

Rarity, trophy hunting and ungulates

L. Palazy^{1,2}, C. Bonenfant¹, J. M. Gaillard¹ & F. Courchamp²

¹ Biométrie et Biologie Évolutive, Villeurbanne, France

² Ecologie, Systématique et Evolution, Orsay, France

Keywords

anthropogenic Allee effect; conservation; hunting management; trophy price; mammals.

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

Editor: Iain Gordon
Associate Editor: John Linnell

Received 24 January 2011;
accepted 16 May 2011

doi:10.1111/j.1469-1795.2011.00476.x

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 wild-life-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 sub-species. 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-Barbérica & 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 km², 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 ($C_{\text{mean}} = 0.42 \pm 8.18$; $P = 0.001$). 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

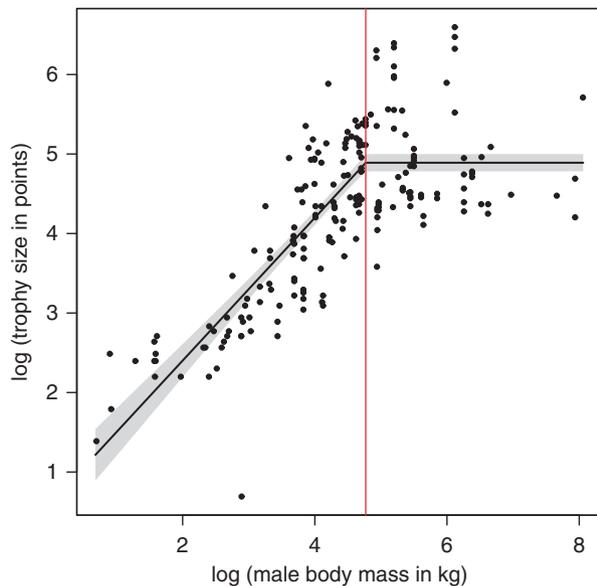


Figure 1 Allometric relationship between log-transformed body mass and log-transformed trophy size for 202 ungulate taxa. Trophy size given in points is the SCI score calculated with official measurement methods. The vertical line corresponds to the threshold body mass (at 117 kg, 95% confidence interval 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.

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).

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	Δ AIC	k	AICw
$P \sim L + M + B + R + M \times B$	0.00	8	0.80
$P \sim L + M + B + R + M \times B + M \times R$	4.80	9	0.07
$P \sim L + M + B + R$	5.40	9	0.05
$P \sim L + M + B + R + M \times B + B \times R$	5.90	9	0.04
$P \sim L + M + R$	7.40	10	0.02

Models were selected according to the Akaike Information Criterion (AIC); Δ AIC 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]
<i>M</i>	0.47	0.06	[0.36; 0.59]
<i>R</i>	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 interval.

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

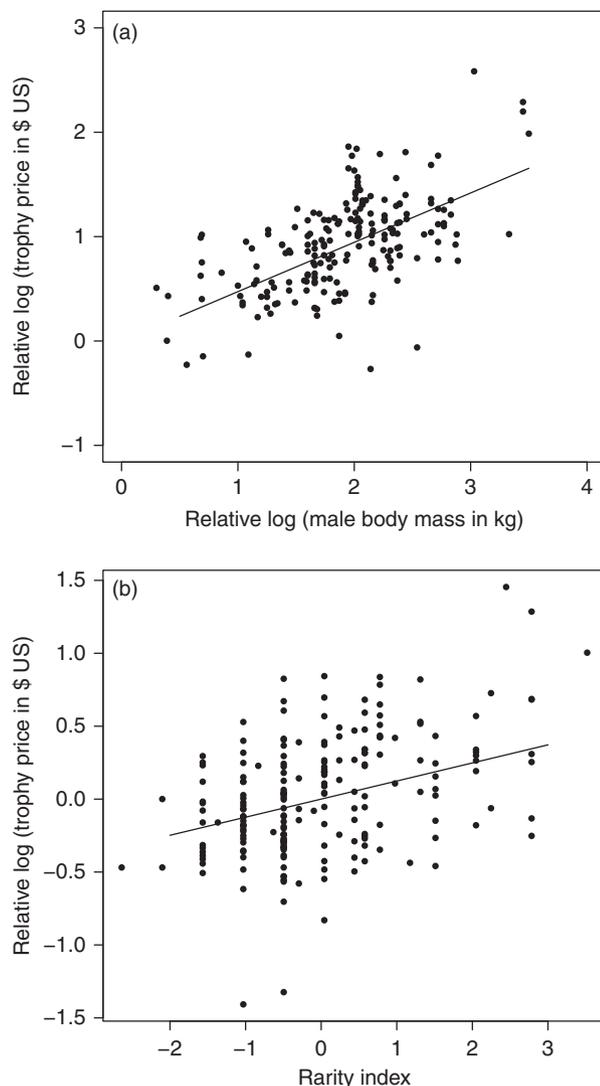


Figure 2 (a) Effect of body mass on log-transformed trophy price in US \$, once the effect of locations has been accounted for. The black line and circles correspond to the best model predictions and observed values, (202 taxa) respectively the Central Canadian Barron Ground caribou *Rangifer tarandus groenlandicus* and the upper point corresponds to the black. (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 rhino *Ceratotherium 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.

Acknowledgements

We are grateful to M. S. Boyce, M. Festa-Bianchet, E.J. Milner-Gulland, S. Gregory and A. Mysterud for their comments. We thank also L. Boitani and C. Rondinini for providing us the IUCN updates before their publication. We acknowledge the financial support from the Agence Nationale de la Recherche, project 'RARE' (ANR-09-PEXT).

The funders had no role in study design, data collection and analysis, decision to publish or preparation of the manuscript.

References

- Anderson, D.R. (2001). The need to get the basics right in wildlife field studies. *Wildl. Soc. Bull.* **29**, 1294–1297.
- Angulo, E. & Courchamp, F. (2009). Rare species are valued big time. *PLoS One* **4**, 1–5.
- Angulo, E., Deves, A.L., Saint Jalmes, M. & Courchamp, F. (2009). Fatal attraction: rare species in the spotlight. *Proc. R. Soc. B* **276**, 1331–1337.
- Baillie, J.E.M., Hilton-Taylor, C. & Stuart, S.N. (2004). *2004 IUCN red list of threatened species: a global species assessment*. Cambridge: IUCN Publication Services Unit.
- Bodmer, R.E., Eisenberg, J.F. & Redford, K.H. (1997). Hunting and the likelihood of extinction of Amazonian mammals. *Conserv. Biol.* **11**, 460–466.
- Booth, V.R. (2009). A comparison of the prices of hunting tourism in southern and eastern Africa. *CIC Tech. Ser. Pub.* **7**, 40.
- Bro-Jørgensen, J. (2007). The intensity of sexual selection predicts weapon size in male bovids. *Evolution* **61**, 1316–1326.
- Burney, D.A. & Flannery, T.F. (2005). Fifty millennia of catastrophic extinctions after human contact. *Trends Ecol. Evol.* **20**, 395–401.
- Burnham, K.P. & Anderson, D.R. (2002). *Model selection and multimodel inference: a practical information-theoretic approach*. 2nd edn. New York: Springer-Verlag.
- Calder, W.A. (1984). *Size, fonction and life history*. Cambridge: Dover Publication Inc.
- Caro, T.M., Pelkey, N., Borner, M., Severre, E.L., Campbell, K.L., Huish, S.A., Ole Kuwai, J., Farm, J.P. & Woodworth, J.L. (1998). The impact of tourist hunting on large mammals in Tanzania: an initial assessment. *J. Anim. Eco.* **36**, 321–346.
- Clark, C.W. (1990). *Mathematical bioeconomics – optimal management of renewable resources*. 2nd edn. New York: Wiley-Interscience.
- Courchamp, F., Angulo, E., Rivalan, P., Hall, R.J., Signoret, L., Bull, L. & Meinard, Y. (2006). Rarity value and species extinction: the anthropogenic Allee effect. *PLoS Biol.* **4**, 2405–2410.
- Cousins, J.A., Sadler, J.P. & Evans, J. (2008). Exploring the role of private wildlife ranching as a conservation tool in South Africa: stakeholder perspectives. *Ecol. Soc.* **13**, 43.
- Damuth, J. (1981). Population-density and body size in mammals. *Nature* **290**, 699–700.
- Davidson, Z., Valeix, M., Loveridge, A.J., Madzikanda, H. & Macdonald, D.W. (2011). Socio-spatial behaviour of an African lion population following perturbation by sport hunting. *Biol. Conserv.* **144**, 114–121.
- Dray, S. & Dufour, A.B. (2007). The ade4 package: implementing the duality diagram for ecologists. *J. Stat. Soft.* **22**, 1–20.

