Ambio

Effects of scarcity, aesthetics and ecology on wildlife auction prices of large African mammals

--Manuscript Draft--

Manuscript Number:	AMBI-D-17-00074R1
Full Title:	Effects of scarcity, aesthetics and ecology on wildlife auction prices of large African mammals
Article Type:	Report
Keywords:	consumer preferences; ecological economics, ecotourism; game farming; hedonic pricing; wildlife
Corresponding Author:	Fredrik Dalerum Universidad de Oviedo SPAIN
Corresponding Author Secondary Information:	
Corresponding Author's Institution:	Universidad de Oviedo
Corresponding Author's Secondary Institution:	
First Author:	Fredrik Dalerum
First Author Secondary Information:	
Order of Authors:	Fredrik Dalerum
	Maria Miranda
	Cristina Muñiz
	Placido Rodriguez
Order of Authors Secondary Information:	
Funding Information:	Ministerio de Economía y Competitividad (RYC-2013-14662) — Dr Fredrik Dalerum
Abstract:	For successful integration of biological conservation into economic markets, economic processes need to capture ecological values. South African wildlife ranching is a tourist based activity that generates unique information on the economic value of wildlife species. We used public data from South African wildlife auctions to evaluate if annual prices 1991-2012 related to species characteristics associated with scarcity, aesthetics and ecology of South African carnivores and ungulates. While none of the species characteristics influenced carnivore prices, ungulate prices were related to characteristics associated with novelty and aesthetics, which relative importance had increased over time. We raise both ecological and economic concern for this apparent focus. Our results also suggest a potential importance of non-species related factors, such as market and buyer characteristics. We encourage further evaluation of the relative influences of species characteristics versus factors that are intrinsically linked to economic processes on price variations in South African wildlife.

AUTHOR BIOGRAPHIES

Fredrik Dalerum is a research fellow at the Research Unit of Biodiversity, University of Oviedo, Spain, although he is also affiliated with University of Pretoria (South Africa) and Stockholm University (Sweden). He is a terrestrial ecologist who focuses his research on the biology and conservation of mammalian carnivores, functional aspects of biodiversity, and general issues of conservation and environmental sustainability.

Address: Research Unit of Biodiversity (UO-CSIC-PA), Mieres Campus, University of Oviedo, 33600 Mieres, Asturias, Spain (address for correspondence); Telephone: +34 985 10 3000 (Ext. 5927)

Address: Department of Zoology, Stockholm University, Sweden

Address: Mammal Research Institute, Department of Zoology, University of Pretoria, South Africa

Maria Miranda is an environmental scientist with a research history of studying mammalian herbivory and trophic interactions.

Address: Research Unit of Biodiversity (UO-CSIC-PA), Mieres Campus, University of Oviedo, Mieres, Asturias, Spain

Cristina Muñiz is an Associate Professor in the Department of Economics at University of Oviedo , Spain. She is mainly focusing her research on leisure economics applying econometric models to study the involvement of individuals in leisure activities, especially sports and cultural activities.

Address: Department of Economics, University of Oviedo, Campus del Cristo, Oviedo, Asturias, Spain

Plácido Rodriguez is a professor in Economy at University of Oviedo. His primary research focus is on the economic impacts of sport activities. He is the chairman and founder of the Sports Economics Observatory Foundation based in Gijon.

Address: Sports Economics Observatory Foundation (FOED), Department of Economics, University of Oviedo, Gijon, Asturias, Spain

Effects of scarcity, aesthetics and ecology on wildlife auction prices of large African mammals

Fredrik Dalerum[1,2,3], María Miranda[1], Cristina Muñiz [4,5] & Plácido Rodríguez[4,5]

[1] Research Unit of Biodiversity (UO-CSIC-PA), Mieres Campus, University of Oviedo, 33600 Mieres, Asturias, Spain (address for correspondence); Telephone: +34 985 10 3000 (Ext. 5927)

[2] Department of Zoology, Stockholm University, Sweden

[3] Mammal Research Institute, Department of Zoology, University of Pretoria, South Africa

[4] Department of Economics, University of Oviedo, Oviedo, Spain

[5] Sports Economics Observatory Foundation (FOED), Gijon, Spain

E-mails: F. Dalerum (correspondence): dalerumjohan@uniovi.es
M. Miranda: maria.mirandaroves@gmail.com
C. Muñiz: cmuniza@uniovi.es
P. Rodríguez: placido@uniovi.es

Article type: Report

Word count, abstract: 149

Word count, total (excluding references): 4980

Number of references: 45

Number of figures: 1

Number of tables: 1

Acknowledgements

Ben Oban kindly provided compiled data on game prices for 1991-2011. FD received financial support from a Ramón y Cajal fellowship from the Spanish Ministry of Economy and Competitiveness.

Abstract

For successful integration of biological conservation into economic markets, economic processes need to capture ecological values. South African wildlife ranching is a tourist based activity that generates unique information on the economic value of wildlife species. We used public data from South African wildlife auctions to evaluate if annual prices 1991-2012 related to species characteristics associated with scarcity, aesthetics and ecology of South African carnivores and ungulates. While none of the species characteristics influenced carnivore prices, ungulate prices were related to characteristics associated with novelty and aesthetics, which relative importance had increased over time. We raise both ecological and economic concern for this apparent focus. Our results also suggest a potential importance of non-species related factors, such as market and buyer characteristics. We encourage further evaluation of the relative influences of species characteristics versus factors that are intrinsically linked to economic processes on price variations in South African wildlife.

Key words

consumer preferences; ecological economics, ecotourism; game farming; hedonic pricing; wildlife

INTRODUCTION

Humanity has induced unprecedented and accelerating negative impacts on Earth's biota during the past few centuries. Following a broad realization of these detrimental environmental impacts, there has been a subsequent recognition that they may lead to dramatic and negative consequences for humanity itself (Ehrlich and Ehrlich 2013). Substantial effort has consequently been invested in attempting to preserve biological resources, and to better align human societies with the biotic environment (Mace 2014). This work is currently putting a large emphasis on finding sustainable interactions between human societies and the environment (Carpenter et al. 2009, Turnhout et al. 2014). However, although much of the key principles of how such interactions should be structured are known, public authorities have not yet been able to accomplish their full incorporation into public policy (Dalerum 2014).

Economic processes regulate much of modern human societies, in particular the distribution of the material dimensions of human welfare. It is therefore not surprising that there have been frequent attempts to find synergies between environmental protection and economic markets. Such synergies have partly focused on monetary valuations of environmental resources (Costanza et al. 1997, Balmford et al. 2002), but also on finding less environmentally damaging ways of structuring economic activities (UNEP 2011). For instance, an evolving ecotourism market is attempting to use consumer experiences as economic commodities in a non-consumptive way (Honey 2008). Ecotourism has been suggested as particularly useful to provide economic incentives for conservation action in impoverished societies (Amin 2016), although the opposite has also been argued (Benjaminsen and Bryceson 2012).

Commercial wildlife ranching in South Africa is a tourism driven industry that is economically important and has the potential to contribute to the biodiversity conservation (Cousins et al. 2008). Following a legislative change in 1991 it became possible to privately own free ranging wildlife in South Africa (Snijders 2012). There has subsequently been a rapid increase in commercially driven wildlife ranches (Taylor et al. 2016). These ranches are primarily generating revenue from ecotourism and trophy hunting, but also through meat production and from selling wildlife to other ranches (Van der Merwe et al. 2004). Wildlife ranching has grown to a considerable industry, consisting of an estimated 9,000 wildlife ranches covering 14% of South Africa's land area (170,000 km^2) (Taylor et al. 2016). Wildlife species are traded between ranches, both through private sales and through official auctions (Bothma et al. 2010). Although the total amount of animals sold privately is unknown, it is estimated to be 4-6 times as high as the number of animals sold at auctions. However, the total live sales are estimated to turnover approximately 320 million USD (Taylor et al. 2016). A recent study suggests that prices in this market are unrelated to species' evolutionary and ecological significance (Dalerum and Miranda 2016), but we still have scant information on what is driving the prices of South African wildlife. A good market alignment with environmentally important characteristics is a requirement for any wildlife based market to actively contribute to environmental sustainability (Dalerum & Miranda 2016).

The hedonic pricing model addresses the marginal trade-offs in the markets performed by consumers and sellers and is often used to evaluate the relative influences of intrinsic and extrinsic values of products (Court 1939). It is intuitive to regard aesthetic and physical attributes as important for the satisfaction tourists get from wildlife. Hence, the hedonic model is well suited for economic evaluations of wildlife, since it primarily focuses on the satisfaction given by attributes of goods (Gray 1995). Under this model, goods can be described as composites of different intrinsic properties, so-called characteristics (Rosen 1974), and consumer's utility depends on the different characteristics that the goods have (Lancaster, 1966). This stand in contrast to the neoclassical economic framework, which assumes that consumers want to purchase goods because of the utilities they directly provide.

Scarcity is a specific characteristic of goods that is central to economic theory. A greater scarcity is often associated with higher prices in the market. Although high prices could hamper consumption, they could also lead to an increasde desire for goods since price can be a quality indicator as well as indicator of the social status of the buyer (Veblen, 1889). Subsequently, the rarity of animals has been related to various aspects of their economic attractiveness. For instance, IUCN (International Union for Conservation of Nature) threat category has been associated to both African trophy hunting prices (Johnson et al. 2010) and to the number of mammals and reptiles traded as exotic pets (Bush et al. 2014). In addition, prices for species of caged birds in Australia have been negatively associated with their abundance in captivity (Val-Ilosera and Cassey 2017). However, we note that the market prices of South African wildlife could be analysed from both demand-side and supply-side perspectives as changes in prices are likely to reflect not only consumer behaviour, but also supply side effects such as the costs associated with housing and maintaining wildlife populations.

In this study we used a 22-year data set on annual average wildlife auction prices from South Africa to evaluate if the prices were associated to species characteristics related to their scarcity, aesthetics and ecology. The analyses were restricted to a sample of mammalian ungulates of the orders Artiodactyla and Perissodactyla as well as to carnivores > 10kg in body size, since these are the species mostly traded in the South African game industry (Taylor et al. 2016). A priori we hypothesized that (i) rarity, both within and among species, would be positively related to prices; (ii) aesthetic values, which have previously been shown important for wildlife values, would be positively related to prices; (iii) certain aspects of species ecology, primarily carnivory, large body size and large home range size, would be negatively related to prices since we believe they would be associated with increased hosting and maintenance costs. Finally, because of an increased environmental awareness during the past 20 years (Mace 2014), we expected that the relationships between prices and species characteristics had shifted over time, with an increased positive association between prices and ecologically relevant characteristics. We envision such a change to have been caused by an increased consumer demand for ecologically relevant species.

METHODS

Compilation of price data

We compiled annual average wildlife auction prices between 1991 and 2012 from the recreational journal *Game and Hunt* (http://www.wildlifehunt.co.za) and from an electronic newsletter from International Council for Game and Wildlife Conservation (http://africanindaba.com; Dalerum and Miranda 2016). Our data included information on 6 species of native large carnivores (>10kg, see Dalerum 2013) and on 37 species of native ungulates (Dalerum and Miranda 2016). We also included information on one exotic large carnivore species (*Panthera tigris*) and 3 species of exotic ungulates (*Dama dama*, *Kobus leche, Oryx dammah*). For 10 ungulates we obtained prices both from the common form as well as from non-native populations or from deviant colour mutations. We treated these prices separately in the analyses (see descriptions below). Apart from bushbuck (*Tragelaphus scriptus*) during 2010-2012, we did not have separate prices for males and females. For this species, we used average prices across both sexes for the years we did have sex specific information. We treated bontebok (*Damaliscus pygargus pygargus*) and blesbok (*Damaliscus pygargus phillipsi*) as separate taxonomic entities in our data. We have presented the prices in the original South African currency (South African Rand, ZAR), but adjusted prices for inflation by using average annual consumer price indices available from Statistics South Africa with 2012 as reference year (http://www.statssa.gov.za). All raw average annual prices are given in Table S1.

