 1 and 2. Further details on the theory underlying the backward-bending supply curve for a population subject to open access exploitation can be found on pages 131–132 of Clark (1990).

A species' perceived rarity will also affect supply, if conservation measures are implemented to increase hunter costs directly through antipoaching patrols and the threat of fines/jail sentences, or indirectly by increasing the opportunity costs of hunting (i.e., through the provision of more profitable alternative livelihoods; Table 1). Increasing hunter costs following a declaration of rarity should shift the supply curve upwards and increase its steepness, thus reducing extinction risk (Figure 1). However, theoretical studies have suggested that conservation efforts such as increasing supply from sustainable sources or increasing the opportunity cost of hunting can have ambiguous effects on hunting pressure. Damania *et al.* (2005) suggest that while increased profitability of agriculture may shift the allocation of labor from hunting to farming, increased income enables the purchase of more efficient hunting equipment, in which selective hunting worsens the conservation status of some species. Equally, wildlife farming may prevent or stimulate illegal

Table 1 Summary of the effects of perceived rarity on hunting pressure. Hunting offtake is affected both directly by the scarcity of the hunted species and indirectly via changes to hunting costs and efficiency induced by conservation interventions. The expectation is that increasing costs per unit catch (via reduced catch per unit effort and/or increased cost per unit hunting effort) will tend to decrease hunting effort, while price rises lead to increased effort.

Effect of rarity	Consequences for hunting	Example
1.1. Reduced stock leads to reduced offtake	Hunter costs per animal caught are rising (normal bioeconomic process)	Fisheries, e.g., herring (Bjorndal Conrad 1987)
1.2. Rarity prompts conservation efforts to directly reduce hunting effort	Hunter costs rise more than proportionally to changes in stock size	Anti-poaching patrols and penalties, e.g., black rhinos (Leader-Williams *et al.* 1990)
1.3. Rarity prompts conservation efforts to reduce hunting effort by promoting alternative livelihoods for hunters	Opportunity cost of hunting increases (but increased income could increase hunter efficiency, so effects on offtake not obvious)	Profits from managed trophy hunting passed to local community, e.g., project CAMPFIRE, Zimbabwe (Bond 2001); COMACO project, Zambia (www.itswild.org)
1.4. Rarity prompts trade restrictions in goods derived from the exploited species	Limited sales opportunities may reduce long-term incentive to hunt, but pre-enforcement hunting effort may increase	Spike in trade in animals in the year prior to CITES uplisting (Rivalan *et al.* 2007)
1.5. Aggregation or avoidance behavior of species changes at lower population sizes	Local changes in Catch Per Unit Effort (CPUE), may also be associated with a change in hunter costs per unit effort, so effects on offtake not obvious	Avoidance behavior reduces CPUE, e.g., tuna (Walters 2003); animals aggregate in protected areas which may increase CPUE, e.g., northern cod (Rose & Kulka 1999)

hunting, depending on market conditions (Bulte & Damania 2005). Nonetheless, empirical support for the negative effects of these conservation interventions remains scarce, and farming has had some notable successes in controlling the exploitation of wild populations, such as the Nile crocodile (Thorbjarnarson 1999).

The demand curve describes the relationship between the quantity on the market and the price consumers are willing to pay; in general, the price increases with market scarcity (Figure 1) and the steepness (elasticity) of this relationship depends on the availability of acceptable alternatives. A species' perceived rarity can affect consumer decisions in various ways (Table 2). Demand for products derived from a locally scarce population of a hunted species will be low if it is more abundant elsewhere (resulting in a flat, or elastic demand curve, Figure 1). However, prices may increase sharply with declining market availability for globally endangered species, especially for consumer groups for which no acceptable alternative products are available (e.g., collectors of specimens and exotic pets, luxury products such as caviar). A species' perceived rarity may stimulate conservation efforts targeted at reducing consumer demand, including ownership restrictions, awareness campaigns appealing to consumer ethics, or the provision of sustainable alternatives through captive breeding (note, however, that the latter

Table 2 Summary of the possible effects of perceived rarity on consumer behavior, as represented by the changes in the quantity purchased at given price (demand). In standard economic theory, the expectation is that price rises lead to reductions in the quantity demanded.

