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Rarity, trophy hunting and ungulates

L. Palazy[1,2], C. Bonenfant[1], J. M. Gaillard[1] & F. Courchamp[2]

1 Biométrie et Biologie Évolutive, Villeurbanne, France
2 Ecologie, Systématique et Evolution, Orsay, France

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Correspondence
Lucille Palazy. Current address: UMR CNRS 5558, Univ Lyon 1, 43 bd 11 nov, 69622 Villeurbanne cedex, France.
Tel: +33 4.72.43.29.35
Email: lucille.palazy@u-psud.fr

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Abstract

The size and shape of a trophy constitute major determinants of its value. We postulate that the rarity of a species, whatever its causes, also plays a major role in determining its value among hunters. We investigated a role for an Anthropogenic Allee effect in trophy hunting, where human attraction to rarity could lead to an over-exploitative chain reaction that could eventually drive the targeted species to extinction. We performed an inter-specific analysis of trophy prices of 202 ungulate taxa and quantified to what extent morphological characteristics and their rarity accounted for the observed variation in their price. We found that once location and body mass were accounted for, trophies of rare species attain higher prices than those of more common species. By driving trophy price increase, this rarity effect may encourage the exploitation of rare species regardless of their availability, with potentially profound consequences for populations.

Introduction

Over-exploitation of natural resources by humans is one of the main causes of the current and dramatic loss of biodiversity (Kerr & Currie, 1995; Burney & Flannery, 2005). Despite occurring worldwide and therefore constituting a common type of natural resource exploitation, trophy hunting is generally considered as a low threat for animal species (Lindsey *et al.*, 2007). In contrast to subsistence hunting, trophy hunting consists of killing few animals, for recreational purposes, both for pleasure, that is, the experience of the hunt, and in order to collect and display trophies made of horns, antlers, skulls, tusks or teeth, in a process akin to hobby collections (Milner, Nilsen & Andreassen, 2007).

Recently, there has been much debate concerning the relationship between sport hunting and conservation (Bodmer, Eisenberg & Redford, 1997; Gordon, Hester & Festa-Bianchet, 2004; Whitman *et al.*, 2004; Loveridge, Reynolds & Milner-Gulland, 2006). On the one hand, hunting is perceived as detrimental for target species for several reasons. Species affected by trophy hunting are usually large and long-lived species whose population dynamics are slow (Fowler, 1988; Owen-Smith, 1988) and typically occur at low local abundance (Damuth, 1981). Harvesting low-density populations of large mammals is likely to have a strong impact on their dynamics and viability (Bodmer *et al.*, 1997). Moreover, the current worldwide trend of increasing wealth, in particular in the Middle East, Russia and China (Dubois & Laurent, 1998; Guriev & Rachinsky, 2009), is likely to be paralleled by a growth in demand for sport hunting. Risks of population collapse are further increased by the current lack of adequate scientific data used to establish hunting quotas and the lack of enforcement of these quotas (Anderson, 2001; Whitman *et al.*, 2004; Packer *et al.*, 2009). In addition, hunters normally target large males, which are in general those that face strong sexual selection pressures, often resulting in a lower survival compared with females (Short & Balaban, 1994). Empirical evidence suggests that such a selective harvest can impact both population structure and long-term population dynamics (Milner *et al.*, 2007). Moreover, trophy hunting has also been shown to modify the behaviour of individuals and the spatial structure of populations (Davidson *et al.*, 2011). Globally, trophy hunting has been shown to be detrimental to several species (Swenson *et al.*, 1997; Caro *et al.*, 1998; Packer *et al.*, 2011). Hunting can, on the other hand, generate substantial income that, at least in part, is directed towards the conservation of hunted species and their habitats (Lewis & Alpert, 1997; Leader-Williams, 2009). For instance, trophy hunting yields around 30 million US dollars a year in Namibia and 100 million in South Africa (Lindsey, Roulet & Romanach, 2007). Furthermore, private ranches, particularly in southern

Africa, are increasingly converting from livestock and agricultural production to game animal production and the restoration of natural habitats. For example, this conversion from agricultural lands to natural habitats is what has been beneficial to white and black rhinos (Leader-Williams *et al*., 2005; Cousins, Sadler & Evans, 2008; Lindsey, Romanach & Davies-Mostert, 2009). For these reasons, the culling of a few individuals can ultimately be beneficial for the hunted population as a whole (Gunn, 2001; Loveridge *et al*., 2006).