Compilation of data on species characteristics

The hedonic pricing approach argues that the price of any good is the sum of the unobserved prices of the bundle of their characteristics. Therefore, we related prices to a series of species specific characteristics associated with rarity, ecology and aesthetics (Table S2). We used the hedonic price function $P_i = f(R_{i1},\ldots,R_{ij}, A_{i1},\ldots,A_{ik}, E_{il},\ldots,E_{il})$, where P_i is the price for a given species defined as a function of specific characteristics associated with rarity ($R_{i1\text{-}j}$), aesthetics ($A_{i1\text{-}k}$), and ecology ($E_{i1\text{-}l}$).

We used three variables to reflect the rarity of a given species of ungulates, and two for carnivores; a species geographic origin, IUCN Red List category, and whether or not it was from a non-native population or had deviant morphology (only for ungulates, Table S2). We scored if each species were native or not to South Africa based on the official IUCN distribution maps. We used the relevant global assessment of the IUCN Red List classification for each year and species from the IUCN Red List database (http://www.iucnredlist.org/). For species where we had prices prior to an initial IUCN assessment, we back-dated the classification each year using the first assessment available. We converted previous Red List classifications to the current ones for consistency. For 10 ungulate species we had prices for either non-native populations (east African populations of buffalo *Syncerus caffer*; Zambian populations of sable *Hippotragus niger*; Livingstone's eland *Taurotragus oryx,* Hartmann's mountain zebra *Equus zebra*) as well as deviant colour mutations for impala (*Aepyceros melampus*), springbok (*Antidorcas marsupialis*), blue wildebeest (*Connochaetes taurinus*), blesbok, gemsbok (*Oryx gazella*), and the greater kudu (*Tragelaphus strepsiceros*). We treated all of these populations and colour forms as deviant forms in our analyses.

We used one character for carnivores and ungulates respectively to reflect aesthetics; colour pattern (carnivores) and horn or tusk length (ungulates). We compiled data on colour patterns for all carnivores, and classed each species as either plain or patterned (i.e., spotted or striped). For ungulates, we compiled data on maximum horn length recorded in southern Africa from Skinner and Chimimba (2005), except for bushpig (*Potamochoerus larvatus*), common warthog (*Phacochoerus africanus*) and hippopotamus (*Hippopotamus amphibious*) for which we instead used the tusk length. For black (*Diceros bicornis*) and white (*Ceratotherium simum*) rhinoceros we only used the length of the front horn.

Finally, we downloaded a series of characters from the PanTHERIA database to reflect species ecology (Jones et al. 2009). These characters included body mass (averaged between males and females), population density, home range size, activity cycle (classed as a categorical variable: diurnal, nocturnal, or both), social group size, and diet breadth (only recorded for ungulates). Data were error checked and missing species data were supplemented with information from other sources (Table S2). The raw data are available in Table S3.

Data analyses

We used mixed linear models to associate these species characteristics to market prices. Following Hector et al. (2010), we ran subset models to maximize the amount of included data for our evaluations of relationships between prices and species characteristics, as well as if these relationships had changed over time. We did not use a sequential approach to model selection based on information theoretic criteria, but rather selected representative characteristics a-priori and evaluated each predictor while retaining all other a-priori selected predictors simultaneously in the model. First, although not directly included in our hedonic price evaluation, we compared prices of carnivores and ungulates using a model including all carnivore and ungulate species for which we had at least one price, but we only included species native to South Africa and only the common colour morph or population. In this model we used the average annual price as the response variable and used taxonomic group (i.e. carnivore or ungulate) as the only fixed effect. Second, we ran two models in which we related prices to species characteristics of carnivores and ungulates separately. In both of these models we used the average annual price as the response. For carnivores we removed predictors that were correlated > 80%, whereas all predictors were correlated < 50% for ungulates. In the carnivore model, we retained IUCN category, origin (native or exotic), activity cycle (diurnal, nocturnal or both) and colour pattern as categorical predictors, and body mass, social group size and home range size as continuous predictors. In the ungulate model, categorical predictors were IUCN category, origin (native or exotic), activity cycle (diurnal, nocturnal or both) and morph type (i.e. common or deviant morphological form or population), while body mass, horn or tusk length, density, social group size, diet breadth and litter size are continuous predictors. For these two models, we calculated the marginal R^2 following Johnson (2014, but see Nakagawa and Schielzeth 2013) as a heuristic way of evaluating the total amount of price variation that was explained by our species characteristics, and the coefficient of determination as defined by Edwards et al. (2008) as a heuristic method of evaluating the relative amount of explained variance for each of our different predictors (i.e. interpretable as a partial R^2 in a linear model). Finally, we ran a fourth model to evaluate the effect of species characteristics on temporal change in prices. In this last model, we only included ungulate species with at least three years of available data. We did not have sufficient data on carnivores for this analysis. This model had the same structure as the previous one, with the exception that we added year as a fixed linear covariate, as well as a 2-way interaction term between year and each of the other fixed predictors. Hence, this model is evaluating differences in a linear temporal trend of prices among factor levels (for categorical predictors) or along the values of continuous predictors. In all models, we log transformed prices following Rosen (1974), and visually inspected the residuals prior to analyses so that they conformed to heteroscedasticity. We added year grouped over species as a random effect structure to account for the temporal and taxonomic structure of our data. We also scaled all continuous variables by subtracting the means and dividing them by their standard deviations. For continuous predictors, this scaling gives coefficients that represent changes in the dependent variable (log price) per standard deviation unit change in the predictor. Hence, through this scaling all beta coefficients are directly comparable.

All statistical analyses were done in the statistical environment R version 3.3.0 for Linux (http://r-project.org) and the used the contributed packages nlme (Pinheiro et al. 2016) and r2glmm (Jaeger 2016).

RESULTS

Native carnivores did not differ significantly in average prices compared to native ungulates in their common form (β = -0.35, SE $_\beta$ = 0.69, P = 0.612). The species characteristics explained 48% of the variation in prices for carnivores and 46% for ungulates. For carnivores, body mass ($R^2_{partial}$ = 0.12), colour pattern ($R^2_{partial}$ = 0.12) and activity patterns (nocturnal $R^2_{partial}$ = 0.12, both nocturnal and diurnal $R^2_{partial}$ = 0.09) had the highest partial R^2values, but none of the biological characteristics had a significant effect on auction prices (Table 1, Fig. 1a,b). For ungulates, type (i.e. either deviant colour morphs of populations, $R^2_{partial}$ = 0.16), horn or tusk length ($R^2_{partial}$ = 0.12) and body mass ($R^2_{partial}$ = 0.07) had the highest partial R^2values (Table 1). Deviant forms sold for significantly higher prices than common ones (Fig. 1c, β = 1.83, SE_{β} = 0.08, P < 0.001). Similarly, horn or tusk length (β = 0.60, SE_{β} = 0.25, P = 0.026) and body mass (β = 0.58, SE_{β} = 0.27, P = 0.044) were significantly positively related to higher prices (Table 1). In addition there were lower prices for species classed as "Near threatened" (β = -0.33, SE_{β} = 0.07, P < 0.001) and "Vulnerable" (β = -0.62, SE_{β} = 0.19, P < 0.001) compared to species classed as "Least concern". Although the prices of both "Endangered" and "Critically endangered" species were comparatively very high (Fig. 1b), these were caused by high prices of a single species, the black rhino.

Overall, prices of ungulates had increased over time (β = 0.05, SE_{β} = 0.01, P < 0.001). However, ungulates of deviant forms had increased more in prices than common forms along the studied period (β = 0.10, SE_{β} = 0.01, P < 0.001), and horn or tusk length was also associated with a larger increase in prices over time (β = 0.02, SE_{β} < 0.01, P < 0.001). Ungulates classed as "Near threatened" (β = -0.03, SE_{β} = 0.01, P = 0.005) and "Critically endangered" (β = -0.15, SE_{β} = 0.07, P = 0.035) had increased less in prices compared to ungulates classed as "Least concern". In addition, body mass, diet breadth and litter size were positively associated with increases in prices over time (Table 1).

DISCUSSION

While a previous study has shown that South African wildlife prices may not be aligned with environmental conservation goals (Dalerum and Miranda 2016), we here show that prices were mostly related to characteristics associated with rarity and aesthetics, and that the importance of these characteristics had increased over time. It is well recognized that humans prefer certain animals before others (Kellert 1996), and that these preferences are often based on aesthetic values (Stokes 2007, Val-Ilosera and Cassey 2017). Body and trophy size have previously been positively related to prices paid for African trophy hunts (Johnson et al. 2010), and we suggest that aesthetic values may be an important driver for the relative values people place on African wildlife species. Since aesthetic preferences often bias conservation efforts (Coursey 1998, Czech et al. 1998), we call for caution in using consumer's revealed preferences through market prices for directing conservation and management of African wildlife.

In our study, the IUCN category did not significantly affect prices, which suggests that not all aspects of rarity may be important. Instead, novelty, in the form of deviant populations or colour mutations, was one of the main factors influencing prices. We argue that a market demand for rarity and novelty may hamper the alignment between economic activities and conservation values through two separate processes. First, a demand for rare species may lead to a disproportionate exploitation of them and subsequently an even further increased extinction risk (Courchamp et al. 2006). Secondly, a demand for novelty may lead to a market focus on oddities, or even the active creation of them (e.g., gene manipulation of antelope for the creation of novel colour morphs, Antelope Specialist Group 2015). Such practices may be problematic for several reasons (Taylor et al. 2016). For instance, the elevated economic values of deviant animals may lead to intensively controlled breeding conditions that do not favour ecological and biodiversity values. In addition, the economic reliance on novelty value alone may eventually lead to price instability or even market collapse similar to large scale collapses of economic bubbles (Shiller 2016).

The South African large carnivore fauna includes some of the most well-known species in the world, many of which are recognized as conservation flagships (Dalerum et al. 2008). However, we did not find that carnivores were more expensive than ungulates, or that any species characteristics appeared to have influenced the relative prices among carnivores. We find this poor relationship between the appreciation by market participants and species' economic values surprising. However, as hypothesized, we suggest that the higher real or perceived cost of farming carnivores compared to herbivores, for instance in terms of increased costs of food supply and larger area requirements, may have caused their prices to be lower than expected.

We provide several potential limitations to our study. First, we used annual prices over an extended period of time that spanned significant political turmoil in South Africa, including the breakdown of the previous apartheid system. Second, we used simple linear relationships to evaluate the relative effects of differences in temporal trends of prices among and within species. Finally, the fixed effects of our respective models explained less than half of the variances in prices of both carnivores and ungulates. While annual prices prevented us from evaluating both buyer and auction specific price variables, they may provide more robust estimates of variation among species, which was the core focus of our study. However, the low amount of explained variance suggests strong effects of non-species related factors on these auction prices. Such factors can likely be related to characteristics of each respective buyer, such as financial assets, current wildlife stock, and personal preferences, but also to characteristics related to the auction event or to general market characteristics. For instance, we have not taken into consideration details on the number of animals sold at each auction event, how many buyers were present at each auction, or how large proportion of animals were sold at auctions versus directly through private sales. Such characteristics have previously been shown important for animal prices (Kassie et al. 2011, Terfa et al. 2013). Similarly, international exchange rates, total number of active wildlife farms, and total number of potential consumers of the products of wildlife farms (e.g., game tourists, trophy hunters and game meat consumers) are all of them likely to influence prices (e.g., Ayele et al. 2006).

To conclude, we found no difference in prices between native carnivores and ungulates, between exotic and native species, nor any effects of species characteristics on the prices on carnivores. However, both conservation status, deviations from the normal colour morph, body size and horn size influences prices of ungulates. We interpret these relationships as indicators of an importance of novelty and aesthetics, and our results suggested that this importance has increased over time. However, species characteristics explained less than 50% of price variation among species. We therefore encourage further work towards a full evaluation of the relative influences of species characteristics versus factors relating to different characteristics of the market participants as well as features of the market that are intrinsically linked to economic processes on the price variations in South African wildlife. Such an evaluation is paramount to fully be able to assess the conservation potential of this particular economic market, and may be highly instructional as a model for evaluating the potential contribution of economic markets towards solutions for the current environmental crisis.

