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ABSTRACT

The devolution of user rights of wildlife in southern Africa has led to a widespread land-use shift from livestock farming to game ranching. The economic advantages of game ranching over livestock farming are significant, but so too are the risks associated with breeding financially valuable game where free-ranging wildlife pose a credible threat. Here, we assessed whether the conservation potential of game ranching, and a decentralized approach to conservation more generally, may be undermined by an increase in human-wildlife conflict. We demonstrate that game rancher tolerance towards free-ranging wildlife has significantly decreased as the game ranching industry has evolved. Our findings reveal a conflict of interest between wealth and wildlife conservation resulting from local decision-making in the absence of adequate centralized governance and evidence-based best practice. As a fundamental pillar of devolution-based natural resource management, game ranching proves an important mechanism for economic growth, albeit at a significant cost to conservation.

INTRODUCTION

The governance of natural resources has historically resided with the state (Child 2004). However, decentralization of governance has produced a devolutionary shift in natural resource management over the past four decades (Parker et al. 2015), particularly in developing countries (Ribot et al. 2006; Larson & Soto 2008). This shift to local resource management is based on the premise that local people are committed to sustainable resource use (Cousins et al. 2008). In southern Africa, policies that once established centralized control over wildlife were replaced by legislative changes that bestowed custodial rights of wildlife to individual property owners (Bothma et al. 2009; Lindsey et al. 2009a). Following the mantra "if it pays, it stays", southern African governments sought to align environmental management objectives with the socio-economic needs of local people (Child 2004). This devolution-based legislation encouraged innovation among the private and communal sectors (Child 2012), resulting in a rapid and widespread land-use shift in rangelands from livestock farming to game ranching (Cloete et al. 2007; Lindsey et al. 2009b).

Game ranching in southern Africa is now synonymous with private- and community-based natural resource management (Bothma et al. 2009). Although largely perceived to benefit environmental conservation through the protection of habitat and biodiversity (Lindsey et al. 2009b), game ranching inherently increases interactions—and potentially conflict—between valuable game species and free-ranging wildlife (Lindsey et al. 2013). Many free-ranging large mammals across southern Africa are ecologically vital as keystone species, and act as biodiversity indicators (Dalerum et al. 2008), but typically accrue little direct financial benefit to

game ranchers. In contrast, commercial game species represent important agricultural assets that represent substantial financial resources (Van Der Merwe et al. 2004). Ranchers are therefore unlikely to tolerate (defined here as the willingness to accept an event despite challenging circumstances; adapted from Treves & Naughton-Treves 2005) free-ranging wildlife potentially threatening those assets through depredation or infrastructure damage. Decreased tolerance may be further intensified by economic instability (Dickman 2010), particularly as agricultural sectors can act as economic buffers during periods of financial crises (Headey et al. 2010), which often result in increased investment and financial reliance on agricultural productivity (Allen & Giovannetti 2010; Headey et al. 2010).

Limpopo Province, South Africa (ca. 125 977 km^2; hereafter 'Limpopo', Fig. 1), has a largely impoverished human population, the highest density of game ranches in South Africa (Carruthers 2008), and an abundance of free-ranging wildlife. Game ranch establishment peaked across South Africa, and particularly in Limpopo (van der Waal & Dekker 2000), during the early 1990s (Van Der Merwe et al. 2004), with expansion subsequently reducing by the turn of the millennium (van der Waal & Dekker 2000; Bothma & Sartorius Von Bach 2010). Game ranching represents a core component of the agricultural sector, and has recently shifted from breeding large numbers of common game species towards breeding fewer high-value species with increasingly intensive management (Lindsey et al. 2009b) (Supporting Information S1). This land-use shift may exacerbate levels of conflict by increasing the financial threat posed by free-ranging wildlife and possibly result in increased adoption of conflict mitigation measures, such as problem animal control, or the use of heavily fortified predator-proof fencing (Lindsey et al. 2011). Here, we assess whether the

conservation potential of game ranching, and a decentralized approach to conservation more generally, may be undermined by an increase in human-wildlife conflict in Limpopo from 2003–2012. We explore the evolution of game ranching practices from extensive to intensive, to better understand the concomitant change in game rancher tolerance of free-ranging wildlife, and integrate this mechanistic understanding into the challenges facing conservation policy making more generally.