A hitherto unsuspected factor is likely to alter these current hunt-based conservation programmes. Recent studies have shown that rare species are often perceived as having a high value, no matter the cause of their rarity (Gault, Meinard & Courchamp, 2008; Angulo & Courchamp, 2009; Angulo *et al*., 2009). Under this theory, named the Anthropogenic Allee effect (AAE hereafter), rare species should be the most valuable and attractive to hunters, and therefore be disproportionately sought after. Several wildlife-related economic markets might be driven by this relationship between rarity and economic value (Courchamp *et al*., 2006). We suggest that trophy hunting could be one of them. Obviously, rare species are the most sensitive to overexploitation and trophy hunting may precipitate their decline and exacerbate their risk of extinction. If rarity leads to a higher economic value and higher attractiveness for sport hunters, this mechanism would impose major concerns for the preservation of rare species.

In a market economy, price is most often accepted as a measure of economic value. The identification of biological and ecological factors that influence trophy price has been the subject of recent investigations (Johnson *et al*., 2010), but many aspects have not been explored. For instance, no study has yet focused on a large range of ungulates that are legally trophy hunted throughout the world. Understanding pricing is crucial to better assess the hunting threat for a given species. Inter-specific and intra-specific variations in trophy price are strongly related to its size (Festa-Bianchet, 2003). Yet, the relative contributions of body mass, trophy size, hunt location and rarity on official trophy price, and how these parameters interact, remain to be quantified.

Here, we aimed to test whether the most threatened ungulate species are also disproportionately valued by trophy hunters. We surveyed 202 ungulate taxa, recording the average body mass of males and a measure of trophy size. We also recovered information on their IUCN conservation status and geographic ranges to assess their rarity (supporting information Table S1). We collected data on trophy price for each species, as a proxy of their attractiveness. As closely related species are likely to share some phenotypic traits, we used phylogenetic generalized least squares (PGLS; Freckleton *et al*., 2002) models to assess which species characteristics (i.e. male body mass, trophy size, trophy type, distribution range location and rarity) determine trophy price and we tested for the possible occurrence of an AAE in ungulate taxa hunted for their trophies.

Methods

Data sources

Hunted species

The Safari Club International (SCI) database (available on subscription at http://www.scirecordbook.org/) provided the list of trophy hunted species. Trophies recorded since 1973 are linked to the following information: hunter, guide and measurer names, date, location, weapon and SCI trophy score. We obtained a list of 427 species and subspecies. We then focused on ungulate taxa for several reasons. First, trophy hunting is mainly focused on ungulates (88%; Baillie, Hilton-Taylor & Stuart, 2004). Second, there is a high variation in body mass, conservation status and trophy price among ungulates. Third, by focusing on ungulates only, we limited heterogeneity in the measurement of trophy size, as trophies recorded for Felidae and Ursidae families are mostly skulls.

Trophy price

To compare trophy prices, we used the ‘trophy fee’. The government decides the amount for this fee, which includes the permit for killing one animal. Interested hunting companies pay trophy fees but are then free to increase the price when they sell it to hunters, to make a profit (Booth, 2009). Hence, the price fixed by the hunting companies is determined by market rules (Kotler *et al*., 2008). Intuitively, if the fee proposed by the government is too high to interest hunters or to permit a sufficient profit margin, the hunting society will not buy it. Thus, the price of the trophy (including both fee and profit) should be adjusted to the demand. This price therefore provides an estimate of the perceived value of the trophy, regardless of the additional costs of the hunt (e.g. guide, material, accommodation), which may differ according to many factors (e.g. country, accommodation type, hunt duration). Thus, a high price should reflect a high demand for the focal species. We collected annual trophy prices from 76 hunting companies, running between 2005 and 2009. Trophy prices were missing for 135 taxa, which were consequently excluded from the analysis. We also excluded hunts in hunting reserves, such as ranches located in the USA (especially in Texas), which offer hunting for species classified as ‘extinct in the wild’ by the IUCN, because these prices were likely to differ from hunting in the natural range of these species. After these exclusions, we obtained trophy prices for 202 unique taxa.

Mean body mass

Male average body mass data were extracted from the literature (Silva & Downing, 1995; Mysterud, Pérez-Barbéria & Gordon, 2001; Bro-Jørgensen, 2007). When several sources were available, we used the median measure as the species-level body mass.