REFERENCES

Antelope Specialist Group. 2015. *IUCN SSC ASG Position Statement on the Intentional Genetic Manipulation of Antelopes Ver. 1.0 (30 April 2015).* IUCN SSC Antelope Specialist Group. URL: https://www.iucn.org/sites/dev/files/import/downloads/asg_igm_posnsment_2015_final_19may_2015.pdf.

Amin, A. 2016. Exploring the role of economic incentives and spillover effects in biodiversity conservation policies in sub-Saharan Africa. *Ecological Economics* 127: 185-191.

Ayele, G., M. A. Jabbar, H. Teklewold, E. Mulugeta and G. Kebede. 2006. Seasonal and inter-market differences in prices of small ruminants in Ethiopia. *Journal of Food Products Marketing* 12: 59-77.

Balmford, A., A. Bruner, P. Cooper, R. Costanza, S. Farber, R. E. Green, M. Jenkins, P. Jefferiss, V. Jessamy, J. Madden, K. Munro, N. Myers, S. Naeem, J. Paavola, M. Rayment, S. Rosendo, J. Roughgarden, K. Trumper, and R. K. Turner. 2002. Economic reasons for conserving wild nature. *Science* 297: 950-953.

Benjaminsen, T. A., and I. Bryceson. 2012. Conservation, green/blue grabbing and accumulation by dispossession in Tanzania. *Journal of Peasant Studies* 39: 335-355.

Bothma, J. P., J. G. du Toit, and J. van Rooyen 2010. Buying and selling wild animals. Pages 619-639 *in* J. P. Bothma, editor. *Game Ranch Management*. Van Schaik, Johannesburg, South Africa.

Bush, E., S. E. Baker, and D. W. Macdonald. 2014. Global trades in exotic pets 2006-2013.

Conservation Biology 28: 663-676.

Carpenter, S. R., H. A. Mooney, J. Agard, D. Capistrano, R. S. DeFries, S. Díaz, T. Dietz, A. K. Duraiappah, A. Oteng-Yeboah, H. Miguel Pereira, C. Perrins, W. V. Reid, J. Sarukhan, R. J. Scholes, and A. Whyte. 2009. Science for managing ecosystem services: Beyond the Millennium Ecosystem Assessment. *Proceedings of the National Academy of Science, USA* 106: 1305-1312.

Courchamp, F., E. Angulo, P. Rivalan, R. J. Hall, L. Signoret, L. Bull, and Y. Meinard. 2006. Rarity value and species extinction: the anthropogenic Allee effect. *PLoS Biology* 4: e415.

Costanza, R., R. d'Arge, R. de Groot, S. Farberk, M. Grasso, B. Hannon, K. Limburg, S. Naeem, R. V. O'Neill, J. Paruelo, R. G. Raskin, P. Suttonkk, and M. van den Belt. 1997. The value of the world's ecosystem services and natural capital. *Nature* 387: 253-260.

Coursey, D. L. 1998. The revealed demand for a public good: Evidence from endangered and threatened species. *New York University Environmental Law Journal* 6: 411–449.

Court, A. T. 1939. Hedonic price indexes with automotive examples. In *The dynamics of automotive demand*, 98-119. New York, General Motors.

Cousins, J. A., J. P. Sadler, and J. Evans. 2008. Exploring the role of private wildlife ranching as a conservation tool in South Africa: Stakeholder perspectives. Ecology and Society 13: 43.

Czech, B., P. R. Krausman, and R. Borkhartaria. 1998. Social construction, political power, and allocation of benefits to endangered species. *Conservation Biology* 12: 1103–1112.

Dalerum, F. 2013. Phylogenetic and functional diversity in large carnivore assemblages. *Proceedings of the Royal Society of London, Series B Biology* 280: 20130049.

Dalerum, F. 2014. Identifying the role of conservation biology for solving the environmental crisis. *Ambio* 43: 839-846.

Dalerum, F., and M. Miranda. 2016. Game auction prices are not related to biodiversity contributions of southern African ungulates and large carnivores. *Scientific Reports* 6: 21922.

Dalerum, F., M. J. Somers, K. E. Kunkel, and E. Z. Cameron. 2008. The potential for large carnivores to act as biodiversity surrogates in southern Africa. *Biodiversity and Conservation* 17: 2939-2949.

Edwards, L. J., K. E. Muller, R. D. Wolfinger, B. F. Qaqish, and O. Schabenberger. 2009. An R^2 statistic for fixed effects in the linear mixed model. *Statistics in Medicine* 27: 6137-6157.

Ehrlich, P. R., and A. H. Ehrlich. 2013. Can a collapse of global civilization be avoided? *Proceedings of the Royal Society of London, Series B Biology* 280: 20122845.

Gray, G. G. 1995. *The human dimensions to wildlife ecology*. Champaign, Il: Illinois University Press.

Hector, A., S. Felten, and B. Schmid. 2010. Analysis of variance with unbalanced data: an update for ecology and evolution. *Journal of Animal Ecology* 79: 308-316.

Honey, M. 2008. *Ecotourism and sustainable development: Who owns paradise?* 2nd edition. Island Press, Washington, D.C., USA.

Jaeger, B. 2016. r2glmm: Computes R squared for mixed (multilevel) models. R package version 0.1.1. https://CRAN.R-project.org/package=r2glmm

Johnson, P. C. D. 2014. Extension of Nakagawa and Schielzeth's R^2_{GLMM} to random slopes models. *Methods in Ecology and Evolution* 5: 944-946.

Johnson, P. J., R. Kansky, A. J. Loveridge, and D. W. Macdonald. 2010. Size, rarity and charisma: valuing African wildlife trophies. *PLoS ONE* 5: e12866.

Jones, K. E., J. Bielby, M. Cardillo, S. A. Fritz, J. O'Dell, C. D. L. Orme, K. Safi, W. Sechrest, E. H. Boakes, C. Carbone, C. Connolly, M. J. Cutts, J. K. Foster, R. Grenyer, M. Habib, C. A. Plaster, S. A. Price, E. A. Rigby, J. Rist, A. Teacher, O. R. P. Bininda-Emonds, J. L. Gittleman, J. L., G. M. Mace, and A. Purvis. 2009. PanTHERIA: a species-level database of life history, ecology, and geography of extant and recently extinct mammals. *Ecology* 90:2648.

Kassie, G. T., A. Abdulai, and C. Wollny. 2011. Heteroscedastic hedonic price model for cattle in the rural markets of central Ethiopia. *Applied Economics* 43:3459-3464.

Kellert, S. R. 1996. *The value of life: Biological diversity and human society.* Island Press, Washington, D.C., USA.

Lancaster, K. 1966. A new approach to consumer theory, *Journal of Political Economy* 74: 132–57.

Mace, G. M. 2014. Whose conservation? *Science* 345: 1558-1560.

Nakagawa, S. and H. Schielzeth. 2013. A general and simplemethod for obtaining R^2 from generalized linearmixed-effectsmodels. *Methods in Ecology and Evolution* 4: 133-142.

Pinheiro, J., D. Bates, S. DebRoy, and D. Sarkar. 2016. *nlme: Linear and nonlinear mixed effect models.* R package version 3.1-127. URL: http://CRAN.R-project.org/package=nlme.

Rosen, S. 1974 . Hedonic prices and implicit markets: product differentiation in pure competition, *Journal of Political Economy* 82: 34–5.

Shiller, R. J. 2016. *Irrational exuberance.* Princeton University Press, Princeton, USA.

Skinner, J. D., and C. Chimimba. 2005. *Mammals of the southern African subregion.* Cambridge University Press, Cambridge, UK.

Snijders, D. 2012. Wild property and its boundaries – on wildlife policy and rural consequences in South Africa. *Journal of Peasant Studies* 39: 503-520.

Stokes, D. 2007. Things we like: human preferences among similar organisms and implications for conservation. *Human Ecology* 35: 361–369.

Taylor, A., P. Lindsey, and H. Davies-Mostert, H. (2016). *An assessment of the economic, social and conservation value of the wildlife ranching industry and its potential to support the green economy in South Africa.* Green economy research report, Developm. Bank of South Africa, Johannesburg, South Africa.

Terfa, Z. G., A. Haile, D. Baker, and G. T. Kassie. 2013. Valuation of traits of indigenous sheep using hedonic pricing in Central Ethiopia. *Agricultural and Food Economics* 1: 6.

Turnhout, E., C. Waterton, K. Neves, and N. Buizer. 2014. Rethinking biodiversity: from goods and services to “living with”. *Conservation Letters* 6:154–161.

Val-Ilosera, M., and P. Cassey. 2017. Physical attractiveness, constraints to the trade and handling requirements drive the variation in species availability in the Australian cagebird trade.

Ecological Economics 131: 407-413.

Van der Merwe, P., M. Saayman, and W. Krugell. 2004. Factors that determine the price of game. *Koedoe* 47: 105–113.

Veblen, T. 1889. *The Theory of the Leisure Class*. Macmillan, New York.

UNEP. 2011. *Towards a green economy: Pathways to sustainable development and poverty eradication – a synthesis for policy makers*. United Nations Environment Programme, Nairobi, Kenya.

Fig. 1. Differences in average annual auction prices between native and exotic carnivores and ungulates of the common form (a), among carnivores and ungulates from different IUCN threat categories (b, LC – "Least concern", NT – "Near threatened", VU = "Vulnerable", EN – "Endangered", CR – "Critically endangered", EW – "Extinct in the wild") and between common and deviant forms of 12 ungulate species that were sold from non-native populations or in deviant colour mutations (c). The massive elevation in prices for EN and CR ungulate species were due to high prices of the black rhino (*Diceros bicornis*). The figure describes average prices calculated from average species prices ± 1 SE of species averages.

Table 1. Partial R^2values (with 95% confidence limits), beta coefficients, their associated standard errors as well as p-values from mixed linear models of the effects of a series of biological predictors on annual prices of carnivores and ungulates. For categorical predictors, the beta coefficients describe the difference between each level and the reference level. For continuous predictors, the coefficients describe the unit of log (price) change over each standard deviation unit of change of the predictor. The magnitude of the beta coefficients is therefore directly comparable among the different continuous characters.

	Carnivores				Ungulates				Ungulates over time		
Class/Predictor	R^2	β	SE_{β}	P	R^2	β	SE_{β}	P	β †	SE_{β}	P
Rarity											
IUCN: NT‡					0.01 (0-0.03)	-0.33	0.07	< 0.001	-0.03	0.01	0.005
IUCN: VU‡	0.07 (0.0-0.27)	2.92	0.69	0.147	0.01 (0-0.02)	-0.62	0.19	< 0.001	-0.03	0.02	0.165
IUCN: EN‡	< 0.01 (0-0.116)	1.53	0.80	0.307	< 0.01 (0-0.01)	-0.36	0.29	0.212	-0.02	0.04	0.596
IUCN: CR‡					< 0.01 (0-0.02)	-0.82	0.48	0.085	-0.15	0.07	0.035
IUCN: EW‡					< 0.01 (0-0.01)	-1.24	2.21	0.579	-0.12	0.09	0.154
Origin: Exotic‡	0.01 (0-0.16)	1.91	0.95	0.293	< 0.01 (0-0.01)	0.24	1.02	0.811	-0.01	0.02	0.489
Form: Deviant ‡					0.16 (0.12-0.21)	1.83	0.08	< 0.001	0.10	0.01	< 0.001
Aesthetics											
Horn length					0.10 (0.06-0.13)	0.60	0.25	0.026	0.02	< 0.01	< 0.001
Colour pattern:	0.12 (0.01-0.34)										
Spotted/striped‡		0.81	0.75	0.473							
Ecology											
Body mass	0.12 (0.0-0.336)	0.65	0.65	0.394	0.07 (0.04-0.10)	0.58	0.27	0.044	-0.01	0.01	0.014
Activity: Nocturnal‡	0.12 (0.01-0.34)	0.71	0.80	0.538	< 0.01 (0-0.01)	-0.59	1.03	0.572	0.04	0.04	0.217
Activity: Both‡	0.09 (0-0.29)	1.69	1.02	0.345		-0.30	0.45	0.504	< 0.01	0.01	0.684
					0.01 (0-0.02)						
Group size	0.02 (0-0.17)	-0.50	0.95	0.636	0.06 (0.03-0.09)	-0.29	0.22	0.204	-0.01	< 0.01	0.002
Litter size					0.05 (0.03-0.08)	-0.44	0.22	0.052	-0.02	0.01	0.000
Density					0.01 (0-0.03)	-0.19	0.24	0.447	< 0.01	0.01	0.381

Home range size	< 0.01 (0-0.12)	0.13	0.88	0.893	0.01 (0-0.03)	0.26	0.33	0.432	0.01	0.01	0.271
Diet breadth					0.01 (0-0.02)	0.14	0.23	0.566	-0.01	< 0.01	0.039

† Interaction coefficients, which for categorical predictors describe the difference in the trend of price over time between each level and the reference level, and for continuous predictors describe the change in trend of price over time per standard deviation change in the predictor.