- Dubois, B. & Laurent, G. (1998). The new age of luxury living. *Financ. Times Mastering Mgmt. Rev.* **437**, 32–35.
- Festa-Bianchet, M. (2003). Exploitative wildlife management as a selective pressure for life-history evolution of large mammals. In *Animal behavior and wildlife conservation*: 191–207. Festa-Bianchet, M. & Apollonio, M. (Eds). Washington, DC: Island Press.
- Fowler, C.W. (1988). Population-dynamics as related to rate of increase per generation. *Evol. Ecol.* **2**, 197–204.
- Freckleton, R.P., Harvey, P.H. & Pagel, M. (2002). Phylogenetic analysis and comparative data: a test and review of evidence. *Am Nat.* **160**, 712–726.
- Gandy, S.E. & Reilly, B.K. (2004). Alternative trophy measuring techniques for African buffalo. *Koedoe* **47**, 119–124.
- Gault, A., Meinard, Y. & Courchamp, F. (2008). Consumers' taste for rarity drives sturgeons to extinction. *Conserv. Lett.* **1**, 199–207.
- Gordon, I.J., Hester, A.J. & Festa-Bianchet, M. (2004). The management of wild large herbivores to meet economic, conservation and environmental objectives. *J. Appl. Ecol.* **41**, 1021–1031.
- Greenacre, M. (1986). *Theory and applications of correspondence analysis*. London: Academic Press.
- Gunn, A.S. (2001). Environmental ethics and trophy hunting. *Ethics Environ.* **6**, 68–95.
- Guriev, S. & Rachinsky, A. (2009). The Evolution of personal wealth in the former Soviet Union and central and eastern Europe. In *Personal wealth from a global perspective*: 134–149. Press, O.U. (Ed.). Helsinki: UNU-WIDER research paper.
- Hall, R.J., Milner-Gulland, E.J. & Courchamp, F. (2008). Endangering the endangered: the effects of perceived rarity on species exploitation. *Conserv. Lett.* **1**, 75–81.
- Johnson, J.B. & Omland, K.S. (2004). Model selection in ecology and evolution. *Trends Ecol. Evol.* **19**, 101–108.
- Johnson, P.J., Kansky, R., Loveridge, A.J. & MacDonald, D.W. (2010). Size, rarity and charisma: valuing African wildlife trophies. *PLoS One* **5**, 1–9.
- Kerr, J.T. & Currie, D.J. (1995). Effects of human activity on global extinction risk. *Conserv. Biol.* **9**, 1528–1538.
- Kotler, P., Armstrong, G., Wong, V. & Saunders, J.A. (2008). *Principles of marketing*. 5th Revised edition edn. London: Pitman publishing.
- Leader-Williams, N. (2009). Conservation and hunting: friends or foes? In: *Recreational hunting, conservation, and rural livelihoods*: 9–24. Dickson, B., Hutton, J. & Adams, W.M. (Eds). London: Wiley-Blackwell.
- Leader-Williams, N., Milledge, S., Adcock, K., Brooks, M., Conway, A., Knight, M., Mainka, S., Martin, E.B. & Teferi, T. (2005). Trophy hunting of Black Rhinos *Diceros bicornis*: proposals to ensure its future sustainability. *J. Int. Wildl. Law Policy* **8**, 1–11.
- Lewis, D.M. & Alpert, P. (1997). Trophy hunting and wildlife conservation in Zambia. *Conserv. Biol.* **11**, 59–68.
- Lindsey, P.A., Alexander, R., Frank, L.G., Mathieson, A. & Romañach, S.S. (2006). Potential of trophy hunting to create incentives for wildlife conservation in Africa where alternative wildlife-based land uses may not be viable. *Anim. Conserv.* **9**, 283–291.
- Lindsey, P.A., Frank, L.G., Alexander, R., Mathieson, A. & Romanach, S.S. (2007). Trophy hunting and conservation in Africa: problems and one potential solution. *Conserv. Biol.* **21**, 880–883.
- Lindsey, P.A., Romanach, S.S. & Davies-Mostert, H.T. (2009). The importance of conservancies for enhancing the value of game ranch land for large mammal conservation in southern Africa. *J. Zool. (Lond.)* **277**, 99–105.
- Lindsey, P.A., Roulet, P.A. & Romanach, S.S. (2007). Economic and conservation significance of the trophy hunting industry in sub-Saharan Africa. *Biol. Conserv.* **134**, 455–469.
- Loveridge, A.J., Reynolds, J.C. & Milner-Gulland, E.J. (2006). Does sport hunting benefit conservation? In *Key topics in conservation biology*: 224–240. Macdonald, D.W. & Service, K. (Eds). Oxford: Blackwell.
- Milner, J.M., Nilsen, E.B. & Andreassen, H.P. (2007). Demographic side effects of selective hunting in ungulates and carnivores. *Conserv. Biol.* **21**, 36–47.
- Mysterud, A., Pérez-Barbérica, F.J. & Gordon, I.J. (2001). The effect of season, sex and feeding style on home range area versus body mass scaling in temperate ruminants. *Oecologia* **127**, 30–39.
- Owen-Smith, R.N. (1988). *Mega-herbivores: the influence of very large body size on ecology*. Cambridge: University Press.
- Packer, C., Brink, H., Kissui, B.M., Maliti, H., Kushnir, H. & Caro, T. (2011). Effects of trophy hunting on lion and leopard populations in Tanzania. *Conserv. Biol.* **25**, 142–153.
- Packer, C., Kosmala, M., Cooley, H.S., Brink, H., Pintea, L., Garshelis, D., Purchase, G., Strauss, M., Swanson, A., Balme, G., Hunter, L. & Nowell, K. (2009). Sport hunting, predator control and conservation of large carnivores. *PLoS One* **4**, 1–8.
- Paradis, E. (2006). *Analysis of phylogenetics and evolution with R*. New York: Springer.
- Pavoine, S., Ollier, S., Pontier, D. & Chessel, D. (2008). Testing for phylogenetic signal in phenotypic traits: new matrices of phylogenetic proximities. *Theor. Popul. Biol.* **73**, 79–91.
- Price, S.A. & Gittleman, J.L. (2007). Hunting to extinction: biology and regional economy influence extinction risk and the impact of hunting on artiodactyls. *Proc. R. Soc. B* **274**, 1845–1851.
- R Development Core Team (2009). *R: A language and environment for statistical computing ISBN 3-900051-07-0*. Vienna: R Development Core Team.
- Short, R.V. & Balaban, E. (1994). *The differences between the sexes*. Cambridge: Cambridge University Press.
- Silva, M. & Downing, J.A. (1995). *CRC handbook of mammalian body masses*. Boca Raton: CRC Press.
- Swenson, J.E., Sandegren, F., Soderberg, A., Bjarvall, A., Franzen, R. & Wabakken, P. (1997). Infanticide caused by hunting of male bears. *Nature* **386**, 450–451.

Ulm, K. (1989). On the estimation of threshold values. *Biometrics* **45**, 1324–1326.

Whitman, K., Starfield, A.M., Quadling, H.S. & Packer, C. (2004). Sustainable trophy hunting of African lions. *Nature* **428**, 175–178.

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.

As a service to our authors and readers, this journal provides supporting information supplied by the authors. Such materials are peer-reviewed and may be re-organized for online delivery, but are not copy-edited or typeset. Technical support issues arising from supporting information (other than missing files) should be addressed to the authors.