Trophy score

For each recorded hunt, trophy measurements were systematically undertaken by an official measurer, according to the SCI Official Measurer's Manual, the reference source for most hunters (116 455 trophies measured in the SCI database; Gandy & Reilly, 2004). The SCI score includes measures of trophy length, thickness and complexity (straight, spiral, volume). Hence, the score is directly proportional to the trophy size. This trophy score is denominated as 'trophy size' in the following text.

Location

Species in the SCI database are directly classified by continents or geographical regions (North America, South-Pacific). We followed this classification in our analysis using a four-level factor for location: Africa, Europe, Asia and North America. In this way, we could account for large-scale cultural or economic differences. We chose to use a continental rather than country scale because all species are not found in the same set of countries and because we could not find sufficient data at the country scale (e.g. trophy prices for widely distributed species were available for only two or three countries).

Rarity

We quantified the hunters' perception of rarity through a combination of conservation status and species distribution area. First, conservation statuses were divided into five categories following the 2008 IUCN red list (available at http://www.iucn.org/): (1) 'critically endangered'; (2) 'endangered'; (3) 'vulnerable'; (4) 'near threatened'; (5) 'least concern'. Second, to obtain distribution maps, we used both the SCI and IUCN databases because they were often different and the SCI database allowed us to include data at the subspecies level. We created geographic distribution categories for each taxon to minimize biases due to database differences (e.g. method used, date of compilation). All taxa were classified into one of seven geographic distribution categories corresponding to 200 000, 580 000, 1 700 000, 4 900 000, 14 000 000, 40 000 000 and more than 40 000 000 km^2, so that each geographic distribution category was 70% larger than the preceding category. This percentage was selected to obtain a reasonable number of categories while conserving a good level of information in the new variable. The reliability of distribution estimates was verified against the *PanTheria* trait database (Price & Gittleman, 2007). Typically, category 1 encompasses endemic taxa, whereas category 7 corresponds to taxa with a continent-wide distribution. Subsequently, we conducted a correspondence analyses (Greenacre, 1986) entering IUCN statuses and geographical distribution categories as variables. We used the scores of species on the first axis (accounting for 63% of total inertia) as a synthetic measure of rarity in the subsequent analyses, therefore reducing the number of degrees of freedom from 10 to 1.

Data analyses

Firstly, we tested three main models to assess the allometric relationship between trophy size and body mass. We first fitted a linear model, then a model including a threshold body mass (Ulm, 1989) and finally a quadratic model to explore a potentially non-linear allometric relationship between trophy size and body mass (Calder, 1984). As body mass and trophy size are positively correlated over most of the range of body mass observations due to allometric constraints (on a log scale: $R^2 = 65.4\%$, $P < 0.001$), we used the residuals of the relationship between log-transformed body mass and log-transformed trophy size (threshold model) to avoid redundant information in our subsequent analyses of trophy price. Such a relative trophy size corresponds to the trophy size corrected for the body mass (i.e. trophy size at a given body mass).

Secondly, we tested for the occurrence of a phylogenetic signal in trophy prices, because closely related taxa would yield non-independent observations. We chose a taxonomy-based tree for the signal test because phenotypic traits are the primary target of hunters. We used the Abouheif's test (Pavoine *et al.*, 2008) implemented in the ADE4 package (Dray & Dufour, 2007) of R 2.9.2 (R Development Core Team, 2009). We found that taxonomy had a marked impact on price variation among taxa ($C_{mean} = 0.42 \pm 8{,}18$; $P = 0.001$). To account for this taxonomic correlation in trophy price, we tested the effect of the explanatory variables on trophy price using PGLS models constrained by a taxonomy-based weight matrix, that is, several closely related species were each given a lower weight compared with one phylogenetically distinct species. The Grafen method (implemented in 'ape' package; Paradis, 2006) that gives a weight to each tree node to attribute branch length was used to build the weight matrix from the taxonomy of ungulate taxa.

Third, we tested for the effects of hunt location, body mass, relative trophy size, rarity index and the two-way interactions among these variables on trophy prices with PGLS models. We entered average body mass first because it is likely to be the main driver of variation in trophy price. There was no detectable correlation between body mass and rarity ($R^2 < 0.0011$). After entering both location and body mass in our model, we then entered relative trophy size and rarity to reduce the risk of detecting a spurious rarity effect that would be caused by physical characteristics. We fitted all the combinations of variables and their two-way interactions, down to a simple linear model with location as the single variable explaining price. We systematically checked the normality of model residuals, which was always acceptable. We checked each model for highly influential points using the Cook's distance and when needed we refit the model again after having excluded outliers and always found the same significant effect. We used the Akaike Information Criterion (AIC) for model selection and computed Akaike weights (AICw) to assess the relative statistical support of the fitted models (Johnson & Omland, 2004). We used the base-10 logarithm for log-transformations.