‡ Categorical predictor. Reference levels: IUCN class = "Least concern", Origin = "Native", Form = "Common", Colour pattern = "Plain", Activity = "Diurnal"

Abstract

For successful integration of biological conservation into economic markets, economic processes need to capture ecological values. South African wildlife ranching is a tourist based activity that generates unique information on the economic value of wildlife species. We used public data from South African wildlife auctions to evaluate if annual prices 1991-2012 related to species characteristics associated with scarcity, aesthetics and ecology ~~evaluated how species characteristics were related to auction prices~~ of South African ~~large~~ carnivores and ungulates~~ during 1991-2012~~. While none of the species characteristics ~~considered~~ influenced carnivore prices, ungulate prices were related to characteristics~~factors~~ associated with novelty and aesthetics, which~~. The~~ relative importance had ~~of these factors had also~~ increased over time. We raise both ecological and economic concern for~~of~~ this apparent focus. Our results also suggest a potential importance of ~~suggested that~~ non-species related factors, such as market and~~for instance market size,~~ buyer characteristics~~ and characteristics of the sale events, had likely been influential~~. We encourage further evaluation~~therefore encourage a quantification~~ of the relative influences of species characteristics versus factors that are intrinsically linked to economic processes on price variations in ~~importance of environmental values versus such economic factors for determining~~ South African wildlife~~ prices~~.

Key words

consumer preferences; ecological economics, ecotourism; game farming; hedonic pricing~~species characteristics~~; wildlife

INTRODUCTION

Humanity has induced ~~during the past few centuries had~~ unprecedented and accelerating negative impacts on Earth's biota during the past few centuries. Following a broad realization~~recognition~~ of these detrimental environmental impacts, there has been a subsequent recognition that they may lead to ~~have~~ dramatic and negative consequences for humanity itself (Ehrlich and Ehrlich 2013). Substantial effort has consequently been invested in attempting to preserve biological resources, and to better align human societies with the biotic environment (Mace 2014). This work is currently putting a large emphasis on finding sustainable interactions between human societies and the environment (Carpenter et al. 2009, Turnhout et al. 2014). However, although much of the key principles of how such interactions should be structured are known, public authorities have not yet been able to accomplish their full incorporation~~we have still not managed to fully incorporate them~~ into public policy (Dalerum 2014).

Economic processes regulate much of modern human societies, in particular the distribution of the material dimensions of human welfare. It is therefore not surprising that there have been frequent attempts to find synergies between environmental protection and economic markets. Such synergies have partly focused on monetary valuations of environmental resources (Costanza et al. 1997, Balmford et al. 2002), but also on finding less environmentally damaging ways of structuring economic activities (UNEP 2011). For instance, an evolving ecotourism market is attempting to use consumer experiences as economic commodities in a non-consumptive way (Honey 2008). Ecotourism has been suggested as particularly useful to provide economic incentives for conservation action in impoverished societies (Amin 2016), although the opposite has also been argued (Benjaminsen and Bryceson 2012).

Commercial wildlife ranching in South Africa is a tourism driven industry that is economically important and has the potential to contribute to the biodiversity conservation (Cousins~~Taylor~~ et al. 2008~~2016~~). Following a legislative change in 1991 it became possible to privately own free ranging wildlife in South Africa (Snijders 2012). There has subsequently been a rapid increase in commercially driven wildlife ranches (Taylor et al. 2016). These ranches are primarily generating revenue from ecotourism and trophy hunting, but also through meat production and from selling wildlife to other ranches (Van der Merwe et al. 2004). Wildlife ranching has grown to a considerable industry, consisting of an estimated 9,000~~9000~~ wildlife ranches covering 14% of South Africa's land area (170,000 km^2) (Taylor et al. 2016). Wildlife species are traded between ranches, both through private sales and through official auctions (Bothma et al. 2010). Although the total amount of animals sold privately is unknown, it is estimated to be 4-6 times as high as the number of animals sold at auctions. However, the total live sales are estimated to turnover approximately 320 million USD (Taylor et al. 2016). A recent study suggests that prices in this market are unrelated to species' evolutionary and ecological significance (Dalerum and Miranda 2016), but we still have scant information on what is driving the prices of South African wildlife. A good market alignment with environmentally important characteristics is a requirement for any wildlife based market to actively contribute to environmental sustainability (Dalerum & Miranda 2016).

The hedonic pricing model addresses the marginal trade-offs in the markets performed by consumers and sellers and is often used to evaluate the relative influences of intrinsic and extrinsic values of products (Court 1939). It is intuitive to regard aesthetic and physical attributes as important for the satisfaction tourists get from wildlife. Hence, the hedonic model is well suited for economic evaluations of wildlife, since it primarily focuses on the satisfaction given by attributes of goods (Gray 1995). Under this model, goods can be described as composites of different intrinsic properties, so-called characteristics (Rosen 1974), and consumer's utility depends on the different characteristics that the goods have (Lancaster, 1966). This stand in contrast to the neoclassical economic framework, which assumes that consumers want to purchase goods because of the utilities they directly provide.

Scarcity is a specific characteristic of goods that is central to economic theory. A greater scarcity is often associated with higher prices in the market. Although high prices could hamper consumption, they could also lead to an increasde desire for goods since price can be a quality indicator as well as indicator of the social status of the buyer (Veblen, 1889). Subsequently, the rarity of animals has been related to various aspects of their economic attractiveness. For instance, IUCN (International Union for Conservation of Nature) threat category has been associated to both African trophy hunting prices (Johnson et al. 2010) and to the number of mammals and reptiles traded as exotic pets (Bush et al. 2014). In addition, prices for species of caged birds in Australia have been negatively associated with their abundance in captivity (Val-Ilosera and Cassey 2017). However, we note that the market prices of South African wildlife could be analysed from both demand-side and supply-side perspectives as changes in prices are likely to reflect not only consumer behaviour, but also supply side effects such as the costs associated with housing and maintaining wildlife populations.

~~Although the commercialisation of South African wildlife has been claimed as a great conservation success, it is still an industry that is largely driven by consumer (i.e. tourist and hunter) preferences (Cousins et al. 2008). The prices paid for wildlife are therefore likely to be at least partly related to consumer demand. Since most economic valuations of environmental resources are based on indirect methods, South African wildlife auctions provide a unique source of information of direct economic values of an environmental asset. This may be important, since any successful merge of market economies and environmental protection rests on a positive alignment between market forces and environmental values. A recent study suggests that prices in this market are unrelated to species' evolutionary and ecological significance (Dalerum and Miranda 2016), but we still have scant information on what is driving the prices of South African wildlife.~~ In this study we used~~use~~ a 22-~~-~~year data set on annual average wildlife auction prices from South Africa to evaluate if the prices were associated to species characteristics related to their scarcity, aesthetics and ecology. The analyses were restricted to a sample of ~~We have restricted the analyses to~~ mammalian ungulates of the orders Artiodactyla and Perissodactyla as well as to carnivores > 10kg in body size, since these are the species mostly traded in the South African game industry (Taylor et al. 2016). A priori we hypothesized that (i) rarity, both within and among species, would be positively related to prices; (ii) aesthetic values, which have previously been shown important for wildlife values, would be positively related to prices; (iii) certain aspects of species ecology, primarily carnivory, large body size and large home range size, would be negatively related to prices since we believe they would be ~~. We deliberately chose characters related to scarcity because of its central role in economic theory. Briefly, people are prepared to pay for a product (i.e. a good or a service) only if it satisfies any of their needs and it is in limited supply. We selected traits~~ associated with increased hosting and maintenance costs. Finally, because of an increased environmental awareness during the past 20 years (Mace 2014), we expected that the relationships between prices and species characteristics had shifted over time, with an increased positive association between prices and ecologically relevant characteristics. We envision such a change to have been caused by an increased consumer demand for ecologically relevant species. ~~aesthetics and ecology since we anticipated that these traits could be associated with consumer preferences for particular species, or to the costs associated with hosting them.~~

METHODS

Compilation of price data

We compiled ~~the~~ annual average wildlife auction prices between 1991 and 2012 from the recreational journal *Game and Hunt* (http://www.wildlifehunt.co.za) and from an electronic newsletter from International Council for Game and Wildlife Conservation (http://africanindaba.com; Dalerum and Miranda 2016). Our data included information on 6 species of native large carnivores (>10kg, see Dalerum 2013) and on 37 species of native ungulates (Dalerum and Miranda 2016). We also included information on one exotic large carnivore species (*Panthera tigris*) and 3 species of exotic ungulates (*Dama dama, Kobus leche, Oryx dammah*). For 10 ungulates we obtained prices both from the common form as well as from non-native populations or from deviant colour mutations. We treated these prices separately in the analyses (see descriptions below). Apart from bushbuck (*Tragelaphus scriptus*) during 2010-2012, we did not have separate prices for males and females. For this species, we used average prices across both sexes for the years we did have sex specific information. We treated bontebok (*Damaliscus pygargus pygargus*) and blesbok (*Damaliscus pygargus phillipsi*) as separate taxonomic entities ~~as a separate species~~ in our data. We have presented the prices in the original South African currency (South African Rand, ZAR), but adjusted prices for inflation by ~~adjusted prices for inflation using 2012 as our reference year~~ using average annual consumer price indices available from~~form~~ Statistics South Africa with 2012 as reference year (http://www.statssa.gov.za). All raw average annual prices are given in Table S1.

Compilation of data on species characteristics

The hedonic pricing approach argues that the price of any good is the sum of the unobserved prices of the bundle of their characteristics. Therefore, we related prices to a series of species specific characteristics associated with rarity, ecology and aesthetics (Table S2). We used the hedonic price function $P_i = f(R_{i1},\ldots,R_{ij}, A_{i1},\ldots,A_{ik}, E_{il},\ldots,E_{il})$, where P_i is the price for a given species defined as a function of specific characteristics associated with rarity (R_{i1-j}), aesthetics (A_{i1-k}), and ecology (E_{i1-l}).

We used three variables to reflect the rarity of a given species of ungulates, and two for carnivores; a species geographic origin, IUCN Red List category, and whether or not it was from a non-native population or had deviant morphology (only for ungulates, Table ~~related prices to a series of species specific characteristics associated with rarity, ecology and aesthetics (table~~ S2). We scored if each species were native or not to South Africa based on the official IUCN distribution maps. We used~~compiled~~ the relevant global assessment of the IUCN Red List classification for each year and species from the IUCN Red List database (http://www.iucnredlist.org/). For species where we had prices prior to an initial IUCN assessment, we back-dated the classification each year using the first assessment available. We converted previous Red List red list classifications to the current ones for consistency. For 10 ungulate species we had prices for either non-native populations (east African populations of buffalo *Syncerus caffer*; Zambian populations of sable *Hippotragus niger*; Livingstone's eland *Taurotragus oryx*, Hartmann's mountain zebra *Equus zebra*) as well as deviant colour mutations for impala (*Aepyceros melampus*), springbok (*Antidorcas marsupialis*), blue wildebeest (*Connochaetes taurinus*), blesbok (for the analyses we treated the bontebok as a separate taxonomic entity), gemsbok (*Oryx gazella*), and the greater kudu (*Tragelaphus strepsiceros*). We treated all of these populations and colour forms as deviant forms in our analyses. For ungulates, we compiled data on maximum horn length recorded in southern Africa from Skinner and Chimimba (2005), except for bushpig (*Potamochoerus larvatus*), common warthog (*Phacochoerus africanus*) and hippopotamus (*Hippopotamus amphibious*) for which we instead used the tusk length. For black (*Diceros bicornis*) and white (*Ceratotherium simum*) rhinoceros we only used the length of the front horn. For carnivores, we compiled data on colour patterns, and classed each species as either plain or patterned (spotted or striped). Finally, we downloaded a series of characters from the PanTHERIA data base (Jones et al. 2009). These characters included body mass (averaged between males and females), population density, home range size, activity cycle (classed as a categorical variable: diurnal, nocturnal, or both), social group size, and diet breadth (only recorded for ungulates). Data were error checked and missing species data were supplemented with information from other sources (Table S2). The raw data are available in Table S3.