COMMENTARY

Rarity, willingness to pay and conservation

M. Festa-Bianchet

Département de Biologie, Université de Sherbrooke, Sherbrooke, QC, Canada

Correspondence

Marco Festa-Bianchet, Département de Biologie, Université de Sherbrooke, Sherbrooke, QC, Canada, J1K 2R1

Email: m.festa@Usherbrooke.ca

doi:10.1111/j.1469-1795.2011.00518.x

In standard economic theory, the price of goods, whether low-fat hamburgers or trophy sheep, is expected to rise when demand increases or supply diminishes. Standard economic theory also assumes that consumers act rationally, but that is another story. All else being equal, rare things tend to be dearer than common things and in some cases, rarity increases value. Conservation biology usually sees rarity as a problem. Rare species, especially at small population size, tend to have higher risk of extinction than common species. When species become rare because of human actions, community ecology may be altered and ecosystem services may diminish. For example, if a sport-hunted species becomes rare, fewer individuals can be sustainably harvested. If some people have a certain willingness to pay to harvest that species, and prices are set by markets, the lower supply should lead to an increase in price. Within this framework, Palazy *et al.* (2012) seek to understand whether rarity may lead to an anthropogenic Allee effect (Courchamp *et al.*, 2006) in the special case of trophy-hunted species. They find that once other variables are controlled for, rarity does tend to increase the cost of trophy hunts, although the effect is rather weak. That result raises two questions: (1) Is this a problem? and (2) What motivates people to hunt endangered species?

The relationship between rarity and willingness to pay for a trophy hunt is not necessarily a problem for conservation. First, let us agree on what we are talking about. This is not a case of rich people wanting to kill pandas, Arabian oryx or Sumatran rhinos. It is a case of people willing to spend more to legally kill a markhor than an ibex, a grizzly than a black bear or a sable antelope than a wildebeest. As long as quotas are ecologically and evolutionarily sustainable, trophy hunting can be a part of a conservation strategy for some endangered species, if some of the funds generated are actually used to protect the species or its habitat (Leader-Williams, Smith & Walpole, 2001). Herein lies a problem: many hunts are trumpeted as 'Conservation Hunting' (Freeman & Wenzel, 2006), but few are. Most trophy hunts of ungulates are sustainable and produce revenues for the guiding industry, but their impact on conservation (if any) is not necessarily positive. One notable

exception is the markhor hunting program in the Torghar area of Pakistan, a species which, interestingly, is largely responsible for the positive effect of rarity on price in the paper by Palazy *et al.* When the rarity–price relationship leads to poaching or corruption in the issue of hunting permits, then we clearly have a real problem, but that is neither the subject of this discussion nor an issue on which Palazy *et al.* provide information. I suggest that a much more deleterious effect of rarity on conservation may be found in luxury goods derived from wildlife, such as certain foods (tuna, shark fins and turtle eggs come to mind) or status symbols (shatoosh, ivory and horned beetles are likely candidates).

If quotas are reduced to account for rarity, and price is determined by supply and demand, rarity should lead to higher trophy fees. The best way to maximize profit would be an auction, with permits sold to those with the highest willingness to pay. Auctions of trophy hunts can be spectacularly successful (Festa-Bianchet, 2003), but are rare. Trophy fees may have a weak relationship with demand because governments have a monopoly and may set fees artificially low. Most profits go to guiding companies, whose willingness to reinvest in conservation would be an interesting area of research. Palazy *et al.* (2012) suggest that high trophy fees are evidence of high demand. As fees increase, however, fewer trophy hunters can afford them. Many hunters can spare \$7000–10 000 to hunt an Asiatic ibex, but very few would even consider spending \$30 000–50 000 to hunt an argali. High fees may be also driven by lower supply. The data used in this paper are weakly related to the actual cost to the hunter, because government-imposed trophy fees are typically a fraction of what hunters pay. For example in Canada, nonresident permits for trophy sheep are typically a few hundred dollars, but guiding fees are in the tens of thousands. In much of Europe, fees vary according to the size of the horns or antlers of the animal taken. Cultural, political and administrative differences between countries make it very difficult to compare the costs of trophy hunts for different species. The method used by Palazy *et al.* is an acceptable first approximation, but a more detailed economic analysis of the amounts that trophy

hunters spend according to rarity and other factors is warranted.

Perhaps the most important question for conservation is the motivation of trophy hunters. We may seek to discourage this activity if it was detrimental to conservation, similarly to efforts to reduce overexploitation of several marine species, or species used in luxury markets, by publicizing the conservation consequences of overharvest and the availability of alternative products. In the battle for public opinion to affect consumer choices, trophy hunting is a powerful tool: most people hate it, much more than they may dislike other forms of hunting. A picture of an overweight middle-aged white guy sitting on a bloody dead bear will attract a lot more attention, emotion and donations than yet another report on fish overharvest or on habitat destruction. On the other hand, to include trophy hunting as part of a conservation strategy (Leader-Williams *et al.*, 2001), we may want to know why anyone would willingly part with a small fortune to kill a goat. Marketing may have a stronger effect than rarity on the cost of a hunt. Many conservationists are aware that hunting within pristine habitat, seeing wildlife and contributing to conservation can be powerful motivators for many hunters. Others may want to exploit the picture of the bloodied bear, as effectively done by animal rights groups. So far, commercial interests, rather than conservationists, have most effectively used marketing to extract money from hunters. Emphasis on the competitive, 'mine is bigger than yours' aspect of trophy hunting has spawned the offer of 'products' such as artificially fed animals with large 'trophies', hybrid oddities marketed as novelty items and canned 'hunts' of semi-captive animals (Knox, 2011). Search 'Texas dall' on Google to see some successful marketing. Negative consequences for conservation include the introduction of exotics, genetic pollution, disease transmission and predator extirpation. These practices also reinforce the negative perception of hunters by much of the public, and make it harder to use trophy hunting as a conservation tool. It is difficult and controversial to support killing animals to promote conservation (Lindsey *et al.*, 2006). The paper by Palazy *et al.* underlines

the need to clarify what 'conservation hunting' really means. It cannot simply mean 'sustainable'; it must involve measurable and transparent benefits to conservation.

Acknowledgments

I thank Wendy King and Rich Harris for comments. My research on wildlife evolutionary ecology and conservation is supported by the Natural Sciences and Engineering Research Council of Canada.

References

- Courchamp, F., Angulo, E., Rivalan, P., Hall, R.J., Signoret, L., Bull, L. & Meinard, Y. (2006). Rarity value and species extinction: the anthropogenic Allee effect. *PLoS Biol.* **4**, 1–6.
- Festa-Bianchet, M. (2003). Exploitative wildlife management as a selective pressure for the life-history evolution of large mammals. In *Animal behavior and wildlife conservation*: 191–207. Festa-Bianchet, M. & Apollonio, M. (Eds). Washington: Island Press.
- Freeman, M.M.R. & Wenzel, G.W. (2006). The nature and significance of polar bear conservation hunting in the Canadian Arctic. *Arctic* **59**, 21–30.
- Knox, W.M. (2011). The antler religion. *Wildl. Soc. Bull.* **35**, 45–48.
- Leader-Williams, N., Smith, R.J. & Walpole, M.J. (2001). Elephant hunting and conservation. *Science* **293**, 2203.
- Lindsey, P.A., Alexander, R., Frank, L.G., Mathieson, A. & Romanach, S.S. (2006). Potential of trophy hunting to create incentives for wildlife conservation in Africa where alternative wildlife-based land uses may not be viable. *Anim. Conserv.* **9**, 283–291.
- Palazy, L., Bonenfant, C., Gaillard, J.M. & Courchamp, F. (2012). Rarity, trophy hunting and ungulates. *Anim. Conserv.* **15**, 4–11.

COMMENTARY

Trophy hunting with uncertain role for population dynamics and extinction of ungulates

A. Mysterud

Centre for Ecological and Evolutionary Synthesis (CEES), Department of Biology, University of Oslo, Oslo, Norway

Correspondence

Atle Mysterud, Centre for Ecological and Evolutionary Synthesis (CEES), Department of Biology, University of Oslo, PO Box 1066 Blindern, NO-0316 Oslo, Norway

Email: atle.mysterud@bio.uio.no

doi:10.1111/j.1469-1795.2011.00519.x

Many species of large mammals are threatened. Overexploitation is involved as a driver for population declines in many cases, and understanding the mechanisms provides a key to mitigative efforts. The population dynamic effects of harvesting vary considerably not only due to differences in hunting pressure, but also due to variable selectivity. Hunters aiming for meat, recreation, trophies or population control will target different kind of individuals (Mysterud, 2011), and different sex and age classes have largely variable contribution to population growth. Understanding the motivation for harvest is thus a key point, and the study by Palazy *et al.* (2012) is a major step forward to understand what is the motivation of trophy hunters at the interspecific level.