Effect of rarity	Consequences for demand	Examples
2.1. No obvious effect/minor effect of rarity; substitutes are available	Standard demand curve, consumers buy less at increased prices	Bushmeat hunting in West Africa (East *et al.* 2005; Wilkie & Godoy 2001)
2.2. No close substitutes for the good; demand remains high when species is rare	Highly inelastic demand curve; price rises do not deter buyers	Specialist collections, e.g., butterflies (Slone *et al.* 1997); ingredients for traditional medicine, e.g., bahaba (Sadovy & Cheung 2003)
2.3. Rarity itself makes the species more desirable	Demand curve shifts upwards and/or becomes less elastic as population declines	Trophy hunting, e.g., *Caprinae* (Courchamp *et al.* 2006); Luxury goods, e.g., caviar (Raymakers 2002)
2.4. Conservation measures target consumers to reduce demand for wild stock	Demand decreases or remains elastic when the species is rare	Consumer awareness campaigns and legal trade bans, e.g., ivory (Bulte & van Kooten 1999)
2.5. Rarity prompts conservation measures to supply sustainable alternatives	Saturation of market with an ethical alternative reduces demand for wild-derived product	Captive breeding, e.g., bulbs of *Galanthus* spp. (Entwistle *et al.* 2002)

can stimulate illegal hunting; Clayton *et al.* 2000; Bulte & Damania 2005).

Population consequences of rarity-fuelled demand

Here we focus on the case of most conservation concern, that is, where a species' perceived rarity fuels increased consumer demand. Proxies for a species' rarity such as threat listing by a conservation organization can be perceived as official verification that it is a "limited edition" (Rivalan *et al.* 2007). This can increase consumer demand if ownership of scarce goods conveys social status, or if consumers believe that this is their last chance to obtain specimens before the species goes extinct. If rare species attract sufficiently high market prices, this may stimulate hunting in spite of rising hunter costs.

We investigated the population consequences of rarity-fuelled hunting using the classic Gordon–Schaefer model for open-access exploitation (Gordon 1954; see also legend of Figure 2). Open-access exploitation assumes that hunters are subject to no restrictions, and has therefore been widely applied to species that are weakly protected by law, where hunting restrictions are weakly enforced and to poaching (Milner-Gulland & Leader-Williams 1992; Bulte 2003; Ling & Milner-Gulland 2006). This model assumes that hunting effort increases when the price for the amount caught outweighs the hunting costs, and decreases otherwise (responding to the marginal change in profit). We also assume that the price hunters receive is proportional to the market price; any intermediate agents between the hunters and the market keep a fixed percentage of the sale price and the rest is passed on to hunters. Finally, we restrict our attention to single-species hunts fuelled by the collections, exotic pets, or luxury markets, while acknowledging that opportunistic "bycatch" of rare species in multi-species hunts may also pose a serious threat.

In the standard Gordon–Schaefer model, the price and the cost per unit hunting effort are assumed to be independent of the hunted population's size. Here we relax this assumption when the population size declines below a "rarity threshold" ($x = x_R$). Hunter costs *per unit catch* increase as the population declines, but additionally we assume that the costs *per unit effort* experience a jump at the rarity threshold, reflecting increased risks of the hunter being caught and penalized if antipoaching enforcement is implemented.

We assume two different responses of price to perceived rarity. First, increased consumer interest in the species after a declaration of rarity can cause the market price to jump to a higher fixed value; further price rises