We used one character for carnivores and ungulates respectively to reflect aesthetics; colour pattern (carnivores) and horn or tusk length (ungulates). We compiled data on colour patterns for all carnivores, and classed each species as either plain or patterned (i.e., spotted or striped). For ungulates, we compiled data on maximum horn length recorded in southern Africa from Skinner and Chimimba (2005), except for bushpig (*Potamochoerus larvatus*), common warthog (*Phacochoerus africanus*) and hippopotamus (*Hippopotamus amphibious*) for which we instead used the tusk length. For black (*Diceros bicornis*) and white (*Ceratotherium simum*) rhinoceros we only used the length of the front horn.

Finally, we downloaded a series of characters from the PanTHERIA database to reflect species ecology (Jones et al. 2009). These characters included body mass (averaged between males and females), population density, home range size, activity cycle (classed as a categorical variable: diurnal, nocturnal, or both), social group size, and diet breadth (only recorded for ungulates). Data were error checked and missing species data were supplemented with information from other sources (Table S2). The raw data are available in Table S3.

Data analyses

We used mixed linear models to associate these species characteristics to market prices. Following Hector et al. (2010), we ran subset models to maximize the amount of included data for our evaluations of relationships between prices and species characteristics, as well as if these relationships had changed over time. We did not use a sequential approach to model selection based on information theoretic criteria, but rather selected representative characteristics a-priori and evaluated each predictor while retaining all other a-priori selected predictors simultaneously in the model~~enable us to test specific hypotheses with the maximum amount of included data~~. First, although not directly included in our hedonic price evaluation, we compared prices of carnivores and ungulates using a model including all carnivore and ungulate species for which we had at least one price, but we only included species native to South Africa and only the common colour morph or population. In this model we used the average annual price as the response variable and used taxonomic group (i.e. carnivore or ungulate) as the only fixed effect. Second, we ran two models in which ~~were~~ we related prices to species characteristics of carnivores and ungulates separately ~~to species characteristics~~. In both of these models we used the average annual price as the response. For carnivores we removed predictors that were correlated > 80%, whereas all predictors were correlated < 50% for ungulates. In the carnivore model, we retained IUCN category, origin (native or exotic), activity cycle (diurnal, nocturnal or both) and colour pattern as categorical predictors, and body mass, social group size and home range size as continuous predictors. In the ungulate model, categorical predictors were ~~we used~~ IUCN category, origin (native or exotic), activity cycle (diurnal, nocturnal or both) and morph type (i.e. common or deviant morphological form or population), while ~~as categorical predictors and~~ body mass, horn or ~~/~~tusk length, density, social group size, diet breadth and litter size are~~as~~ continuous predictors. For these two models, we calculated the marginal R^2 following Johnson (2014, but see Nakagawa and Schielzeth 2013) as a heuristic way of evaluating the total amount of price variation that was explained by our species characteristics, and the coefficient of determination as defined by Edwards et al. (2008) as a heuristic method of evaluating the relative amount of explained variance for each of our different predictors (i.e. interpretable as a partial R^2 in a linear model). ~~.~~Finally, we ran a fourth model to evaluate the effect of species characteristics on temporal change in prices. In this last model,~~model~~ we only included ungulate species with at least three years of available data. We did not have sufficient data on carnivores for this analysis. This model had the same structure as the previous one, with the exception that we added year as a fixed linear covariate~~continuous fixed co-variate~~, as well as a 2-way interaction term between year and each of the other fixed predictors. Hence, this model is evaluating differences in a linear temporal trend of prices among factor levels (for categorical predictors) or along the values of continuous predictors. In all models, we log transformed prices following Rosen (1974), and visually inspected the residuals prior to analyses so that they conformed to heteroscedasticity. We ~~to account for heteroschedasticity, and we~~ added year grouped over species as a random effect structure to account for the temporal~~spatial~~ and taxonomic structure of our data. We also scaled all continuous variables by subtracting the means and dividing them by their standard deviations. For continuous predictors, this scaling gives coefficients that represent changes in the dependent variable (log price) per standard deviation unit change in the predictor. Hence, through this scaling ~~, to make~~ all beta coefficients are directly comparable.

All statistical analyses were done in the statistical environment R version 3.3.0 for Linux (http://r-project.org) and the used the contributed packages~~package~~ nlme (Pinheiro et al. 2016) and r2glmm (Jaeger 2016).

RESULTS

Native carnivores did not differ significantly in average prices compared to native ungulates in their common form ($\beta = -0.35$, $SE_{\beta} = 0.69$, $P = 0.612$). The species characteristics explained 48% of the variation in prices for carnivores and 46% for ungulates. For carnivores, body mass ($R^2_{partial} = 0.12$), colour pattern ($R^2_{partial} = 0.12$) and activity patterns (nocturnal $R^2_{partial} = 0.12$, both nocturnal and diurnal $R^2_{partial} = 0.09$) had the highest partial R^2values, but none of the biological characteristics had a significant effect on auction prices (Table 1, Fig. 1a,b). For ungulates, type (i.e. either deviant colour morphs of populations, $R^2_{partial} = 0.16$), horn or tusk length ($R^2_{partial} = 0.12$) and body mass ($R^2_{partial} = 0.07$) had the highest partial R^2values (Table 1). Deviant forms sold for significantly higher prices than common ones (Fig. 1c, $\beta = 1.83$, $SE_{\beta} = 0.08$, $P < 0.001$). Similarly, horn or tusk length ($\beta = 0.60$, $SE_{\beta} = 0.25$, $P = 0.026$) and body mass ($\beta = 0.58$, $SE_{\beta} = 0.27$, $P = 0.044$) were significantly positively related to higher prices (Table 1). In addition there were lower prices for species classed as "Near threatened" ($\beta = -0.33$, $SE_{\beta} = 0.07$, $P < 0.001$) and "Vulnerable" ($\beta = -0.62$, $SE_{\beta} = 0.19$, $P < 0.001$) compared to species classed as "Least concern". Although the prices of both "Endangered" and "Critically endangered" species were comparatively very high (Fig. 1b), these were caused by high prices of a single species, the black rhino.

Native carnivores did not differ significantly in average prices compared to native ungulates in their common form ($\beta = -0.35$, $SE_{\beta} = 0.69$, $P = 0.612$). Similarly, exotic species did not differ in prices from native ones for either carnivores ($\beta = 1.91$, $SE_{\beta} = 0.95$, $P = 0.293$) or ungulates ($\beta = 0.24$, $SE_{\beta} = 1.02$, $P = 0.811$) (Fig. 1a). For carnivores, none of the biological characteristics had a significant effect on auction prices (Table 1). For ungulates, there were lower prices for species classed as "Near threatened" ($\beta = -0.33$, $SE_{\beta} = 0.07$, $P < 0.001$) and "Vulnerable" ($\beta = -0.62$, $SE_{\beta} = 0.19$, $P < 0.001$) compared to species classed as "Least concern". Although the prices of both "Endangered" and "Critically endangered" species were comparatively very high (Fig. 1b), these were caused by

~~high prices of a single species, the black rhino. However, deviant forms sold for significantly higher prices than common ones (Fig. 1c, $\beta = 1.83$, $SE_{\beta} = 0.08$, $P < 0.001$). In addition, horn/tusk length ($\beta = 0.60$, $SE_{\beta} = 0.25$, $P = 0.026$) and body mass ($\beta = 0.58$, $SE_{\beta} = 0.27$, $P = 0.044$) were associated with higher prices (Table 1). The species characteristics explained 48% of the variation in prices for carnivores and 46% in the ungulates.~~

Overall, prices of ungulates had increased over time ($\beta = 0.05$, $SE_{\beta} = 0.01$, $P < 0.001$). However, ungulates of ~~Ungulates of~~ deviant forms had increased more in prices than common forms along the studied period ($\beta = 0.10$, $SE_{\beta} = 0.01$, $P < 0.001$), and horn or ~~maximum horn/~~tusk length was also associated with a larger increase in prices over time ($\beta = 0.02$, $SE_{\beta} < 0.01$, $P < 0.001$). Ungulates classed as “Near threatened” ($\beta = -0.03$, $SE_{\beta} = 0.01$, $P = 0.005$) and “Critically endangered” ($\beta = -0.15$, $SE_{\beta} = 0.07$, $P = 0.035$) had increased less in prices compared to ungulates classed as “Least concern”. In addition, body mass, diet breadth and litter size were positively associated with increases in prices over time (Table 1).

DISCUSSION

While a previous study has shown that South African wildlife prices may not be aligned with environmental conservation goals (Dalerum and Miranda 2016), we here show that prices~~they~~ were mostly related to characteristics associated with rarity ~~novelty~~ and aesthetics, and that the importance of these characteristics ~~novelty and aesthetics~~ had increased over time. It is well recognized that humans prefer certain animals before others (Kellert 1996), and that these preferences are often based on aesthetic values (Stokes 2007, Val-Ilosera and Cassey 2017). Body and trophy size have previously been positively related to prices paid for African trophy hunts (Johnson et al. 2010), and we suggest that aesthetic values may be an important driver for the relative values people place on African wildlife species. Since aesthetic preferences often bias conservation efforts (Coursey 1998, Czech et al. 1998), we call for caution in using consumer’s revealed preferences through market prices~~public preferences, such as market prices,~~ for directing conservation and management of African wildlife.

In our study~~Scarcity is a central component in microeconomic theory (e.g., Smith 1776, Brock 1968), where scarce products generally are regarded as more desirable than common ones (Lynn 1991). In line with these economic realizations~~, the IUCN category did not significantly affect prices, which suggests that not all aspects of rarity may be important. ~~rarity of animals has been related to various aspects of their economic attractiveness. For instance, IUCN threat category has been associated to both African trophy hunting prices (Johnson et al. 2010) and to the number of mammals and reptiles traded as exotic pets (Bush et al. 2014), and prices for species of caged birds in Australia have been negatively associated with their abundance in captivity (Vall-Ilosera and Cassey 2017). In our study, however, the IUCN category did not significantly affect prices.~~ Instead, novelty, in the form of deviant populations or colour mutations, was one of the main factors influencing prices. We argue that a market demand for rarity and novelty ~~scarce products~~ may hamper the alignment between economic activities and conservation values through two separate processes. First, a demand for rare species may lead to a disproportionate exploitation of them and subsequently an even further increased extinction risk (Courchamp et al. 2006). Secondly, a demand for novelty~~rarity~~ may lead to a market focus on oddities, or even the active creation of them (e.g., gene manipulation of antelope for the creation of novel colour morphs, Antelope Specialist Group 2015). Such practices may be problematic for several reasons (Taylor et al. 2016). For instance, the elevated economic values of deviant animals may lead to intensively controlled breeding conditions that do not favour ecological and biodiversity values. In addition, the economic reliance on novelty value alone may eventually lead to price instability or even market collapse similar to large scale collapses of economic bubbles (Shiller 2016).