Palazy *et al.* (2012) analyse a huge dataset on trophy fees of 427 ungulate species. The important insight yielded is how pricing of trophies varies as a function of animal traits, both morphological and in terms of rarity. The analysis is sophisticated, so there is no reason to doubt the patterns reported. Palazy *et al.* (2012) further suggest that trophy hunters' attraction for rarity could lead to an 'overexploitation chain reaction', being a mechanism for an anthropogenic Allee effect (AAE). This claim appears more speculative. Palazy *et al.* (2012) claim that 'Globally, trophy hunting has been shown to be detrimental to several species'. However, the three references provided give no clear evidence that ungulates in general are negatively affected by trophy hunting. For example, one case is the brown bear (*Ursus arctos*) from Scandinavia documenting that removal of a dominant male represent a risk of increased infanticide by immigrating males (Swenson *et al.*, 1997). However, this is not typical trophy hunting, as the hunters are not selective (Bischof *et al.*, 2009). Even with this infanticide mechanism present, this brown bear population has among the highest growth rates recorded worldwide, suggesting sustainable harvesting.

When is trophy harvesting likely to cause an AAE? Key questions for the argument of AAE is what demographic class of animal is the target of hunting, what is the mating

system and what happens to the conception of a trophy when animals get rare.

(1) In general, prime-aged males from the most sexually dimorphic species appear the typical target of trophy hunting. There is a clear link between large sexual body size dimorphism, male size and the level of polygyny in ungulates (Loison *et al.*, 1999). With high levels of polygyny, male-biased harvesting must be intense before females are not inseminated, and often younger males take over as sires (Mysterud, Coulson & Stenseth, 2002). Indeed, despite extremely skewed sex ratios in many populations of deer, the main problems are often those related to overabundance (McShea & Underwood, 1997). The single documented case in which a skew in sex ratio has caused severe population decline is for the saiga antelope (*Saiga tataricus*), when the proportion of adult males reached < 2% of the population (Milner-Gulland *et al.*, 2003). For saiga, medicinal use was the main motivation for hunting, not trophies. One may also argue that trophy hunters target the most viable males, but the link between survival and trophy size is weak at best (Bonenfant *et al.*, 2009). We would, however, expect stronger effects of harvesting males in general for monogamous species (Parker, Rosell & Mysterud, 2007). These species, however, have lower trophy prices in ungulates (Palazy *et al.*, 2012).

(2) Females may be a target for trophy hunters if sexual body size dimorphism is small or other secondary sexual characters are absent, this will largely increase the population dynamic effect of trophy hunting. For Bovids, for example in oryx (*Oryx gazella*) and eland (*Taurotragus oryx*), female horns are often also valued by trophy hunters being longer (though thinner) than male horns. Indeed, the best case of unsustainable sport hunting reported by Caro *et al.* (1998) was for eland. If trophy hunting was driving extinction in cases where females possess horns, we would expect a different effect in Cervids and Bovids, as female Cervids do not possess antlers (apart from reindeer). Palazy *et al.* (2012) report no difference in pricing between Cervids and Bovids, and pricing increased rather than decreased

with male size. However, such factors may explain why the two case studies of detrimental trophy hunting come from carnivores having less marked sexual dimorphism and often a different mating system (Caro *et al.*, 1998; Packer *et al.*, 2011).

(3) Lastly, trophy hunting could cause an AAE if trophy hunters stop being picky on size (or sex) when animals get rare, if *any* trophy will increase in value for rare species. If so, the following can be predicted: for rare species, within species variance in trophy pricing is small ('any trophy from a rare species would do'). For common species, variance in trophy pricing is high ('extreme value to the largest'), as there is much to choose from, and because all trophy hunters know the scale – realizing this one is a big individual.

Clearly, Palazy *et al.* (2012) provide one major step forward in understanding pricing of trophies among species. Hopefully, they will continue their important work to understand the variation of prices also within species, and to provide explicit links to population dynamics.

References

- Bischof, R., Swenson, J.E., Yoccoz, N.G., Mysterud, A. & Gimenez, O. (2009). The magnitude and selectivity of natural and multiple anthropogenic mortality causes in hunted brown bears. *J. Anim. Ecol.* **78**, 656–665.
- Bonenfant, C., Pelletier, C., Garel, M. & Bergeron, P. (2009). Age-dependent relationship between horn growth and survival in wild sheep. *J. Anim. Ecol.* **78**, 161–171.
- Caro, T.M., Pelkey, N., Borner, M., Severre, E.L.M., Campbell, K.L.I., Huish, S.A., Kuwai, J.O., Farm, B.P. & Woodworth, B.L. (1998). The impact of tourist hunting on large mammals in Tanzania: an initial assessment. *Afr. J. Ecol.* **36**, 321–346.
- Loison, A., Gaillard, J.-M., Pélabon, C. & Yoccoz, N.G. (1999). What factors shape sexual size dimorphism in ungulates? *Evol. Ecol. Res.* **1**, 611–633.
- McShea, W.J. & Underwood, H.B. (1997). *The science of overabundance. Deer ecology and population management*. Washington, DC: Smithsonian Institution Press.
- Milner-Gulland, E.J., Bukreeva, O.M., Coulson, T., Lushchekina, A.A., Kholodova, M.V., Bekenov, A.B. & Grachev, I.A. (2003). Reproductive collapse in saiga antelope harems. *Nature* **422**, 135.
- Mysterud, A. (2011). Selective harvesting of large mammals: how often does it result in directional selection? *J. Appl. Ecol.* **48**, 827–834.
- Mysterud, A., Coulson, T. & Stenseth, N.C. (2002). The role of males in the population dynamics of ungulates. *J. Anim. Ecol.* **71**, 907–915.
- Packer, C., Brink, H., Kissui, B.M., Maliti, H., Kushnir, H. & Caro, T. (2011). Effects of trophy hunting on lion and leopard populations in Tanzania. *Conserv. Biol.* **25**, 142–153.
- Palazy, L., Bonenfant, C., Gaillard, J.-M. & Courchamp, F. (2012). Rarity, trophy hunting and ungulates. *Anim. Conserv.* **15**, 4–11.
- Parker, H., Rosell, F. & Mysterud, A. (2007). Harvesting of males delays female breeding in a socially monogamous mammal; the beaver. *Biol. Lett.* **3**, 106–108.
- Swenson, J.E., Sandegren, F., Söderberg, A., Bjärvall, A., Franzén, R. & Wabakken, P. (1997). Infanticide caused by hunting of male bears. *Nature* **386**, 450–451.

RESPONSE

Response: rarity, trophy hunting and ungulatesL. Palazy^{1,2}, C. Bonenfant¹, J. M. Gaillard¹ & F. Courchamp²

1 Biométrie et Biologie Évolutive, Villeurbanne, France

2 Ecologie, Systématique et Evolution, Orsay, France

Correspondence

Lucille Palazy, Biométrie et Biologie Evolutive, UMR-CNRS 5558, Univ Lyon 1, 69622 Villeurbanne, France

Email: lucille.palazy@u-psud.fr

doi:10.1111/j.1469-1795.2012.00521.x

Trophy hunting has become a particularly burning issue since the emergence of its possible use as a conservation tool. For trophy hunting-based conservation programmes to be sustainable, there is a need to (1) understand how trophy hunting works economically and socially, and (2) assess any potential threats to the conservation of the species that are being exploited.

In Palazy *et al.* (2012), we showed that trophy hunters attribute a higher value to rare species. This valuation of rarity could lead to increased exploitation (driven by demand and the economic return to the communities), in turn leading to even further rarity, and so on. This process, called the anthropogenic Allee effect (AAE; Courchamp *et al.*, 2006), represents a potential threat which should be taken into account when setting up trophy hunting management schemes.