We hypothesized that given the economic reliance on agriculture during times of financial crises, investment within the agricultural sector (e.g., game ranching) should have increased around the global economic crisis of 2008, which severely impacted South Africa (Allen & Giovannetti 2010). We expected that as game ranching profitability increases, tolerance towards free-ranging wildlife that threaten game ranching assets should decrease. Finally, we predicted that decreased tolerance should lead to increased problem animal control, and increased predator-proof fencing, in an attempt to reduce interactions between valuable game and free-ranging wildlife that pose a significant threat.

METHODOLOGY

Measuring the scale and profitability of game ranching

Limpopo's annual game auction records, comprising numbers of game sold, average price, and annual turnover (i.e., annual sales volume) for each species, were obtained from the Vleissentraal online database (www.vleissentraal.co.za; accessed December 2013). Livestock auction records of economically important breeds (e.g., Bonsmara cattle *Bos taurus*, Merino and Dorper sheep *Ovis aries*) were obtained from Farmer's Weekly archives (National Library of South Africa, Pretoria). Game

were categorized into common breeds and high-value breeds based on their maximum average price (common game ≤ ZAR 10 000; high-value game > ZAR 10 000 per animal) over the study period. Return of investment (i.e., amount of financial return relative to investment cost) of game and livestock was quantified by pooling males and females of adults only, using their value at auction. National and provincial economic data were obtained from Statistics South Africa (www.statssa.gov.za; statistical release P0441, accessed December 2013) from 2003–2012. Auction and economic data were standardized using the buying power (1 + (Consumer Price Index / 100) * yearly value) of the South African Rand (CPI source: www.inflation.eu).

Identifying land-use types

Using a geographic information system (GIS), we divided Limpopo into different land-use types by overlaying formally registered game ranches (Exemption Property Database, LEDET), protected areas (World Database on Protected Areas; IUCN and UNEP-WCMC, accessed December 2014), natural and man-made water bodies (Department of Agriculture, Forestry and Fisheries), urban and rural settlements (Statistics South Africa), and agricultural land (Department of Agriculture, Forestry and Fisheries), with the remainder comprising mixed farms. Mixed farms in Limpopo predominantly practice game ranching, interspersed with livestock farming. Game ranches may act as small pseudo-protected areas by restoring habitat and introducing species, but are fundamentally different to protected areas in how they are managed (Bond et al. 2004). Game ranch management is profit-orientated with emphasis on the commercial production of ungulate species (Bothma & Sartorius

Von Bach 2010), whereas protected area management is largely conservation-orientated (Leverington et al. 2010). Therefore, to avoid potential bias relating to the management of protected areas (e.g., problem animal control on protected areas is likely driven by underlying conservation objectives such as disease control, rather than financial motivations), we excluded protected areas from our analyses. Land-use types were then categorized into 'non-game ranches' comprising agricultural land and urban and rural settlements, and 'game ranches' comprising formally registered game ranches and mixed farms.

Measuring conflict as a proxy for landowner tolerance

In Limpopo, problem animal permits are issued to landowners by the Limpopo Department of Economic Development, Environment and Tourism (LEDET), for the destruction of animals that reputedly pose a risk to human life or livelihoods. To measure conflict, we used the number of problem animal permit applications issued from 2003–2012 (Wildlife Trade and Regulation Archives, LEDET). Problem animal permit applications, whether approved or rejected, represent the intent of a landowner to destroy a putative problem animal, and therefore provides a reliable gauge of tolerance. We acknowledge that human attitudes towards nuisance wildlife are multi-dimensional (Kansky et al. 2014), yet justify our approach on the basis that tolerance levels likely degrade to a point where landowners perceive legal destruction as a potential solution. Free-ranging wildlife that potentially threaten the profitability of the game ranching industry include black-back jackal *Canis mesomelas*, brown hyaena *Hyaena brunnea*, caracal *Caracal caracal*, cheetah *Acinonyx jubatus*, lion *Panthera leo*, leopard *Panthera pardus*, spotted hyaena

Crocuta crocuta, and African elephant *Loxodonta africana* (collectively referred to as 'nuisance wildlife'). We also collected problem animal permit applications for greater kudu *Tragelaphus strepsiceros* and common duiker *Sylvicapra grimmia* ('non-nuisance wildlife'), as these two common ungulate species are frequently complicit in human-wildlife conflict, but represent a minimal threat to game ranching profitability. Global positioning system (GPS) coordinates for the property location of each problem animal permit application were obtained from the Chief Surveyor General's registered property database (Cadastral Spatial Information, Pretoria). Permit locations were projected across Limpopo, and assigned a land-use category based on the underlying property.