The South African large carnivore fauna includes some of the most well-~~-~~known species in the world, many of which are recognized as conservation flagships (Dalerum et al. 2008). However, we did not find that carnivores were more expensive than ungulates, or that any species characteristics appeared to have influenced the relative prices among carnivores. We find this poor relationship between the appreciation by market participants and species' ~~public recognition and~~ economic values surprising. However, as hypothesized, we suggest that the higher real or perceived cost of farming carnivores compared to herbivores, for instance in terms of increased costs of food supply and larger area requirements, may have caused their prices to be lower than expected. ~~based on the public attention many of these species get.~~

We provide several potential limitations to our study. First, we used annual prices over an extended period of time that spanned significant political turmoil in South Africa, including the breakdown of the previous apartheid system. Second, we used simple linear relationships to evaluate the relative effects of differences in temporal trends of prices among and within species. Finally, the ~~The~~ fixed effects of our respective models explained less than half of the variances in prices of both carnivores and ungulates. While annual prices prevented us from evaluating both buyer and auction specific price variables, they may provide more robust estimates of variation among species, which was the core focus of our study. However, the low amount of explained variance suggests strong effects~~We interpret these results as a strong effect~~ of non-species related factors on these auction prices. Such factors can likely be related to characteristics of each respective buyer, such as financial assets, current wildlife stock, and personal preferences, but also to characteristics related to the auction event or to general market characteristics. For instance, we have not taken into consideration details on the number of animals sold at each auction event, how many buyers were present at each auction, or how large proportion of animals were sold at auctions versus directly through private sales. Such characteristics have previously been shown important for animal prices (Kassie et al. 2011, Terfa et al. 2013). Similarly, international exchange rates, total number of active wildlife farms, and total number of potential consumers of the products of wildlife farms (e.g., game tourists, trophy hunters and game meat consumers) are all of them likely to influence prices (e.g., Ayele et al. 2006). ~~likely to all influence prices. We encourage further work towards a full evaluation of the relative influences of species characteristics versus factors that are intrinsically linked to economic processes on the price variations in South African wildlife. Such an~~

~~evaluation is paramount to fully be able to evaluate the conservation potential of this particular economic market, and may be highly instructional as a model for evaluating the potential contribution of economic markets towards solutions for the current environmental crisis.~~

To conclude, we found no difference in prices between native carnivores and ungulates, between exotic and native species, nor any effects of species characteristics on the prices on carnivores. However, both conservation status, deviations from the normal colour morph, body size and horn size influences prices of ungulates. We interpret these relationships as indicators of an importance of novelty and aesthetics, and our results suggested that this importance has increased over time. However, species characteristics explained less than 50% of price variation among species. We therefore encourage further work towards a full evaluation of the relative influences of species characteristics versus factors relating to different characteristics of the market participants as well as features of the market that are intrinsically linked to economic processes on the price variations in South African wildlife. Such an evaluation is paramount to fully be able to assess the conservation potential of this particular economic market, and may be highly instructional as a model for evaluating the potential contribution of economic markets towards solutions for the current environmental crisis.

REFERENCES

Antelope Specialist Group. 2015. *IUCN SSC ASG Position Statement on the Intentional Genetic Manipulation of Antelopes Ver. 1.0 (30 April 2015).* IUCN SSC Antelope Specialist Group. URL: https://www.iucn.org/sites/dev/files/import/downloads/asg_igm_posnsment_2015_final_19may_2015.pdf.

Amin, A. 2016. Exploring the role of economic incentives and spillover effects in biodiversity conservation policies in sub-Saharan Africa. *Ecological Economics* 127: 185-191.

Ayele, G., M. A. Jabbar, H. Teklewold, E. Mulugeta and G. Kebede. 2006. Seasonal and inter-market differences in prices of small ruminants in Ethiopia. *Journal of Food Products Marketing* 12: 59-77.

Balmford, A., A. Bruner, P. Cooper, R. Costanza, S. Farber, R. E. Green, M. Jenkins, P. Jefferiss, V. Jessamy, J. Madden, K. Munro, N. Myers, S. Naeem, J. Paavola, M. Rayment, S. Rosendo, J. Roughgarden, K. Trumper, and R. K. Turner. 2002. Economic reasons for conserving wild nature. *Science* 297: 950-953.

Benjaminsen, T. A., and I. Bryceson. 2012. Conservation, green/blue grabbing and accumulation by dispossession in Tanzania. *Journal of Peasant Studies* 39: 335-355.

Bothma, J. P., J. G. du Toit, and J. van Rooyen 2010. Buying and selling wild animals. Pages 619-639 *in* J. P. Bothma, editor. *Game Ranch Management*. Van Schaik, Johannesburg, South Africa.

~~Brock, T. C. 1968. Implications of commodity theory for value change. Pages 243-275 *in* (eds. A. G. Greenwald, T. C. Brock, and T. M. Ostrom, editors. *Psychological foundations of attitudes*. Academic Press., New York, USA.~~Bush, E., S. E. Baker, and D. W. Macdonald. 2014. Global trades in exotic pets 2006-2013. *Conservation Biology* 28: 663-676.

Carpenter, S. R., H. A. Mooney, J. Agard, D. Capistrano, R. S. DeFries, S. Díaz, T. Dietz, A. K. Duraiappah, A. Oteng-Yeboah, H. Miguel Pereira, C. Perrins, W. V. Reid, J. Sarukhan, R. J. Scholes, and A. Whyte. 2009. Science for managing ecosystem services: Beyond the Millennium Ecosystem Assessment. *Proceedings of the National Academy of Science, USA* 106: 1305-1312.

Courchamp, F., E. Angulo, P. Rivalan, R. J. Hall, L. Signoret, L. Bull, and Y. Meinard. 2006. Rarity value and species extinction: the anthropogenic Allee effect. *PLoS Biology* 4: e415.

Costanza, R., R. d'Arge, R. de Groot, S. Farberk, M. Grasso, B. Hannon, K. Limburg, S. Naeem, R. V. O'Neill, J. Paruelo, R. G. Raskin, P. Suttonkk, and M. van den Belt. 1997. The value of the world's ecosystem services and natural capital. *Nature* 387: 253-260.

Coursey, D. L. 1998. The revealed demand for a public good: Evidence from endangered and threatened species. *New York University Environmental Law Journal* 6: 411–449.

Court, A. T. 1939. Hedonic price indexes with automotive examples. In *The dynamics of automotive demand*, 98-119. New York, General Motors.

Cousins, J. A., J. P. Sadler, and J. Evans. 2008. Exploring the role of private wildlife ranching as a conservation tool in South Africa: Stakeholder perspectives. Ecology and Society 13: 43.

Czech, B., P. R. Krausman, and R. Borkhartaria. 1998. Social construction, political power, and allocation of benefits to endangered species. *Conservation Biology* 12: 1103–1112.

Dalerum, F. 2013. Phylogenetic and functional diversity in large carnivore assemblages. *Proceedings of the Royal Society of London, Series B Biology* 280: 20130049.

Dalerum, F. 2014. Identifying the role of conservation biology for solving the environmental crisis. *Ambio* 43: 839-846.

Dalerum, F., and M. Miranda. 2016. Game auction prices are not related to biodiversity contributions of southern African ungulates and large carnivores. *Scientific Reports* 6: 21922.

Dalerum, F., M. J. Somers, K. E. Kunkel, and E. Z. Cameron. 2008. The potential for large carnivores to act as biodiversity surrogates in southern Africa. *Biodiversity and Conservation* 17: 2939-2949.

Edwards, L. J., K. E. Muller, R. D. Wolfinger, B. F. Qaqish, and O. Schabenberger. 2009. An R^2 statistic for fixed effects in the linear mixed model. *Statistics in Medicine* 27: 6137-6157.

Ehrlich, P. R., and A. H. Ehrlich. 2013. Can a collapse of global civilization be avoided? *Proceedings of the Royal Society of London, Series B Biology* 280: 20122845.

Gray, G. G. 1995. *The human dimensions to wildlife ecology*. Champaign, Il: Illinois University Press.

Hector, A., S. Felten, and B. Schmid. 2010. Analysis of variance with unbalanced data: an update for ecology and evolution. *Journal of Animal Ecology* 79: 308-316.

Honey, M. 2008. *Ecotourism and sustainable development: Who owns paradise?* 2nd edition. Island Press, Washington, D.C., USA.

Jaeger, B. 2016. r2glmm: Computes R squared for mixed (multilevel) models. R package version 0.1.1. https://CRAN.R-project.org/package=r2glmm

Johnson, P. C. D. 2014. Extension of Nakagawa and Schielzeth's R^2_{GLMM} to random slopes models. *Methods in Ecology and Evolution* 5: 944-946.

Johnson, P. J., R. Kansky, A. J. Loveridge, and D. W. Macdonald. 2010. Size, rarity and charisma: valuing African wildlife trophies. *PLoS ONE* 5: e12866.

Jones, K. E., J. Bielby, M. Cardillo, S. A. Fritz, J. O'Dell, C. D. L. Orme, K. Safi, W. Sechrest, E. H. Boakes, C. Carbone, C. Connolly, M. J. Cutts, J. K. Foster, R. Grenyer, M. Habib, C. A. Plaster, S. A. Price, E. A. Rigby, J. Rist, A. Teacher, O. R. P. Bininda-Emonds, J. L. Gittleman, J. L., G. M. Mace, and A. Purvis. 2009. PanTHERIA: a species-level database of life history, ecology, and geography of extant and recently extinct mammals. *Ecology* 90:2648.

Kassie, G. T., A. Abdulai, and C. Wollny. 2011. Heteroscedastic hedonic price model for cattle in the rural markets of central Ethiopia. *Applied Economics* 43:3459-3464.

Kellert, S. R. 1996. *The value of life: Biological diversity and human society.* Island Press, Washington, D.C., USA.

Lancaster, K. 1966. A new approach to consumer theory, *Journal of Political Economy* 74: 132–57.

~~Lynn, M. 1991. Scarcity effects on value: A quantitative review of the commodity theory literature. Psychology and Marketing 8: 43-57.~~

Mace, G. M. 2014. Whose conservation? *Science* 345: 1558-1560.

Nakagawa, S. and H. Schielzeth. 2013. A general and simplemethod for obtaining R^2 from generalized linearmixed-effectsmodels. *Methods in Ecology and Evolution* 4: 133-142.

Pinheiro, J., D. Bates, S. DebRoy, and D. Sarkar. 2016. *nlme: Linear and nonlinear mixed effect models.* R package version 3.1-127. URL: http://CRAN.R-project.org/package=nlme.

Rosen, S. 1974 . Hedonic prices and implicit markets: product differentiation in pure competition, *Journal of Political Economy* 82: 34–5.

Shiller, R. J. 2016. *Irrational exuberance.* Princeton University Press, Princeton, USA.

Skinner, J. D., and C. Chimimba. 2005. *Mammals of the southern African subregion.* Cambridge University Press, Cambridge, UK.

Smith, A. 1776. *An inquiry into the nature and causes of the wealth of nations.* W. Strahan. , London, UK.Snijders, D. 2012. Wild property and its boundaries – on wildlife policy and rural consequences in South Africa. *Journal of Peasant Studies* 39: 503-520.

Stokes, D. 2007. Things we like: human preferences among similar organisms and implications for conservation. *Human Ecology* 35: 361–369.

Taylor, A., P. Lindsey, and H. Davies-Mostert, H. (2016). *An assessment of the economic, social and conservation value of the wildlife ranching industry and its potential to support the green economy in South Africa.* Green economy research report, Developm. Bank of South Africa, Johannesburg, South Africa.

Terfa, Z. G., A. Haile, D. Baker, and G. T. Kassie. 2013. Valuation of traits of indigenous sheep using hedonic pricing in Central Ethiopia. *Agricultural and Food Economics* 1: 6.

Turnhout, E., C. Waterton, K. Neves, and N. Buizer. 2014. Rethinking biodiversity: from goods and services to "living with". *Conservation Letters* 6:154–161.

Val-Ilosera, M., and P. Cassey. 2017. Physical attractiveness, constraints to the trade and handling requirements drive the variation in species availability in the Australian cagebird trade. *Ecological Economics* 131: 407-413.

Van der Merwe, P., M. Saayman, and W. Krugell. 2004. Factors that determine the price of game. *Koedoe* 47: 105–113.

Veblen, T. 1889. *The Theory of the Leisure Class*. Macmillan, New York.

UNEP. 2011. *Towards a green economy: Pathways to sustainable development and poverty eradication – a synthesis for policy makers*. United Nations Environment Programme, Nairobi, Kenya.