While it is true that species' extinction due to trophy hunting has never been reported, as stated in Mysterud's (2012) commentary, there are documented cases of unsustainable trophy hunting. Among the most topical examples is the decline of the lion (*Panthera leo*) and cheetah (*Acinonyx jubatus*) populations because of trophy hunting (Whitman *et al.*, 2004; Packer *et al.*, 2009, 2011). It is also the case that we still lack clear evidence that populations of ungulates in particular are pushed towards extinction by trophy hunting; however, there are clear examples of unsustainable exploitation related to male hunting in eland *Taurotragus oryx*, sable antelope *Hippotragus niger* and reedbeek *Redunca arundinum* (Caro *et al.*, 1998, 2009). That some species benefit from trophy hunting, such as the Markhor *Capra falconeri* pointed out by Festa-Bianchet (2012), is very encouraging; however, individual cases should not mask how uncommon such situations are, nor understate the threat that trophy hunting can represent when exemplary management is not achieved.

Our claim in Palazy *et al.* (2012) is not that trophy hunting cannot be sustainable, but rather that the irrational value put on rare species can jeopardize the good management of rare species for conservation. Other studies have provided evidence of the valuation of rarity in trophy

hunting and the relationship between trophy prices and demand: for example, a recent study assessing the valuation of African species hunted for their trophies showed that rarity was an important factor (Johnson *et al.*, 2010). Upgrading the International Union for Conservation of Nature status (increasingly threatened) of the trophy species has been linked to an increase in trophy prices related to a higher demand in African bovids (Prescott *et al.*, 2011) and other taxonomic groups (Palazy *et al.*, unpubl. data). Lastly, an unexpected positive correlation between protection status and hunting pressure has also been found in trophy-hunted felid species (Palazy *et al.*, 2011); trophy hunting of lions, panthers (*Panthera pardus*), pumas (*Puma concolor*) and cheetahs increased despite worrying declines in their populations. Beyond this evidence, we totally agree with Festa-Bianchet (2012) that trophy hunting is not the only wildlife-based economic market that can trigger an AAE. In fact, we have already highlighted this process, for instance in luxury goods, ecotourism and animal collections (Gault, Meinard & Courchamp, 2008; Hall, Milner-Gulland & Courchamp, 2008).

We also agree with Mysterud (2012) that rarity may not be the sole characteristic motivating trophy hunters. Size does matter and always will, especially given the existence of record books for hunting trophies. Rarity cannot and should not be considered as the sole motivator for trophy hunters. However, when rarity per se is valued along with other species characteristics, then there is a risk of racing for the remaining trophy animals and any risk should be given proper, case-by-case, consideration. In Palazy *et al.* (2012), we showed that trophy hunters would pay high sums of money to hunt rare species, regardless of the trophy size. This is supported by the general absence of price variation according to trophy size for rare species as compared with a positive relationship in common species in the trophy price lists proposed on hunting tourist operator websites. In our analyses, the effect of species' rarity on the trophy price is obvious despite its lower effect as compared with body mass. With an R^2 of more than 10%, the effect of rarity cannot be considered to be weak. When removing the

Markhor from the model, which as suggested by Festa-Bianchet (2012) could have a strong influence on the pattern we reported, the effect of rarity retains an explanatory power more than 10% (R^2 of 11.2 vs. 12.7, Edwards *et al.*, 2008). In the database, six other 'rare' species (excluding rhino species) with a trophy size below the average are priced above US\$10 000.

Lastly, as noted by Festa-Bianchet (2012), while it is true that increased fees will put the rare trophies out of reach of the vast majority of hunters, it is however unlikely to have a bearing on the AAE. The important question should be how many of the most wealthy hunters are willing to pay to hunt those rare individuals. When some species are reduced to a few hundred individuals, even small hunting pressure applied by a few wealthiest hunters might be sufficient to endanger them. In addition, although we generally agree with Festa-Bianchet's (2012) comments, we do not believe that the AAE we discussed in Palazy *et al.* (2012) is restricted to legal hunting. On the contrary, if rarity is disproportionately valued, and quotas of legal harvesting are lower than the demand, there is an increased risk of illegal hunting to meet the demand (Clayton *et al.*, 2000; Bulte & Damania, 2005; Hall *et al.*, 2008; Palazy *et al.*, 2011). Illegal hunting generally escapes direct management policies of trophy hunting, thus we urge managers to include our AAE results when setting management plans for rare species.

The AAE is a feedback loop that precipitates the decline in the population sizes of rare species towards extinction. As such, the AAE is difficult to demonstrate in living species, as it relies on the availability of ecological and economical data on an exploited species that is often plummeting towards extinction or has already disappeared. When empirical data are not available, one need to be aware of the possibility of an AAE in an economic market based on wildlife trade and insure that it will be avoided. For this reason, we strongly agree with Festa-Bianchet (2012) that understanding the motivations of trophy hunters is key to circumvent AAEs and implement the most sustainable management. We are currently working on this topic and hope to provide yet another step towards a better understanding of the relationships between trophy hunting and conservation biology.

References

- Bulte, E.H. & Damania, R. (2005). An economic assessment of wildlife farming and conservation. *Conserv. Biol.* **19**, 1222–1233.
- Caro, T.M., Pelkey, N., Borner, M., Severre, E.L., Campbell, K.L., Huih, S.A., Ole Kuwai, J., Farm, J.P. & Woodworth, J.L. (1998). The impact of tourist hunting on large mammals in Tanzania: an initial assessment. *Afr. J. Ecol.* **36**, 321–346.
- Caro, T.M., Young, C.R., Cauldwell, A.E. & Brown, D.D.E. (2009). Animal breeding systems and big game hunting: models and application. *Conserv. Biol.* **142**, 909–929.
- Clayton, L.M., Milner-Gulland, E.J., Sinaga, D.W. & Mustari, A.H. (2000). Effects of a proposed ex situ conservation program on in situ conservation of the babirusa, an endangered suid. *Conserv. Biol.* **14**, 382–385.
- Courchamp, F., Angulo, E., Rivalan, P., Hall, R.J., Signoret, L., Bull, L. & Meinard, Y. (2006). Rarity value and species extinction: the anthropogenic Allee effect. *PLoS Biol.* **4**, 2405–2410.
- Edwards, L.J., Muller, K.E., Wolfinger, R.D., Qaqish, B.F. & Schabenberger, O. (2008). An R^2 statistic for fixed effects in the linear mixed model. *Statist. Med.* **27**, 6137–6157.
- Festa-Bianchet, M. (2012). Rarity, willingness to pay and conservation. *Anim. Conserv.* **15**, 12–13.
- Gault, A., Meinard, Y. & Courchamp, F. (2008). Consumers' taste for rarity drives sturgeons to extinction. *Conserv. Lett.* **1**, 199–207.
- Hall, R.J., Milner-Gulland, E.J. & Courchamp, F. (2008). Endangering the endangered: the effects of perceived rarity on species exploitation. *Conserv. Lett.* **1**, 75–81.
- Johnson, P.J., Kansky, R., Loveridge, A.J. & MacDonald, D.W. (2010). Size, rarity and charisma: valuing African wildlife trophies. *PLoS ONE* **5**, 1–7.
- Mysterud, A. (2012). Trophy hunting with uncertain role for population dynamics and extinction of ungulates. *Anim. Conserv.* **15**, 14–15.
- Packer, C., Brink, H., Kissui, B.M., Maliti, H., Kushnir, H. & Caro, T. (2011). Effects of trophy hunting on lion and leopard populations in Tanzania. *Conserv. Biol.* **25**, 142–153.
- Packer, C., Kosmala, M., Cooley, H.S., Brink, H., Pintea, L., Garshelis, D., Purchase, G., Strauss, M., Swanson, A., Balme, G., Hunter, L. & Nowell, K. (2009). Sport hunting, predator control and conservation of large carnivores. *PLoS ONE* **4**, 1–8.
- Palazy, L., Bonenfant, C., Gaillard, J.M. & Courchamp, F. (2011). Cat dilemma: too protected to escape trophy hunting? *PLoS ONE* **6**, e22424.
- Palazy, L., Bonenfant, C., Gaillard, J.M. & Courchamp, F. (2012). Rarity, trophy hunting and ungulates. *Anim. Conserv.* **15**, 4–11.
- Prescott, G.W., Johnson, P.J., Loveridge, A.J. & Macdonald, D.W. (2011). Does change in IUCN status affect demand for African bovid trophies? *Anim. Conserv.* In press. doi:10.1111/j.1469-1795.2011.00506.x
- Whitman, K., Starfield, A.M., Quadling, H.S. & Packer, C. (2004). Sustainable trophy hunting of African lions. *Nature* **428**, 175–178.