Results

Our best model indicated that trophy size is non-linearly related to body mass as suggested by AIC values of 451.7, 387.6 and 412.6 for the linear, threshold and quadratic models, respectively. Hence, the best model included a threshold body mass of 117 [92–181, 95% CI] kg below which trophy size is linearly related to body mass and above which trophy size varies among species independent of their size (Fig. 1).

The five models best accounting for the observed trophy price variation among species included location, body mass and rarity (Table 1). The model having the strongest statistical support (AICw, $w_i = 0.80$) accounted for 29.8% of the observed variation in trophy price and included the additive effects of location, body mass and rarity (supporting information Table S2). On average, trophy prices were higher in Asia and Europe than in Africa and North America (partial $R^2 = 0.12$ for this categorical variable in the best model, Table 2). Body mass accounted for most of the variation in price (partial $R^2 = 0.27$, Fig.2a).

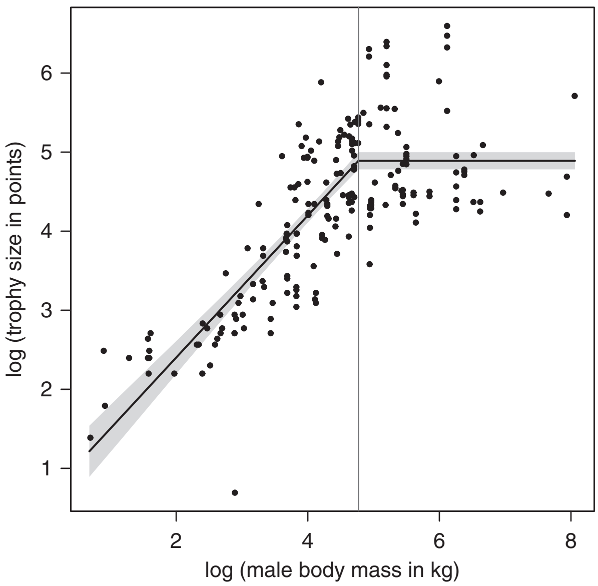

Figure 1 Allometric relationship between log-transformed body mass and log-transformed trophy size for 202 ungulate taxa. Trophy size given in points is the SCI score calculated with official measurement methods. The vertical line corresponds to the threshold body mass (at 117 kg, 95% confidence interval between 92 and 181) separating two subsets of observations according to the best regression model. Black line is the model predictions and the grey shading represents the 95% confidence limits of the predictions.

Consistent with the AAE hypothesis, trophy prices were positively correlated with the rarity index of the species, regardless of the physical characteristics (partial $R^2 = 0.14$; Fig. 2b). On average, the trophy price of the rarest taxa (with a rarity index above zero, 64 taxon) was over twice higher than the trophy price of the most common taxa (with a rarity index below zero, 128 taxon; 86 vs. 42 US$/kg of body mass).

Lastly, once the effects of location, body mass, trophy size and rarity were accounted for, we did not find any support for an effect of trophy type (i.e. *Bovidae* with lifetime growing horns, *Cervidae* with deciduous antlers, and other trophy types found in *Rhinocerotidae* and *Moschidae*) on trophy price.

Discussion

On the basis of 202 taxa, we provide the most rigorous and up to date inter-specific analysis of factors influencing trophy prices. Physical characteristics of animals are used both by hunters as cues for targeting animals and by trophy hunting societies to compare trophies. As such, they are commonly expected to be the main determinant of trophy price (Festa-Bianchet, 2003). Accordingly, we show that body mass is a strong determinant of trophy prices. Trophy size has no significant effect on trophy price.