Fig. 1. Differences in average annual auction prices between native and exotic carnivores and ungulates of the common form (a), among carnivores and ungulates from different IUCN threat categories (b, LC – “Least concern”, NT – ”Near threatened”, VU = ”Vulnerable”, EN – “Endangered”, CR – “Critically endangered”, EW – “Extinct in the wild”) and between common and deviant forms of 12 ungulate species that were sold from non-native populations or in deviant colour mutations (cb). The massive elevation in prices for EN and CR ungulate species were due to high prices of the black rhino (*Diceros bicornis*). The figure describes average prices calculated from average species prices ± 1 SE of species averages.

Table 1. Partial R^2 values (with 95% confidence limits), beta~~Beta~~ coefficients, their associated standard errors as well as p-values from mixed linear models of the effects of a series of biological predictors on annual prices of carnivores and ungulates. For categorical predictors, the beta coefficients describe the difference between each level and the reference level. For continuous predictors, the coefficients describe the unit of log (price) change over each standard deviation unit of change of the predictor. The magnitude of the beta coefficients is therefore directly comparable among the different continuous characters.

	Carnivores				Ungulates				Ungulates over time		
Class/Predictor	R^2	β	SE_β	P	R^2	β	SE_β	P	$\beta^{\dagger}$	SE_β	P
Rarity											
IUCN: NT‡					0.01 (0-0.03)	-0.33	0.07	< 0.001	-0.03	0.01	0.005
IUCN: VU‡	0.07 (0.0-0.27)	2.92	0.69	0.147	0.01 (0-0.02)	-0.62	0.19	< 0.001	-0.03	0.02	0.165
IUCN: EN‡	< 0.01 (0-0.116)	1.53	0.80	0.307	< 0.01 (0-0.01)	-0.36	0.29	0.212	-0.02	0.04	0.596
IUCN: CR‡					< 0.01 (0-0.02)	-0.82	0.48	0.085	-0.15	0.07	0.035
IUCN: EW‡					< 0.01 (0-0.01)	-1.24	2.21	0.579	-0.12	0.09	0.154
Origin: Exotic‡	0.01 (0-0.16)	1.91	0.95	0.293	< 0.01 (0-0.01)	0.24	1.02	0.811	-0.01	0.02	0.489
Form: Deviant ‡					0.16 (0.12-0.21)	1.83	0.08	< 0.001	0.10	0.01	< 0.001
Aesthetics											
Horn length					0.10 (0.06-0.13)	0.60	0.25	0.026	0.02	< 0.01	< 0.001
Colour pattern: Spotted/striped‡	0.12 (0.01-0.34)	0.81	0.75	0.473							
Ecology											
Body mass	0.12 (0.0-0.336)	0.65	0.65	0.394	0.07 (0.04-0.10)	0.58	0.27	0.044	-0.01	0.01	0.014
Activity: Nocturnal‡	0.12 (0.01-0.34)	0.71	0.80	0.538	< 0.01 (0-0.01)	-0.59	1.03	0.572	0.04	0.04	0.217
Activity: Both‡	0.09 (0-0.29)	1.69	1.02	0.345		-0.30	0.45	0.504	< 0.01	0.01	0.684
					0.01 (0-0.02)						
Group size	0.02 (0-0.17)	-0.50	0.95	0.636	0.06 (0.03-0.09)	-0.29	0.22	0.204	-0.01	< 0.01	0.002
Litter size					0.05 (0.03-0.08)	-0.44	0.22	0.052	-0.02	0.01	0.000
Density					0.01 (0-0.03)	-0.19	0.24	0.447	< 0.01	0.01	0.381

Home range size	< 0.01 (0-0.12)	0.13	0.88	0.893	0.01 (0-0.03)	0.26	0.33	0.432	0.01	0.01	0.271
Diet breadth					0.01 (0-0.02)	0.14	0.23	0.566	-0.01	< 0.01	0.039

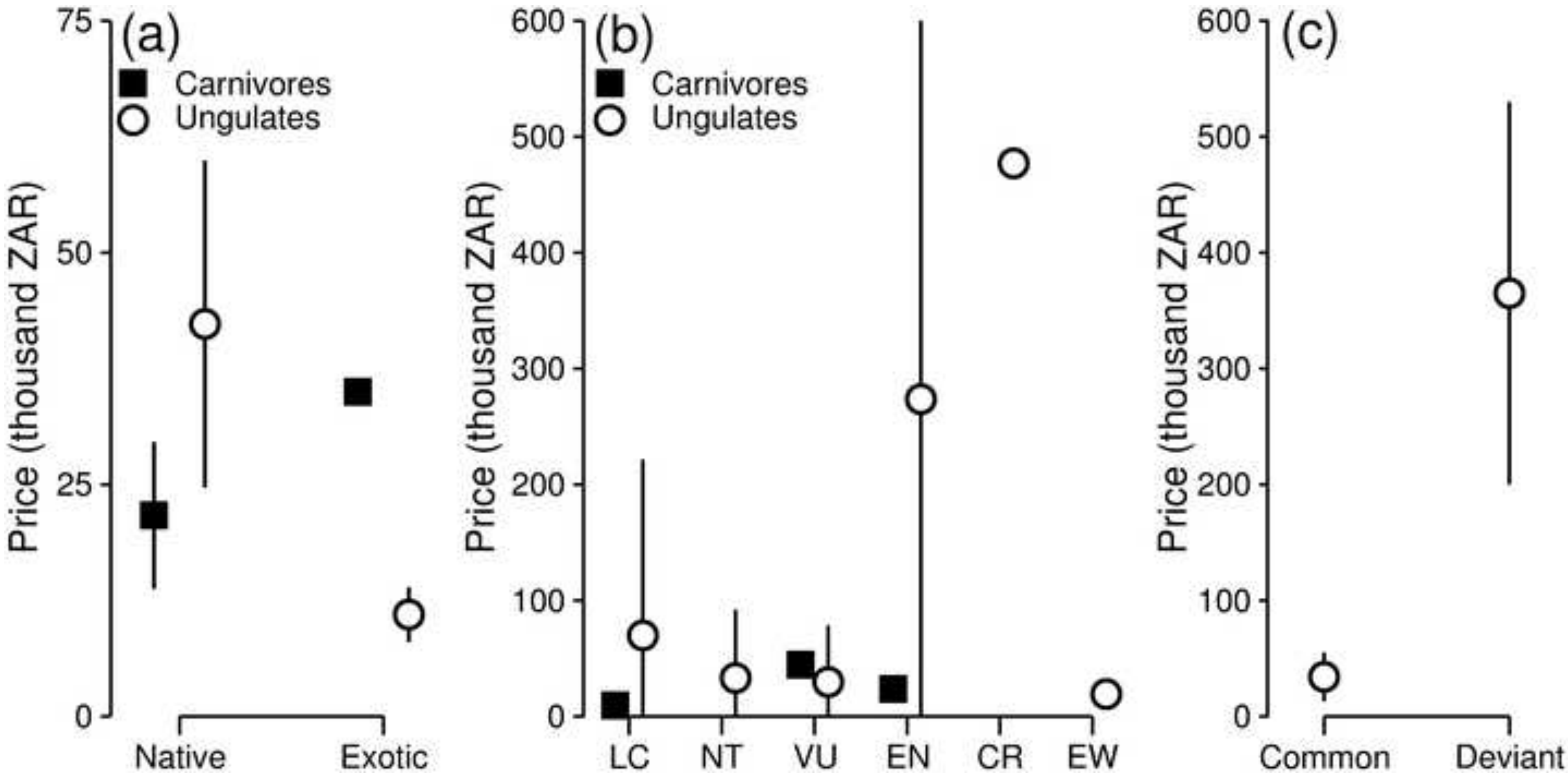
	Carnivores			Ungulates			Ungulates over time		
	β	$SE_β$	P	β	$SE_β$	P	β†	$SE_β$	P
‡									
IUCN: NT‡				-0.33	0.07	< 0.001	-0.03	0.01	0.005
IUCN: VU‡	2.92	0.69	0.147	-0.62	0.19	0.001	-0.03	0.02	0.165
IUCN: EN‡	1.53	0.80	0.307	-0.36	0.29	0.212	-0.02	0.04	0.596
IUCN: CR‡				-0.82	0.48	0.085	-0.15	0.07	0.035
IUCN: EW‡				-1.24	2.21	0.579	-0.12	0.09	0.154
Origin: Exotic‡	1.91	0.95	0.293	-0.24	1.02	0.811	-0.01	0.02	0.489
Form: Deviant‡				-1.83	0.08	< 0.001	-0.10	0.01	< 0.001
Body mass	0.65	0.65	0.394	-0.58	0.27	0.044	-0.01	0.01	0.014
Horn length				-0.60	0.25	0.026	-0.02	< 0.01	< 0.001
Colour pattern: Spotted/striped‡	-0.81	0.75	0.473						
Activity: Nocturnal‡	-0.71	0.80	0.538	-0.59	1.03	0.572	-0.04	0.04	0.217
Activity: Both‡	-1.69	1.02	0.345	-0.30	0.45	0.504	< 0.01	0.01	0.684
Group size	-0.50	0.95	0.636	-0.29	0.22	0.204	-0.01	< 0.01	0.002
Litter size				-0.44	0.22	0.052	-0.02	0.01	0.000
Density				-0.19	0.24	0.447	< 0.01	0.01	0.381
Home range size	-0.13	0.88	0.893	-0.26	0.33	0.432	-0.01	0.01	0.271
Diet breadth				-0.14	0.23	0.566	-0.01	< 0.01	0.039

† Interaction coefficients, which for categorical predictors describe the difference in the trend of price over time between each level and the reference level, and for continuous predictors describe the change in trend of price over time per standard deviation change in the predictor.

‡ Categorical predictor. Reference levels: IUCN class = "Least concern", Origin = "Native", Form = "Common", Colour pattern = "Plain", Activity = "Diurnal"

Figure 1

Click here to download Figure Fig1.tiff



Supplementary Material, Table S1

Click here to access/download
Supplementary Material
ESM-Table-S1.csv

Supplementary Material, Table S2

Click here to access/download
Supplementary Material
ESM-Table-S2.pdf

Click here to access/download
Supplementary Material
ESM-Table-S3.csv

Associate Editor Jeffrey McNeely:

This is an interesting paper, but you will see that the reviewers have both called for major revisions for roughly the same reasons: the paper needs to state more clearly what are the hypotheses to be tested. It would also be helpful to state what are the limitations of the paper (perhaps drawing on the suggested future work in the paper's final paragraph).

We have largely re-written the final section of the introduction (lines 55-91), and in doing so attempted to provide a better justification for our study and what hypotheses we tested.

We have re-written the final two paragraphs of the discussion (lines 250-280), partly to better highlight some caveats, and partly to link these to suggestions for further research.

A problem in the line 122-123 sentence is that it should say "where" instead of "were". Also, in line 26, please revise to avoid the use of "we", when it is not clear who "we" are, and especially since you use "we" frequently to review to the authors; better to say something like, "....they have still not been fully incorporated into public policy."

We have re-worded both the sentence on prevoius line 26 as well as the one on previous line 122-123.

I really liked this paper, and with the major revision called for, it will be a significant contribution to the literature. I do hope that you will be able to make the changes requested.

We are grateful for these positive comments.

COMMENTS FOR AUTHORS:

Reviewer #1:

GENERAL COMMENTS:
The paper uses data from South African wildlife auctions during the 1991-2012 period to assess determinants of wildlife prices. This is an interesting topic, and the authors must have put a tremendous effort into collecting the data. However, I think they need to be a lot clearer about what their research hypotheses are and how they test those hypotheses. More specifically, they clearly have a number of assumptions about what the underlying economic relationships are likely to look like and how those relationships might influence the prices, but it would be much easier to follow what is done in the paper if they stated those assumptions explicitly. The economic relationships will depend not only on the hunters' and other tourists' demand for the different animals, but also on the ease with which these animals can be bred and relocated. The authors are aware of this, obviously, but spelling out some kind of supply-and-demand model, with the supply depending on the biology and ecology of the species in question, would make it easier for the reader to see what to expect.

We have largely re-written the final three paragraphs of the introduction (lines 55-91). In doing so, we have introduced the concept of hedonic pricing, which is directly relevant for our study, as well as provided some more clearly defined a-priori expectations.