1 **Appendix 1: Data set collected for the analyses reported in the paper.**

2 For each species (indicated in both scientific (Latin names) and vernacular (English
 3 names) formulations) are given the trophy price (P, in US \$), male body mass (M, in kg),
 4 IUCN conservation status (C), distribution area category (D), and S (SCI trophy score).

5

Scientific name	English name	P	M	C	D	S	L
<i>Aepyceros melampus melampus</i>	Southern Impala	426	55.2	5	4	69	Africa
<i>Aepyceros melampus petersi</i>	Black faced impala	2820	55.2	3	1	67	Africa
<i>Aepyceros melampus rendilis</i>	East African Impala	663	55.2	5	3	77	Africa
<i>Alcelaphus buselaphus caama</i>	Red hartebeest	999	143.0	5	3	81	Africa
<i>Alcelaphus buselaphus cokei</i>	Coke Hartebeest	2254	143.0	5	2	73	Africa
<i>Alcelaphus buselaphus lelwel</i>	Lelwel Hartebeest	747	143.0	2	4	76	Africa
<i>Alcelaphus buselaphus major</i>	Western Hartebeest	1164	143.0	4	3	79	Africa
<i>Alcelaphus lichtensteini</i>	Lichtenstein Hartebeest	923	178.3	5	5	76	Africa
<i>Alces alces alces</i>	European Moose	2865	400.0	5	6	364	Europe
<i>Alces alces andersoni</i>	Western Canada Moose	1400	453.5	5	5	557	North-America
<i>Alces alces buturlini</i>	Chukotka Moose	7450	453.5	5	4	648	Asia
<i>Alces alces cameloides</i>	Amur Moose	6750	453.5	5	4	250	Asia
<i>Alces alces gigas</i>	Alaska-Yukon Moose	8400	453.5	5	3	731	North-America
<i>Ammotragus lervia</i>	Aoudad or Barbary Sheep	4767	112.0	3	3	166	Africa
<i>Antidorcas marsupialis hofmeyri</i>	Kalahari Springbok	515	39.2	5	3	50	Africa
<i>Antidorcas marsupialis marsupialis</i>	Black springbok	628	39.2	5	3	42	Africa
<i>Antilocapra americana</i>	Pronghorn	300	47.3	5	4	99	North-America
<i>Antilope cervicapra</i>	Blackbuck	2241	45.2	4	4	81	Asia
<i>Axis axis</i>	Axis Deer	3008	53.0	5	4	178	Asia
<i>Axis porcinus</i>	Hog Deer	6250	44.5	2	2	95	Africa
<i>Bison bison</i>	American Bison	3000	678.2	4	6	79	North-America
<i>Bison bonasus</i>	European Bison	7496	749.3	3	1	70	Europe
<i>Bos javanicus</i>	Banteng	8650	750.0	2	2	79	Asia
<i>Bubalus bubalis</i>	Water Buffalo	2528	780.7	2	1	162	Africa
<i>Budorcas taxicolor bedfordi</i>	Golden Takin	11500	282.7	3	1	61	Asia
<i>Budorcas taxicolor tibetana</i>	Sichuan Takin	11000	282.7	3	2	68	Asia
<i>Capra aegagrus aegagrus</i>	Bezoar Ibex	5600	60.2	3	4	133	Asia
<i>Capra aegagrus creticus</i>	Kri Kri Ibex	11200	60.2	3	1	77	Asia
<i>Capra caucasica caucasica</i>	Mid-Caucasian Tur	6450	86.3	2	1	160	Asia
<i>Capra caucasica dinniki</i>	West Caucasian Tur	17450	86.3	2	1	170	Asia
<i>Capra cylindricornis</i>	East Caucasian Tur	6700	88.2	4	1	179	Asia
<i>Capra falconeri falconeri</i>	Astor Markhor	70000	90.0	2	1	114	Asia
<i>Capra ibex</i>	Alpine Ibex	12211	85.0	5	1	113	Europe
<i>Capra pyrenaica hispanica</i>	Beceite Ibex	7800	72.5	5	1	81	Europe

<i>Capra pyrenaica victoriae</i>	Gredos Ibex	7800	72.5	5	1	101	Europe
<i>Capra sibirica alaiana</i>	Mid-Asian Ibex	4633	110.0	5	3	142	Asia
<i>Capra sibirica hagenbecki</i>	Gobi Ibex	3975	110.0	5	3	119	Asia
<i>Capra sibirica hemalayanus</i>	Himalayan Ibex	4900	110.0	5	2	119	Asia
<i>Capra sibirica sibirica</i>	Siberian Ibex	3050	110.0	5	3	124	Asia
<i>Capreolus capreolus</i>	European Roe Deer	2216	25.9	5	5	77	Europe
<i>Capreolus pygargus pygargus</i>	Siberian Roe Deer	2533	42.0	5	6	95	Asia
<i>Cephalophus callipygus</i>	Peters Duiker	1957	18.4	5	3	18	Africa
<i>Cephalophus dorsalis</i>	Bay Duiker	529	19.6	5	4	24	Africa
<i>Cephalophus harveyi</i>	Harvey Red Duiker	750	14.5	5	2	15	Africa
<i>Cephalophus leucogaster</i>	Gabon or White-bellied Duiker	286	14.8	5	3	16	Africa
<i>Cephalophus monticola</i>	Blue Duiker	703	4.9	5	5	9	Africa
<i>Cephalophus natalensis</i>	Natal Red Duiker	1300	13.3	5	3	13	Africa
<i>Cephalophus nigrifrons</i>	Black-fronted Duiker	508	13.8	5	4	14	Africa
<i>Cephalophus ogilbyi</i>	Ogilby Duiker	381	20.7	5	3	16	Africa
<i>Cephalophus rufilatus</i>	Red-flanked Duiker	491	10.1	5	4	13	Africa
<i>Cephalophus silvicultor</i>	Yellow-backed Duiker	1140	61.6	5	5	22	Africa
<i>Cephalophus spadix</i>	Abbott duiker	308	5.0	2	1	15	Africa
<i>Ceratotherium simum cottoni</i>	Northern White Rhinoceros	84000	2800.0	1	1	67	Africa
<i>Ceratotherium simum simum</i>	Southern White Rhinoceros	55000	2800.0	4	1	109	Africa
<i>Cervus albirostris</i>	White-lipped or Thorold Deer	6875	204.2	3	3	256	Asia
<i>Cervus elaphus alashanicus</i>	Alashan Wapiti	8500	180.5	5	3	204	Asia
<i>Cervus elaphus hippelaphus</i>	European Red Deer	5900	180.5	5	4	567	Europe
<i>Cervus elaphus hispanicus</i>	Spanish Red Deer	4500	180.5	5	3	387	Europe
<i>Cervus elaphus kansuensis</i>	Gansu Deer	5500	180.5	5	3	258	Asia
<i>Cervus elaphus nelsoni</i>	Rocky Mountain Elk	1400	180.5	5	4	598	North-America
<i>Cervus elaphus sibiricus</i>	Altai Wapiti	4600	180.5	5	4	394	Asia
<i>Cervus elaphus songaricus</i>	Tian Shan Wapiti or Maral	5500	180.5	5	3	447	Asia
<i>Cervus nippon</i>	Sika deer	767	47.6	5	2	211	Asia
<i>Cervus unicolor</i>	Sambar	4563	215.0	3	5	189	Asia
<i>Connochaetes gnou</i>	Black Wildebeest	1119	151.4	5	1	101	Africa
<i>Connochaetes taurinus albojubatus</i>	White-bearded Wildebeest	1154	206.1	5	1	94	Africa
<i>Connochaetes taurinus cooksoni</i>	Cookson Wildebeest	1338	206.1	5	1	94	Africa
<i>Connochaetes taurinus johnstoni</i>	Nyasa Wildebeest	1154	206.1	5	2	95	Africa
<i>Connochaetes taurinus taurinus</i>	Blue Wildebeest	1065	206.1	5	4	97	Africa
<i>Dama dama</i>	European Fallow Deer	1877	67.0	5	5	359	Africa
<i>Damaliscus dorcas dorcas</i>	Bontebok	1596	68.0	4	1	50	Africa
<i>Damaliscus dorcas phillipsi</i>	Common Blesbok	469	68.0	5	2	52	Africa
<i>Damaliscus lunatus jimela</i>	Topi	910	140.7	5	3	67	Africa
<i>Damaliscus lunatus korrigum</i>	Korrigum	2269	140.7	3	4	75	Africa
<i>Damaliscus lunatus lunatus</i>	Tsessebe	2250	140.7	5	3	57	Africa
<i>Damaliscus lunatus tiang</i>	Tiang	400	140.7	5	3	73	Africa
<i>Diceros bicornis</i>	Black rhinoceros	150000	1059.7	1	3	89	Africa
<i>Elaphodus cephalophus</i>	West China Tufted Deer	4200	18.0	4	4	2	Asia