We also found that species rarity is a strong determinant of the observed price. Indeed, the trophy price of a rare taxon is higher than that of a common one, after accounting for the effect of phylogeny, location and body mass (Fig. 2b). This result could be understood in two ways. First, because prices reflect the interaction between supply and demand in economic markets, the high prices of the rarest species seem not only to be driven solely by virtue of their lower availability but also by a genuine attractiveness to rare

Table 1 Five best phylogenetic generalized least square models of variation in trophy price

Model	ΔAIC	*k*	AICw
P*∼L + *M* + *B* + *R* + *M* × *B	**0.00**	**8**	**0.80**
P∼L + *M* + *B* + *R* + *M* × *B* + *M* × *R*	4.80	9	0.07
P∼L + *M* + *B* + *R*	5.40	9	0.05
P∼L + *M* + *B* + *R* + *M* × *B* + *B* × *R*	5.90	9	0.04
P∼L + *M* + *R*	7.40	10	0.02

Models were selected according to the Akaike Information Criterion (AIC); ΔAIC is the difference in AIC between the current and the best model, AICw is the Akaike weight (Burnham & Anderson, 2002), and each model has k parameters of freedom. The model with the best statistical support is emphasized in bold. The best fitting model accounted for a statistically significant proportion of variation in trophy price, *P*, and combined four different covariates: the location (L), the male average body mass (*M*), the relative trophy size (*B*, measured as the residuals from the regression of trophy size on body mass on the log-scale), the trophy type (T; horn, antlers or other) and rarity (*R*).

Table 2 Estimated coefficients of the best model parameters

Parameter	β	SE	CI
Intercept	2.29	0.12	[2.05; 2.53]
L-Asia	0.34	0.08	[0.19; 0.51]
L-Europe	0.41	0.12	[0.17; 0.64]
L-North America	−0.01	0.12	[−0.22; 0.25]
M	0.47	0.06	[0.36; 0.59]
R	0.12	0.02	[0.08; 0.17]

The trophy price is explained by four different covariates: the location, L (the location taken as a reference in the model is Africa), the male average body mass, *M*, the relative trophy size, *B* (measured as the residuals from the regression of trophy size on body mass on the log-scale) and rarity (*R*). For each coefficient, β is the estimate, SE is the standard error and CI is the confidence internal.

species. Rarity is a special case of wildlife-related economics: high prices induced by the reduction of availability do not lead to a decrease in the demand, as it is usually the case. Rising prices of rare species are counter-intuitively paralleled by an increase in the demand (Hall, Milner-Gulland & Courchamp, 2008). Bio-economic models predict that an AAE arises when rarity value is sufficiently strong such that market prices overcome the increasing costs of harvesting rare individuals (Hall *et al.*, 2008). In this context, the significantly higher prices of the rarest trophies suggest that there is a potential for an AAE to occur in trophy hunting. Given the fragility of these rare species, it is thus worrying to find that rarity itself provides an intrinsic value and an associated incentive for exploitation.

Alternatively, the higher trophy price for rare species may result from the need to raise more capital for the conservation of these species. The trophy fee could be set at an artificially inflated price, with the idea that hunters will pay a high price for a rare species and thereby provide a large amount of money for its preservation. This hypothesis could be supported by the fact that trophy hunters generally display an interest in conservation, but the majority are willing to hunt exotic species (Lindsey *et al.*, 2006). Unfortunately, we are currently missing data to distinguish among these competing explanations and no published material suggests that the higher rare species trophy prices we observe are driven by conservation incentives.

The recently challenged contention that economic extinction of a species' exploitation should always precede its ecological extinction, in the hypothetical situation whereby hunting is the sole threat to the species (Clark, 1990), should raise awareness for trophy hunted species. Trophy prices can be surprisingly high for the most coveted species. When quotas only allow for a small number of individuals of a

