

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

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## 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

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## 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<sup>2</sup>) (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 relevant characteristics is important for optimised contributions of any wildlife based market towards 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 view historically contrasted the neoclassical economic framework, which originally assumed 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 increased 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-Iloera 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 restrict 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  $P_i = f(R_{i1}, \dots, R_{ij}, A_{i1}, \dots, A_{ik}, E_{i1}, \dots, E_{il})$ , 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 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).

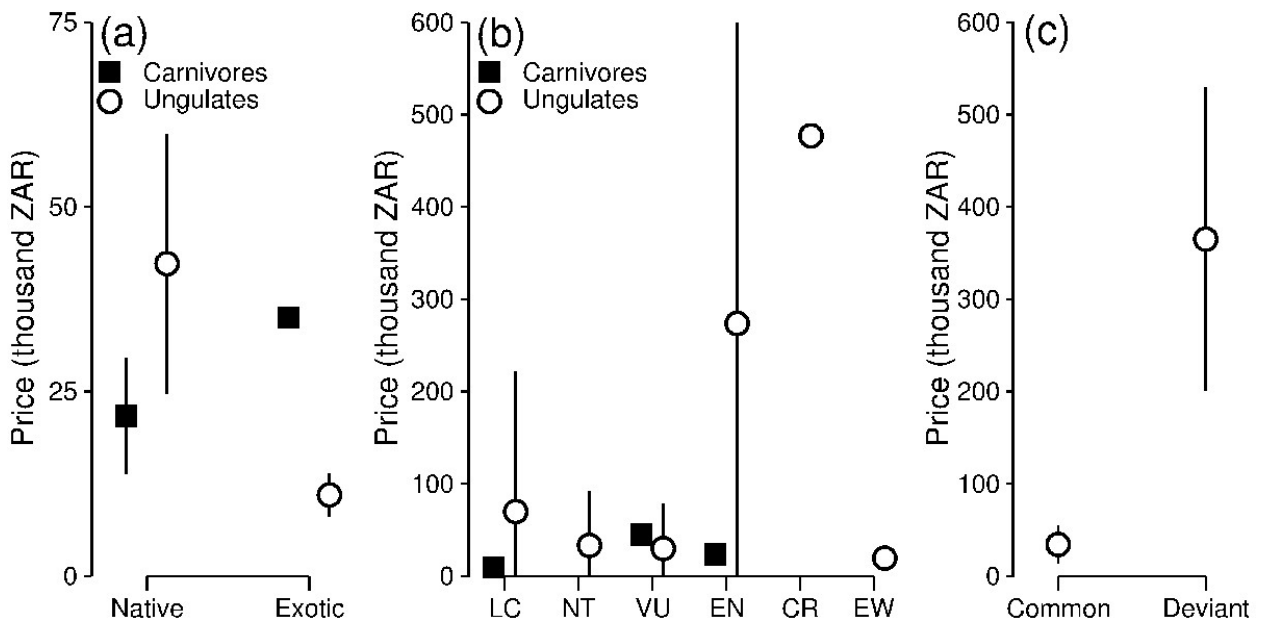
## RESULTS

Native carnivores did not differ significantly in average prices compared to native ungulates in their common form ( $\beta = -0.35$ ,  $SE_{\beta} = 0.69$ ,  $P = 0.612$ ). The species characteristics explained 48% of the variation in prices for carnivores and 46% for ungulates. For carnivores, body mass ( $R^2_{\text{partial}} = 0.12$ ), colour pattern ( $R^2_{\text{partial}} = 0.12$ ) and activity patterns (nocturnal  $R^2_{\text{partial}} = 0.12$ , both nocturnal and diurnal  $R^2_{\text{partial}} = 0.09$ ) had the highest partial  $R^2$  values, 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,  $R^2_{\text{partial}} = 0.16$ ), horn or tusk length ( $R^2_{\text{partial}} = 0.12$ ) and body mass ( $R^2_{\text{partial}} = 0.07$ ) had the highest partial  $R^2$  values (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.

Overall, prices of ungulates had increased over time ( $\beta = 0.05$ ,  $SE_{\beta} = 0.01$ ,  $P < 0.001$ ). However, 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 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 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



**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  $\pm 1$  SE of species averages.

**Table 1.** Partial  $R^2$  values (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.

Class/Predictor	Carnivores				Ungulates				Ungulates over time		
	$R^2$	$\beta$	$SE_{\beta}$	P	$R^2$	$\beta$	$SE_{\beta}$	P	$\beta^{\dagger}$	$SE_{\beta}$	P
<u>Rarity</u>											
IUCN: NT <sup>‡</sup>					0.01 (0-0.03)	-0.33	0.07	< 0.001	-0.03	0.01	0.005
IUCN: VU <sup>‡</sup>	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 <sup>‡</sup>	< 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 <sup>‡</sup>					< 0.01 (0-0.02)	-0.82	0.48	0.085	-0.15	0.07	0.035
IUCN: EW <sup>‡</sup>					< 0.01 (0-0.01)	-1.24	2.21	0.579	-0.12	0.09	0.154
Origin: Exotic <sup>‡</sup>	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 <sup>‡</sup>					0.16 (0.12-0.21)	1.83	0.08	< 0.001	0.10	0.01	< 0.001
<u>Aesthetics</u>											
Horn length					0.10 (0.06-0.13)	0.60	0.25	0.026	0.02	< 0.01	< 0.001
Colour pattern: Spotted/striped <sup>‡</sup>	0.12 (0.01-0.34)	0.81	0.75	0.473							
<u>Ecology</u>											
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 <sup>‡</sup>	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 <sup>‡</sup>	0.09 (0-0.29)	1.69	1.02	0.345		-0.30	0.45	0.504	< 0.01	0.01	0.684
Group size	0.02 (0-0.17)	-0.50	0.95	0.636	0.01 (0-0.02)						
Litter size					0.06 (0.03-0.09)	-0.29	0.22	0.204	-0.01	< 0.01	0.002
Density					0.05 (0.03-0.08)	-0.44	0.22	0.052	-0.02	0.01	0.000
Home range size	< 0.01 (0-0.12)	0.13	0.88	0.893	0.01 (0-0.03)	-0.19	0.24	0.447	< 0.01	0.01	0.381
Diet breadth					0.01 (0-0.02)	0.26	0.33	0.432	0.01	0.01	0.271
						0.14	0.23	0.566	-0.01	< 0.01	0.039

<sup>†</sup> 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.

<sup>‡</sup> Categorical predictor. Reference levels: IUCN class = “Least concern”, Origin = “Native”, Form = “Common”, Colour pattern = “Plain”, Activity = “Diurnal”

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, or 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.

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