<i>Gazella granti granti</i>	Southern Grant Gazelle	560	73.4	5	2	75	Africa
<i>Gazella granti notata</i>	Northern Grant Gazelle	220	73.4	5	2	77	Africa
<i>Gazella granti robertsi</i>	Roberts Gazelle	558	73.4	5	1	66	Africa
<i>Gazella soemmerringi berberana</i>	Soemmerring Gazelle	1300	39.5	3	2	53	Africa
<i>Gazella subgutturosa subgutturosa</i>	Persian Goitered Gazelle	1800	27.7	3	4	44	Asia
<i>Gazella subgutturosa yarkandensis</i>	Yarkand Goitered Gazelle	1500	27.7	3	4	40	Asia
<i>Gazella thomsoni thomsoni</i>	Thomson Gazelle	557	21.8	4	2	44	Africa
<i>Hemitragus jemlahicus</i>	Himalayan Tahr	5600	101.7	4	2	51	Africa
<i>Hippopotamus amphibius</i>	Common Hippopotamus	2328	2126.7	3	4	88	Africa
<i>Hippotragus equinus equinus</i>	Southern Roan Antelope	9350	272.7	5	4	86	Africa
<i>Hippotragus equinus koba</i>	Western Roan Antelope	3634	272.7	5	4	89	Africa
<i>Hippotragus niger niger</i>	Common Sable antelope	5278	231.6	5	4	128	Africa
<i>Hydropotes inermis</i>	Chinese Water Deer	495	12.4	3	2	10	Asia
<i>Hylochoerus meinertzhageni</i>	Giant Forest Hog	1253	140.0	5	4	36	Africa
<i>Kobus ellipsiprymnus crawshayi</i>	Crawshay Defassa Waterbuck	1800	231.9	5	3	77	Africa
<i>Kobus ellipsiprymnus defassa</i>	East African Defassa Waterbuck	676	231.9	4	4	87	Africa
<i>Kobus ellipsiprymnus ellipsiprymnus</i>	Common or Ringed Waterbuck	1956	231.9	5	4	92	Africa
<i>Kobus ellipsiprymnus unctuosus</i>	Sing-sing Waterbuck	1123	231.9	5	4	85	Africa
<i>Kobus kob kob</i>	Western African Kob	625	83.8	3	4	64	Africa
<i>Kobus kob thomasi</i>	Uganda Kob	2750	74.9	5	2	64	Africa
<i>Kobus leche kafuensis</i>	Kafue Flats Lechwe	3530	106.4	3	1	88	Africa
<i>Kobus leche leche</i>	Red Lechwe	2944	106.4	5	2	79	Africa
<i>Kobus leche smithemani</i>	Black Lechwe	3725	106.4	3	1	71	Africa
<i>Kobus vardoni</i>	Puku	707	83.3	4	2	58	Africa
<i>Litocranius walleri sclateri</i>	Northern Gerenuk	1500	40.0	4	3	48	Africa
<i>Litocranius walleri walleri</i>	Southern Gerenuk	2988	40.0	4	3	59	Africa
<i>Loxodonta africana</i>	African Elephant	14846	3160.0	4	5	302	Africa
<i>Madoqua guentheri</i>	Guenther Dik-dik	100	3.6	5	3	11	Africa
<i>Madoqua kirki kirki</i>	Kirk Dik-dik	425	4.9	5	3	12	Africa
<i>Madoqua kirkii damarensis</i>	Damara Dik-dik	2050	4.9	5	2	11	Africa
<i>Madoqua saltiana saltiana</i>	Salt Dik-dik	170	2.5	5	3	12	Africa
<i>Moschus moschiferus</i>	Musk deer	800	11.0	3	6	9	Asia
<i>Muntiacus reevesi</i>	Reeves Muntjac	859	15.7	5	4	32	Asia
<i>Naemorhedus goral</i>	Himalayan Goral	10000	32.0	4	2	22	Asia
<i>Neotragus batesi</i>	Bates Pygmy Antelope	455	2.5	5	3	6	Africa
<i>Neotragus moschatus kirchenpaueri</i>	East African Suni	713	4.8	5	3	11	Africa
<i>Neotragus moschatus livingstonianus</i>	Livingstone Suni	1650	4.8	5	3	14	Africa
<i>Neotragus pygmaeus</i>	Royal Antelope	635	2.0	5	2	4	Africa
<i>Oreotragus oreotragus</i>	Klipspringer	1111	11.8	5	5	16	Africa
<i>Oryx gazella gazella</i>	Kalahari Gemsbok	1094	192.9	5	3	111	Africa
<i>Ourebia ourebi ourebi</i>	Common Oribi	645	14.4	5	5	19	Africa
<i>Ovibos moschatus moschatus</i>	Barren Ground Muskox	150	346.4	5	3	90	North-America
<i>Ovibos moschatus wardi</i>	Greenland Muskox	1075	346.4	5	3	85	North-America
<i>Ovis ammon adametzi</i>	Kuruktag Argali	14000	117.4	4	1	166	Asia
<i>Ovis ammon ammon</i>	Altai Argali	33500	165.3	4	2	260	Asia