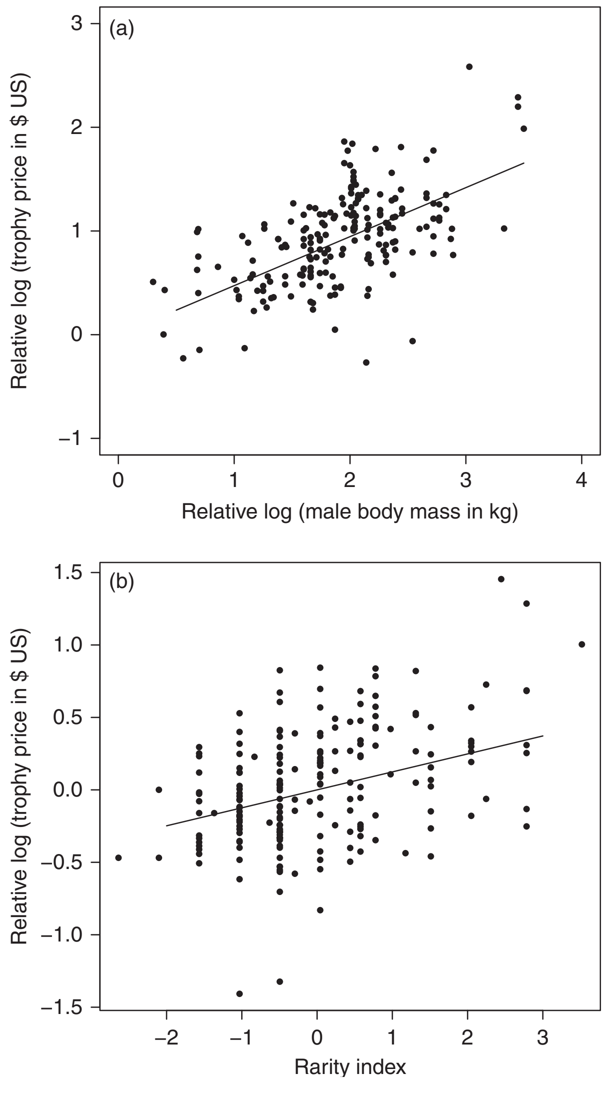

Figure 2 (a) Effect of body mass on log transformed trophy price in US $, once the effect of location has been accounted for. The black line and circles correspond to the best model predictions and observed values respectively (202 taxa). The upper point corresponds to the black rhino *Diceros bicornis*. (b) Effect of rarity on the relative trophy price (i.e. trophy price once the effects of location and body mass have been accounted for). We used the rarity index of each species (i.e. the score of the species on the first axis of the correspondence analysis conducted with IUCN statuses and geographical distribution information as variable loadings) as a continuous variable. The three upper points with high rarity scores are, from the left to the right, the Astor markhor *Capra falconeri falconeri*, the black rhino *Diceros bicornis* and the northern white hinos *Cerathoterium simum cottoni*. The two lower points are the Barren Ground muskox *Ovibos moschatus moschatus*. They should not be considered as outliers according to the Cook's distance.

species to be hunted, prices for the limited trophy fees may escalate in private auctions. For example, one single bighorn sheep *Ovis canadensis* reached over US$ 400 000 during such an auction (Festa-Bianchet, 2003). A sociological study of hunter motivation and willingness to pay high prices for trophies would be of great interest to develop our understanding of trophy pricing further and to provide conservation agencies with efficient management tools to modulate hunter's attraction for a target species.

In the context of an AAE, high hunting prices may promote a disproportionate harvest of species that are the least abundant, therefore escalating their threat of extirpation or extinction. Indeed, over-hunting and poaching are recognized by the IUCN as the primary cause of decline for 30 out of the 39 species in our database considered as threatened. For example, trophy hunting is thought to be the main threat to the endangered *Bos javanicus* in the Asian mainland (2008 IUCN red list). In other taxa, trophy hunting has also been shown as potentially dangerous for hunted populations. For example, declines of lion and leopard populations in Tanzania have recently been attributed to trophy hunting (Packer *et al.*, 2011).

Trophy hunting is a particular aspect of sport hunting and the generalization of our results to sport hunting is unclear. Trophy hunting is obviously strongly sex biased and age biased. This selective harvest is less true for sport hunting because hunters are also motivated by the desire to maximize meat yield or recreational opportunities. In addition, sport hunting mostly deals with abundant species, for which management policies aim at population control rather than conservation issues. Finally, because population control requires many hunters, hunting fees can generally not reach as high prices as those reported in trophy hunting. Overall, we do not think that the results of this analysis are transposable to sport hunting as a whole. However, these findings might be relevant for vulnerable species at a local scale that are subject to non-selective sport hunting.

If well managed, trophy hunting can be beneficial for both human communities and hunted species. Our study, however, demonstrates that rare species should be treated cautiously and as special cases. In particular, we stress that as much as 40% of the trophy-hunted ungulates are considered to be at some form of risk according to the 2008 IUCN red list. In addition, the value of rare species may be a strong incentive for illegal hunting, against which conservation remains mostly powerless. This is especially cogent in the case of AAE.

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Supplementary material

Additional Supporting Information may be found in the online version of this article:

Table S1. Data set collected for the analyses reported in the paper.

Table S2. Complete list of PGLS models fitted.

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