I'll be frank and state that I think spelling out an explicit theoretical framework may be quite difficult and will probably lead to a need to redo parts of the analysis. So this is not an entirely easy task. However, I think it would add a lot of value to the paper, and that that additional value would be needed in order to justify publishing the paper.

As indicated above, we have introduced the concept of hedonic pricing, and attempted to provide better justifications for our analyses including a-priori predictions. We have not re-done our analyses, as we regard them to be germane in relation to the questions we have asked, although we have introduced partial R^2 values partly to answer a request from reviewer 2.

SPECIFIC COMMENTS:
- A twenty year time period is a long time in which to study hunting and other tourism, and it would help if the authors were clearer about what their time trend variables look like in those regressions where they have explicit time components. (The regressions where they don't have explicit time components are, to be honest, probably not that meaningful in economic terms - there is no particular reason to think that e.g. prices shortly before the end of sanctions should follow the same pattern as prices today in an industry dependent on foreign tourism.)

We have clarified that we added time as a linear co-variate (lines 177), and that our 2-way interactions of time x species characteristics evaluate the relative differences in any time trends among factor levels (categorical predictors) or along the values of continuous predictors (lines 178-180).

We do not agree with the reviewer that average prices accumulated across the full time span of our study are not meaningful, and have therefore retained these analyses on the full set of data.

- The authors briefly discuss the auctions and how the setup of an individual auction might affect the prices paid. If the number of buyers and sellers is sufficiently small that we cannot assume competitive pricing, as the authors imply in their discussion, the economic model should be adjusted for that. Have the authors considered bringing in explicit auction theory elements, or otherwsie handling the low level of competition in some auctions, into their framework?

In this manuscript we have used average annual auction prices, and not prices form individual auctions. This has been stated in the introduction (line 78), methods (lines 95), and we have also pointed it out as a potential shortcoming in the discussion (lines 250-251, 255-258). We have also highlighted the need for a further study evaluating the relative effects of species characteristics and other market elements, such as the auction specific variables the reviewer refers to here (lines 274-280).

MANDATORY TO ANSWER QUESTION 1 TO 4

1. Does the subject of the manuscript fall within the scope of Ambio? (exploring the link between anthropogenic activities and the environment; especially encouraged are multi- or interdisciplinary submissions with explicit management or policy recommendations).
Yes/No - Yes
Comment:

N/A

2. Is it comprehensible not only to specialists but also to scientists in other fields and interested laymen?
Yes/No - Yes
Comment:

N/A

3. Is this a new and original contribution?
Yes/No - Yes
Comment:

N/A

4. Are the results of sufficiently high impact and global relevance for publication in Ambio? Is the manuscript set in an international context and does it demonstrate how it builds on previous work on the subject?
Yes/No
Comment: They probably would be if I trusted the underlying economic model, but since we're not told what the theoretical model is, it's hard to say for sure.

We have tried to provide a better theoretical justification for our approach by re-writing the final three paragraphs of the introduction, and in doing so introdcued the henonic model (lines 55-91), which we have further specified in the methods (lines 113-118).

OPTIONAL TO ANSWER QUESTION 5 to 15

5. Are the interpretations and conclusions sound, justified by the data and consistent with the objectives?
Yes/No - No
Comment: They may be, but while the data are impressive, the analysis needs to be supported by a clear theoretical framework.

See our response to the previous question.

6. Does the title of the manuscript clearly reflect its contents? Will it catch the reader's attention?
Yes/No

Comment: Could probably be made a bit punchier

We have replaced the title with “Effects of scarcity, aesthetics and ecology on wildlife auction prices of large African mammals”.

7. Is the abstract sufficiently informative, especially when read in isolation?
Yes/No - Yes
Comment:

N/A

8. Is the statement of objectives of the manuscript adequate and appropriate in view of the subject matter?
Yes/No - No
Comment: As I stated above, the authors need to be much clearer about what their assumptions and hypotheses are

We have re-written the final section of the introduction to better clarify these issues (lines 78-91).

9. Are the methods correctly described and sufficiently informative to allow replication of the research?
Yes/No
Comment:

N/A

10. Is the rigour of the statistics applied in this paper satisfactory? [Please indicate to us if you feel you are not sufficiently proficient in statistics to judge this aspect of the paper yourself]
Yes/No
Comment:

N/A

11. Is the organization satisfactory and are the results clearly presented?
Yes/No
Comment:

N/A

12. Are the figures and tables all necessary and are the captions adequate and informative?
Yes/No
Comment:

N/A

13. Are the references adequate for the subject and the length of the manuscript?
Yes/No
Comment:

N/A

14. Is the quality of the English satisfactory?
Yes/No
Comment:

N/A

15. Is the length of the paper appropriate to the content and/or can you suggest changes, brief additions or deletions (words, phrases) that will increase the value of this manuscript for an international audience?
Yes/No
Comment:

N/A

Reviewer #2:

GENERAL COMMENTS:
The loss of the world's biological diversity, and its economic and ecological consequences, is now widely accepted as an environmental issue of urgent global concern. The convention on biodiversity recognises that the causes species and ecosystem losses are diffuse in nature, involving many different sectors. To address the underlying causes of the problem, the convention underscores the need for multi-stakeholder processes aimed at protecting biodiversity at the genetic, species, an ecosystem level through national-level actions, and on the need to integrate conservation and development objectives in government planning and practice. For this reason, this manuscript is important and germane to the scope of AMBIO: Journal of the Human Environment. However, there are several issues that require attention before the paper can be accepted for publication. Therefore, I recommend major revisions. The specific comments that informed this decision now follow:

We thank the reviewer for the positive remarks, and have responded to each specific comment in detail below.

SPECIFIC COMMENTS:

Abstract
Authors should re-write this section indicating what specific methods/techniques they used in collecting and analyzing the data.

We have included some information of what data was used in the abstract (lines 4-6). However, with an abatract word limit of 150 words, we do not regard it justified to mention statistical methodology in the abstract.

Where and how did they obtain the data? Was it mainly primary or secondary or both?

We have included some information of what data was used in the abstract (lines 4-6).

In the results, what was the order of importance (either decreasing or increasing) of the various predictors of ungulate prices in the multivariate model?

With the tight word limit of the abstract, we regard it more efficient to mention the broad results and conclusions rather than report more specific results as the reviewer suggests. However, we have also introduced partial R^2 values to the results (lines 171-173, lines 195-200, Table 1), to enable a better evaluation of the relative importance of the different effects.

On the whole, how do the magnitudes of species-related factors/predictors compare with non-species related factors?

Our analysis did only include species related factors. We have highlighted both in the abstract (lines 11-13) and in the discussion (lines 274-280) that a full analyses evaluating the relative influence of species characteristics and other aspects of the markets would be highly informative.

Some of the specific points/numbers in the section on compilation of price data should be placed in the abstract to give readers a sense of the scope of the study.

We have included some information of what data was used in the abstract (lines 4-5).

Introduction
This section is well-written. It reads in good logical sequence. However, the authors can make the statement of the problem much stronger. Apart from the fact that little is known about the drivers of the market prices of these species in South Africa, what else is not known that warrants this study?

We have largely re-written the end of the introduction to better justify our study.

Methods
Data analyses
This section mentioned testing of hypotheses. However, the authors failed to indicate, a priori, what their underlying hypotheses were. Authors should state specific objectives, including any pre-specified hypotheses. This is necessary to ascertain which of the hypotheses were rejected or failed to be rejected.

We largely agree with the reviewer in this comment, and we have introduced some a-priori hypotheses in the final paragraph of the introduction (lines 82-91).

Authors should re-word the sentence on line 122-123 on page 6, as is, it is quite awkward.

We have re-worded this sentence.

How did the authors build the multivariate linear regression model? What factors influenced the choice of the predictors or independent variables? This is unclear. Typically, parsimony, theoretical relevance, model fit, etc are considered before the predictors are selected.

This reviewer seems to assume the use of what generally is classed as an information theoretic approach to statistical modelling. While we appreciate that such a sequential approach often is useful and informative, it also has strong drawbacks. In our case, we have regarded it most useful to use a set of a-priori identified predictors and simultaneously evaluate these in the same model. In our mind, this adds simplicity and clarity of the analyses and results. We have justified this approach in the beginning of the data analysis section in the methods (lines 152-155).

We are well aware of an ongoing and active debate as to how best to model data using multiple predictors. For instance, proponents of sequential model selection (whether it is forwards or back-wards selection) often state that it is a more objective form of evaluation, since some formal criterion (often AIC or other penalized likelihood scores) are used to select the optimal model structure rather than using an arbitrary set of predictors and include all these simultaneously in the model. However, opponents to this view highlight that any given data can be explained by an indefinite set of candidate models, and hence any defined set of candidate models have already been exposing the data to a-priori subjective filtering. Since we do not regard it germane for our study to take up journal space with this on-going statistical debate, we have simply stated that we did not use a sequential selection approach in the initial sentences of the data analysis section (lines 152-155).

How were the predictors entered into the multivariate model? The order of entry of the predictors can potentially influence the parameter estimates of the models.

We did not use a sequential modelling approach and selected some optimal model from a set of selected candidate models. Hence, this comment stand as mute, since we have evaluated all model terms in the presence of all other model terms of the same level of complexity (i.e. main effects for our main effects only models and time x characteristic interaction in our co-variance models). We have clarified this in the initial sentences of the data analysis section (lines 152-154).

Results

Authors should give both unadjusted estimates (zero-order/bivariate relationships) and confounder-adjusted estimates and their precision (eg, 95% confidence interval). In this study, the authors focused only on the latter. This is quite problematic since it is difficult to identify which factors act as suppressors and mediators of the relationship between market prices and the species-related factors as well as non-species related factors. They should also make clear which confounders were adjusted for and why they were included.

We disagree with the reviewer here. We do not see how single predictor models would add any information to the multi-predictor ones we now have presented. We are a bit confused regarding the request for parameter estimates and their precision, since he have reported exactly this, i.e. the estimated parameter value as well as its standard error. Finally, we have clearly stated which predictors were included in the models (lines 165-170), so we do not understand the final request, “i.e. They should also make clear which confounders were adjusted for and why they were included.“ However, to enable an easier comparison of the relative effects of the different predictors, we have also included partial R2 values to our results (lines 171-173, lines 195-200, Table 1).

The interpretation of some of the unstandardized coefficients are difficult to follow.

We are confused by this comment, since we have clearly stated that all coefficients for our continuous predictors were calculated on scaled (and centered) variables, i.e. the coefficients are given in units of predictor standard deviation rather than in raw predictor units. For categorical predictors, standardization of the parameters are mute (i.e. in all factors each factor level are assumed to be equally different). We have added a sentence to the method section to further highlight this approach (lines 184-187).

Discussion

I searched in vain for the limitations of the study. Limitations are defining characteristics of every study. Limitations are those elements over which the researcher has no control. In most instances, any assumption you

make becomes a limitation. Assumptions are made about (a) the theory under investigation, (b) the phenomenon under investigation, (c) the instrument, (d) the method, (e) the analysis, (f) the power to find significance, (g) the sample/unit of analysis in the study, and (h) the results. Consequently, the authors should identify the limitations of the study in the discussion section.

We have introduced a paragraph presenting several caveats to our study (lines 250-267).

Conclusion
This section is well-written.

N/A

MINOR EDITS: Authors should re-word the sentence on line 122-123 on page 6, as is, it is quite awkward.

We have re-worded this sentence

MANDATORY TO ANSWER QUESTION 1 TO 4

1. Does the subject of the manuscript fall within the scope of Ambio? (exploring the link between anthropogenic activities and the environment; especially encouraged are multi- or interdisciplinary submissions with explicit management or policy recommendations).
Yes/No
Comment: Yes

N/A

2. Is it comprehensible not only to specialists but also to scientists in other fields and interested laymen?
Yes/No
Comment: Yes

N/A
3. Is this a new and original contribution?
Yes/No
Comment: Yes

N/A

4. Are the results of sufficiently high impact and global relevance for publication in Ambio? Is the manuscript set in an international context and does it demonstrate how it builds on previous work on the subject?
Yes/No
Comment: Yes

N/A