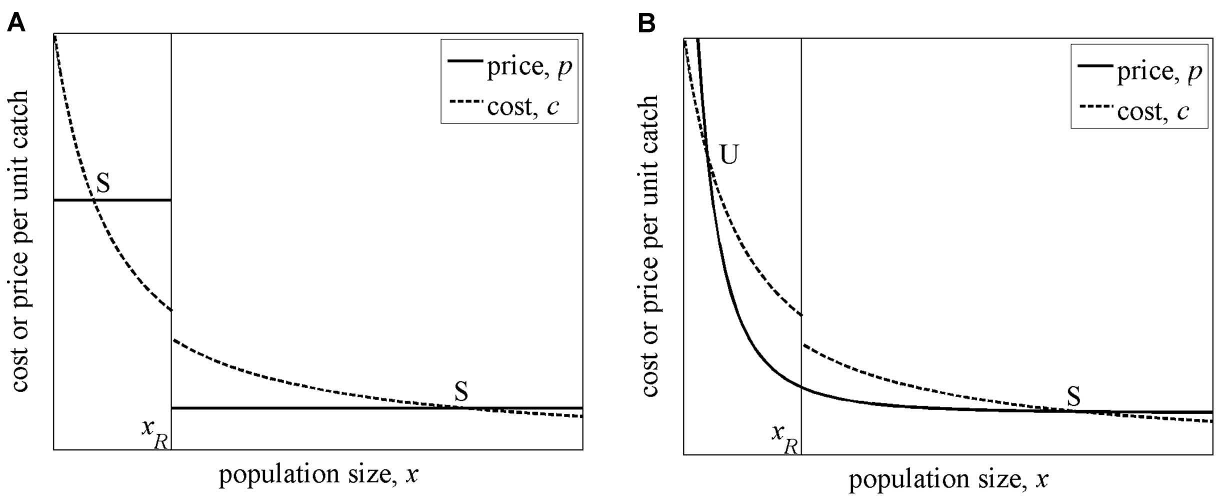

Figure 2 The price (bold line) and cost (dashed line) as functions of population size for a species subject to open-access exploitation; the population is in equilibrium at the intersections of the price and cost curves, and the stability of this equilibrium is denoted by S (stable) or U (unstable). Changes in the exploited population size (x) and hunter effort (E) are described by the Gordon–Schaefer model: $dx/dt = rx(1 - x/K) - qEx$; $dE/dt = \alpha\,(pqEx - cE)$. In the absence of exploitation, the population grows according to the logistic equation with rate r and carrying capacity K. The hunting offtake is qEx, where the constant q describes the species' catchability. Hunting effort is proportional (with rate α) to the difference between the total price for the quantity caught and the total cost of the associated hunting effort. The price per unit catch is p and the cost per unit hunting effort is c; both are assumed constant when the species is abundant, leading to a stable population equilibrium. When the population declines below the critical density $x = x_R$, the cost jumps to a new (constant) value. In (a) the price also jumps to a new fixed level below the rarity threshold, resulting in the creation of a second stable equilibrium (a "poaching pit"). In (b), the price increases continuously as the population declines, creating an unstable equilibrium below which (to the left of U) the species is hunted to extinction (an anthropogenic Allee effect).

are prevented because alternatives from other wild or captive-bred populations are available. Plotting the price and cost per unit catch as functions of population size enables the equilibrium population size under exploitation to be determined (Figure 2a). When perceived rarity results in a price jump, a stable equilibrium exists below the rarity threshold; elevated levels of hunting trap the species at a low population size (a "poaching pit" *sensu* Bulte 2003), at which it is vulnerable to extinction through stochasticity or natural Allee effects. Whether the population can escape this "poaching pit" depends on the reversibility of perceived rarity among consumers: a species that has been declared rare may forever be associated with rarity (and hence value), in which case the "rare" population equilibrium becomes globally stable.

A second possible consumer response to a species' perceived rarity is *demand inelasticity*, where the price continues to increase as wild stocks and their market availability decline (Figure 2b). If demand is sufficiently high that the price increase outstrips the hunting costs at low population sizes, an unstable equilibrium exists, below which ever-increasing hunting effort leads to the species' eventual extinction (an anthropogenic Allee effect *sensu* Courchamp *et al.* 2006). We have tacitly assumed a "best-case" scenario for the species in the absence of hunting, that is, the per capita population growth rate is positive at low population sizes. This enables us to disentangle the direct effects of rarity-fuelled hunting and to show when hunting pressure alone is sufficient to threaten species with extinction. In reality, extrinsic factors such as habitat loss may slow or prevent the species' recovery from low population sizes so that the additional effect of hunting is severe.

Under this scenario, the population size at which the species is perceived as rare (x_R) may itself become the extinction threshold, if elevated levels of hunting reduce the species density into the range where other factors drive it to extinction. Second, the approach to extinction may be accelerated by the "double whammy" of natural decline and a scramble by hunters to obtain the last few specimens. This may explain the demise of the great auk (*Pinguinus impennis*), where a combination of hunting and climate change resulted in a declining population, but it was a rush by museum collectors desperate to obtain specimens that resulted in the death of the last known individual (Fuller 1999).