<i>Ovis ammon collium</i>	Karaganda Argali	9000	139.1	4	2	211	Asia
<i>Ovis ammon dalailamae</i>	Gansu Argali	11250	117.4	4	2	212	Asia
<i>Ovis ammon darwini</i>	Gobi Argali	23333	101.0	4	2	226	Asia
<i>Ovis ammon hodgsoni</i>	Tibetan Argali	12000	102.5	4	3	181	Asia
<i>Ovis ammon karelini</i>	Tian Shan Argali	15167	111.7	4	2	217	Asia
<i>Ovis ammon littledalei</i>	Littledale Argali	11000	117.4	4	2	220	Asia
<i>Ovis ammon polii</i>	Marco Polo Argali	14050	127.2	4	1	244	Asia
<i>Ovis ammon sairensis</i>	Sair Argali	11000	117.4	4	2	230	Asia
<i>Ovis canadensis canadensis</i>	Rocky Mountain Bighorn Sheep	12000	104.6	5	3	210	North-America
<i>Ovis dalli dalli</i>	Dall Sheep	7807	89.4	5	3	196	North-America
<i>Ovis dalli stonei</i>	Stone Sheep	12000	94.8	5	2	185	North-America
<i>Ovis gmelini gmelini</i>	Armenian Mouflon	4352	51.4	3	1	138	Asia
<i>Ovis gmelini isphahanica</i>	Esfahan Mouflon	1904	84.0	3	2	134	Asia
<i>Ovis gmelini laristanica</i>	Laristan Mouflon	2538	36.9	3	2	141	Asia
<i>Ovis gmelini musimon</i>	European Mouflon	3648	49.6	3	4	160	Africa
<i>Ovis nivicola alleni</i>	Okhotsk Snow Sheep	15500	107.0	5	1	171	Asia
<i>Ovis nivicola koriakorum</i>	Koryak Snow Sheep	19000	107.0	5	1	151	Asia
<i>Ovis nivicola lydekkeri</i>	Yakutia Snow Sheep	9950	107.0	5	4	164	Asia
<i>Ovis nivicola nivicola</i>	Kamchatka Snow Sheep	14650	107.0	5	2	176	Asia
<i>Ovis vignei arkal</i>	Transcaspian Urial	4452	65.0	3	2	170	Asia
<i>Ovis vignei cycloceros</i>	Afghan Urial	8000	57.5	3	2	151	Asia
<i>Pelea capreolus</i>	Vaal Rhebok	1382	28.1	5	2	27	Africa
<i>Phacochoerus aethiopicus</i>	Warthog	454	71.0	5	5	49	Africa
<i>Potamochoerus larvatus</i>	Bushpig	493	61.0	5	5	23	Africa
<i>Potamochoerus porcus</i>	Red River Hog	632	61.7	5	5	25	Africa
<i>Pseudois nayaur nayaur</i>	Himalayan Blue Sheep	3700	54.4	5	2	140	Asia
<i>Pseudois nayaur szechuanensis</i>	Chinese blue sheep	2500	54.4	5	3	138	Asia
<i>Pseudois schaeferi</i>	Dwarf Blue Sheep	13900	54.4	2	1	102	Asia
<i>Rangifer tarandus caribou</i>	Mountain Caribou	3625	138.7	5	4	547	North-America
<i>Rangifer tarandus groenlandicus</i>	Central Canada Barren Ground Caribou	80	138.7	5	4	17	North-America
<i>Raphicerus campestris</i>	Steenbok	339	11.0	5	4	17	Africa
<i>Raphicerus melanotis</i>	Cape Grysbok	618	10.4	5	1	13	Africa
<i>Raphicerus sharpei</i>	Sharpe Grysbok	653	7.2	5	4	9	Africa
<i>Redunca arundinum</i>	Common Reedbuck	883	59.8	5	4	35	Africa
<i>Redunca fulvorufula chanleri</i>	Chanler Mountain Reedbuck	700	31.1	3	2	15	Africa
<i>Redunca fulvorufula fulvorufula</i>	Southern Mountain Reedbuck	2428	31.1	5	2	18	Africa
<i>Redunca redunca bohor</i>	Abyssinian Bohor Reedbuck	350	45.8	5	3	26	Africa
<i>Redunca redunca nigeriensis</i>	Nigerian Bohor Reedbuck	625	45.8	5	3	24	Africa
<i>Redunca redunca redunca</i>	Nagor Reedbuck	1294	45.8	5	3	21	Africa
<i>Redunca redunca wardi</i>	Eastern Bohor Reedbuck	605	45.8	5	3	27	Africa
<i>Rupicapra rupicapra balcanica</i>	Balkan Chamois	4900	40.0	5	1	30	Europe
<i>Rupicapra rupicapra carpatica</i>	Carpathian Chamois	2500	40.0	5	1	31	Europe
<i>Rupicapra rupicapra caucasica</i>	Caucasian Chamois	4450	40.0	5	2	25	Asia
<i>Rupicapra rupicapra rupicapra</i>	Alpine Chamois	3700	27.5	5	2	29	Europe
<i>Rupicapra pyrenaica parva</i>	Cantabrian Chamois	4900	23.8	5	1	23	Europe

<i>Rupricapra pyrenaica pyrenaica</i>	Pyrenean Chamois	4900	23.8	5	1	28	Europe
<i>Sus scrofa scrofa</i>	Eurasian wild boar	1206	85.0	5	7	41	Asia
<i>Sylvicapra grimmia abyssinicus</i>	East African Bush Duiker	303	17.9	5	4	15	Africa
<i>Sylvicapra grimmia coronata</i>	Western Bush Duiker	383	17.9	5	4	15	Africa
<i>Sylvicapra grimmia grimmia</i>	Southern Bush Duiker	367	17.9	5	5	19	Africa
<i>Syncerus caffer aequinoctialis</i>	Nile Buffalo	1500	522.0	5	3	115	Africa
<i>Syncerus caffer brachyceros</i>	Central African Savanna Buffalo	1021	522.0	5	3	96	Africa
<i>Syncerus caffer caffer</i>	Cape buffalo	7408	522.0	5	5	141	Africa
<i>Syncerus caffer nanus</i>	Dwarf Forest Buffalo	2664	522.0	5	4	72	Africa
<i>Syncerus caffer planiceros</i>	West African Savanna Buffalo	1631	522.0	5	5	81	Africa
<i>Taurotragus derbianus gigas</i>	Central African Giant Eland	2739	680.0	5	3	143	Africa
<i>Taurotragus oryx livingstonei</i>	Livingstone Eland	2620	590.0	5	4	119	Africa
<i>Taurotragus oryx oryx</i>	Cape eland	2272	590.0	5	3	116	Africa
<i>Taurotragus oryx pattersonianus</i>	East African Eland	2125	590.0	5	3	111	Africa
<i>Tayassu tajacu</i>	Collared Peccary or Javelina	594	20.3	4	4	19	N_Am
<i>Tetracerus quadricornis</i>	Four-horned Antelope or Chousingha	900	19.1	3	4	22	Asia
<i>Tragelaphus angasii</i>	Nyala	2746	111.0	5	2	84	Africa
<i>Tragelaphus buxtoni</i>	Mountain Nyala	5000	216.0	2	1	117	Africa
<i>Tragelaphus euryceros</i>	Bongo	3525	227.0	4	4	91	Africa
<i>Tragelaphus imberbis</i>	Lesser Kudu	3064	93.3	4	3	86	Africa
<i>Tragelaphus scriptus decula</i>	Abyssinian Bushbuck	350	46.1	5	3	40	Africa
<i>Tragelaphus scriptus delameri</i>	East African Bushbuck	748	46.1	5	3	53	Africa
<i>Tragelaphus scriptus meneliki</i>	Menelik Bushbuck	2000	46.1	5	1	45	Africa
<i>Tragelaphus scriptus roualeyni</i>	Limpopo Bushbuck	1048	46.1	5	2	53	Africa
<i>Tragelaphus scriptus scriptus</i>	Harnessed Bushbuck	820	46.1	5	5	40	Africa
<i>Tragelaphus scriptus sylvaticus</i>	Cape bushbuck	798	46.1	5	2	53	Africa
<i>Tragelaphus spekii gratus</i>	Forest Sitatunga	2451	102.0	5	4	84	Africa
<i>Tragelaphus spekii selousi</i>	Zambezi Sitatunga	4500	102.0	5	3	86	Africa
<i>Tragelaphus spekii spekii</i>	East African Sitatunga	2771	102.0	5	2	78	Africa
<i>Tragelaphus strepsiceros bea</i>	East African Greater Kudu	3500	244.0	5	3	145	Africa
<i>Tragelaphus strepsiceros burlacei</i>	Western Greater Kudu	4028	244.0	5	2	127	Africa
<i>Tragelaphus strepsiceros chora</i>	Abyssinian Greater Kudu	1340	244.0	5	3	136	Africa
<i>Tragelaphus strepsiceros strepsiceros</i>	Eastern Cape Greater Kudu	1513	244.0	5	1	141	Africa
<i>Tragelaphus strepsiceros strepsiceros</i>	Southern Greater Kudu	1988	244.0	5	4	158	Africa

1 **Appendix 2: Complete list of PGLS models fitted.** The response variable is the trophy
 2 price, P, and models contain combinations of 4 different covariates: the location (L), the
 3 male average body mass (M), the relative trophy size (B, measured as the residuals from
 4 the regression of trophy size on body mass on the log-scale), and rarity (R).

Model	ΔAIC	k	AICw
$P \sim L + M + B + R + M*B$	0.0	10	0.5501
$P \sim L + M + B + R + M*B + M*R$	2.4	11	0.1657
$P \sim L + M + B + R$	3.8	9.0	0.0823
$P \sim L + M + B + R + M*B + B*R$	3.9	11	0.0783
$P \sim L + M + R$	4.1	8	0.0708
$P \sim L + M + B + R + B*R$	6.4	10	0.0224
$P \sim L + M + B + R + M*R$	7.5	10	0.0129
$P \sim L + M + B + R + M*B + M*R + B*R$	8.1	12	0.0096
$P \sim L + M + R + M*R$	8.9	9	0.0064
$P \sim L + M + B + R + M*R + B*R$	12.0	11	0.0014
$P \sim L + M + B$	22.6	8	0.0000
$P \sim L + M$	23.0	7	0.0000
$P \sim L + M + B + M*B$	23.2	9	0.0000
$P \sim L + R$	50.1	7.0	0.0000
$P \sim L + B + R + B*R$	51.7	9	0.0000
$P \sim L + B + R$	51.9	8	0.0000
$P \sim 1$	63.5	3	0.0000
$P \sim L + B$	67.5	7	0.0000

5

6