Identifying game ranching practices

An online survey was conducted to assess how Limpopo's game ranching practices have changed over the study period (respondent sample size = 116; Supporting Information S2). Given the increasing prices of game across southern Africa (Van Der Merwe et al. 2004), ranchers were asked whether they (1) breed rare game (e.g., roan antelope *Hippotragus equinus*, sable antelope *Hippotragus niger*, buffalo *Syncerus caffer*), (2) breed colour variants (e.g., black impala *Aepyceros melampus*, copper springbok *Antidorcas marsupialis*), and (3) breed extralimital game (i.e., species that do not occur naturally in their region). Only rare game and colour variants were considered 'high-value' species. Finally, given the increasing scientific debate around fencing for wildlife (Woodroffe et al. 2014), ranchers were asked whether they used predator-proof fencing. All questions required the year in which the particular practice was first adopted.

Generalized linear models were used to assess trends over time in game auction sales, game ranching practices, and problem animal permit applications. All statistical analyses were conducted within R v.3.2.0 (R Core Team 2015). All data used in the analyses are available in Supporting Information S3.

RESULTS

Economic contribution of game ranching

Limpopo's agricultural industry generated ZAR 27.64 billion (US$ 1.96 billion) from 2003–2012. The global economic crisis of 2008 lead to an economic recession in South Africa (Supporting Information S4), which resulted in negative growth for all industries other than agriculture (Supporting Information S5). Game ranching contributed 2.8 ± 0.3% (SE) to the growth in Limpopo's agricultural gross domestic product (GDP) prior to the recession (2003–2007), and 12.8 ± 4.6% (SE) during and after the recession (2008–2012). High-value game breeding was a far greater contributor to GDP than common game breeding over the 10-year period (Fig. 2b). Investing in high-value game breeding in 2008 would have resulted in a return on investment (ROI) of 187% by the end of 2012, whereas breeding common game would have returned 57% over the same period. Compared to high-value game, breeding of South Africa's common livestock species, such a Bonsmara cattle (ROI: 60%), or Merino (ROI: 103%) and Dorper sheep (ROI: 7%), would have resulted in far smaller returns on investment.

Game ranching practices and trends in Limpopo

The average price (Table 1a; Fig. 3b) and annual turnover (Table 1b; Fig. 3c) of game sold in Limpopo increased significantly over the 10-year study period. This primarily reflected a significant increase in the number (Table 1c; Fig. 3a) and price (Table 1d; Fig. 3b) of high-value species sold by game ranchers, particularly after 2008. In contrast, the number of common species sold decreased significantly over the 10-year period (Table 1e; Fig. 3a). Game ranchers consistently paid higher prices for female high-value game, than for males (Fig. 2a), highlighting the importance of breeding rather than hunting. As the number of game ranchers breeding high-value species significantly increased over the 10-year period (Table 1f; Fig. 4a; n = 104), so did the number of ranchers using predator-proof fencing (Table 1g; Fig. 4b; n = 94).

Measuring conflict and understanding game rancher tolerance

From 2003–2012, landowners submitted 693 problem animal permit applications for nuisance wildlife, and 999 for non-nuisance wildlife. Most (79%) applications originated from game ranches. For nuisance wildlife, leopard were the most common putative problem animal (68%), followed by elephant (20%), lion (4%), brown hyaena (3%), black-backed jackal (2%), caracal (2%), cheetah (0.5%), and spotted hyaena (0.5%). Applications by game ranchers for nuisance wildlife increased significantly (Table 1h; Supporting Information S6a) over the 10-year period, whereas no significant relationship was detected for nuisance wildlife on non-game ranches (Table 1i; Supporting Information S6b). Applications for non-nuisance wildlife on game ranches however approached significance (Table 1j; Supporting Information S6c), indicating an underlying positive trend. The number of

applications for nuisance wildlife increased significantly with the number of game ranchers breeding high-value species (Table 1k; Fig. 5a), and with the use of predator-proof fencing (Table 1l; Fig. 5b). Problem animal permit applications for elephant, which damage fences (Mutinda et al. 2014), began only once the use of predator-proof fencing had markedly risen from 2008 (Fig. 4b).