Discussion

Human responses to a species' perceived rarity can have wide-ranging impacts on its population dynamics; the benefits arising from increased protection and habitat preservation are well documented, but the potential for rarity itself to stimulate exploitation is just beginning to be explored. The case studies presented in this article have highlighted both the positive and negative effects of conservation measures designed at preventing the extinction of rare species, while the modeling framework has highlighted two alarming possible outcomes for populations of species subject to rarity-fuelled exploitation, namely, that elevated hunting pressure may drive the species to extinction, or trap it at a low population size where it is vulnerable to extinction from other causes. Other bioeconomic models of hunting have shown that species extinction can arise if the cost of finding the last individuals is relatively low (Clark 1973), or through bycatch in a multi-species system (Milner-Gulland & Leader-Williams 1992), but this is the first explicit exploration of how human responses to perceived rarity can further endanger species. While this article has focused on the effects of hunting (removing individuals from wild populations) in response to perceived rarity, it is possible that similar problems may arise through wildlife watching, if some species face disproportionate anthropogenic disturbance resulting from increased interest in observing threatened species in the wild (Bain 2002).

Standard economic theory suggests that hunting pressure can be reduced by increasing hunter costs (either through increased risk of being caught and penalized, or via the provision of alternative livelihoods). Clearly, if such measures are to overcome rarity-driven price increases, hunter costs need to increase at least as rapidly as the price. Unfortunately, effective species protection is often extremely costly (Burton 1999), and sufficient funds for antipoaching enforcement may not be available, particularly if rare species attract high sale prices. Increasing the opportunity cost of hunting by channeling money gained from poaching fines and ecotourism into local communities can reduce poaching (Martin 1986; Lewis & Alpert 1997). However, when hunting is coordinated by organized gangs, as is often the case for species with a rarity-based cachet, such local methods are unlikely to be as effective.

Given the high costs of protecting species, conservation strategies aiming to reduce consumer demand may be a more effective solution. It is tempting to suggest that withholding information on species abundance from the public domain would avoid an increase in demand triggered by a rarity effect. Aside from the moral and technical difficulties of achieving this, a valuable opportunity for raising conservation funds driven by increased public awareness of a species' plight could be lost. Nonetheless, increased regulation of the type of information available in the public domain is advisable. In

Britain, information posted on the Internet by birdwatchers eager to share unusual bird sightings has been used by egg-collectors to locate and rob nests of protected species (Thomas *et al.* 2001). Awareness campaigns by the Royal Society for the Protection of Birds and local ornithological societies have proved effective at promoting greater self-regulation in the birding community when sharing information on sensitive species.

Conservation interventions appealing to consumer ethics provide another means to combat rarity-fuelled demand. Changing the perception that it is fashionable or prestigious to own products derived from rare species has met with some success in curbing demand for products derived from ivory and fur in Europe and the United States (Bulte & Damania 2005). The provision of sustainable alternatives such as organized safari hunting or "green labeling" of sustainably hunted products (Lindsey *et al.* 2007) can control demand for products derived from wild populations. However, restricted legal trade can stimulate an increase in illegal hunting if hunters believe that a market exists for illegally derived stocks (Bulte & van Kooten 1999; Clayton *et al.* 2000), especially in market situations where a small number of suppliers mediate purchases from hunters and supply to consumers (Bulte & Damania 2005).

The exploration of factors affecting consumer demand provides insight into determining those species that might be most at risk from rarity-fuelled exploitation. At-risk species include those that are undergoing well-documented declines that are likely to result in them being assigned conservation status, especially in taxa that are already popular in hobby collections, such as amphibians. Scarce species that have attributes for which there may be no acceptable alternatives to consumers, will also be particularly at risk. These attributes include extreme size or morphology (e.g., the Goliath frog *Conraua goliath*), attractiveness or bright colors (e.g., the blue poison frog *Dendrobates azureus*), a distinctive taste (caviar from sturgeon species), or those perceived to have particular cultural significance or medicinal properties (e.g., American ginseng *Panax quiquefolius*). It is also hoped that the analyses presented in this article will help conservationists to identify warning signals highlighting when a species may be experiencing rarity-fuelled exploitation. Careful monitoring *at the time of a change in the species' threat status* is essential; for example, data on international trade volumes during their uplisting in CITES appendices has revealed an effect of rarity-fuelled demand (Rivalan *et al.* 2007). Other potential warning signals include an increase in numbers of poachers apprehended per unit of antipoaching effort, evidence of increased buyer interest in rare species (e.g., sharp rises in sale prices or hits on wildlife trading websites), or behavioral changes in the quarry species consistent with a response to hunting pressure (e.g., increased vigilance or flocking).

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