DISCUSSION

The global shift from centrally driven decision-making to a decentralized, local participatory process is argued to represent a more legitimate and inclusive governance system that improves local livelihoods and conservation outcomes (Parker et al. 2015). Game ranching is widely heralded as a conservation success and epitomizes the devolutionary rights-based approach to natural resource management in southern Africa (Carruthers 2008; Cousins et al. 2008). Yet, here we highlight the hidden costs of local decision-making in the absence of adequate centralized regulation and evidence-based best practice necessary to uphold conservation objectives. We demonstrate that game ranching has become an important and highly lucrative sector within the agricultural industry. Game ranching practices have become more intensive, to facilitate the breeding of high-value game species. In response to the increased profitability of game breeding, ranchers have adopted a dual-pronged approach to asset management by increasing predator-proof fencing to keep free-ranging wildlife out, and reducing populations of nuisance wildlife through legal destruction. Our findings demonstrate that the proportional increase in problem animal control of nuisance wildlife has far outweighed the proportional increase in game ranching trends towards more intensive practices—

suggesting that intolerance is growing in momentum. The consequences of decreased tolerance towards ecologically important free-ranging wildlife is likely to have significant detrimental impacts on species persistence and ecological systems more broadly (Ripple et al. 2014; 2015).

Unreported and illegal killing of wildlife is a pertinent issue across southern Africa (St John et al. 2012; Thorn et al. 2013; Kahler & Gore 2015). Human-mediated carnivore mortality is widespread, especially amongst livestock and game ranchers in Limpopo (St John et al. 2012). A recent study on leopards in Limpopo demonstrated that legal mortality is unsustainable (Pitman et al. 2015), and camera-trapping surveys conducted during and after the study period indicate that leopard populations are declining (Supporting Information S7). Elephant populations in the region are increasing at 4% per annum (Blanc 2008), but this growth is primarily confined to protected areas (a land-use type removed from this study). Interestingly, permit applications for elephants only began from 2008—the same year in which predator proof fencing markedly increased. This may suggest that predator proof fencing has not only failed to mitigate some forms of conflict in Limpopo, but actively contributed to decreased tolerance towards elephants. Game ranch expansion into new territories decelerated by the late 1990's (van der Waal & Dekker 2000; Bothma & Sartorius Von Bach 2010), which suggests that game ranching territory has not increased over the study period. Notably, Limpopo's human population has markedly grown (8.2% increase from 2001 to 2011; Statistics South Africa 2011), which has left the majority of suitable wildlife habitat in a highly fragmented state (Swanepoel et al. 2013).

Given the high returns on investment, the shift towards high-value game breeding has been, and continues to be, rapidly adopted across the region. From an economic standpoint, game ranching is a significant contributor and is likely to remain an important component on political and economic agendas. Agricultural sectors are considered informal economic safety nets during periods of financial crises (Headey et al. 2010). This is particularly relevant for developing countries where agricultural products are not highly exported, and the inherent inelasticity of the agricultural sector to economic downturn (Shovan 2004; Headey et al. 2010). Given the increased economic reliance on agricultural productivity, and the increased financial risk associated with intensive high-value game breeding, decreased tolerance among landowners towards putative problem animals appears inevitable. The adoption of integrated conservation and development projects (ICDPs), and local resource management more generally, is often put forward as a viable conflict mitigation option (Treves et al. 2009). However, the effectiveness of ICDPs have been mixed, particularly in regard to human-wildlife conflict (Gandiwa et al. 2013). Attitudes around human-wildlife coexistence are primarily influenced by how conflict is managed, and importantly, the severity of conflict events (Don Carlos et al. 2009). As the value of commercial game increases, and consequently the severity of conflict, attitudes towards nuisance wildlife become increasingly antagonistic. The propensity to erect predator-proof fencing in response to conflict raises further concerns (Woodroffe et al. 2014), as it can fragment habitat and significantly alter interactions between species, leading to detrimental impacts on ecosystem functions (Terborgh et al. 2001; Ripple et al. 2014).

The top three species killed as putative problem animals (leopards, elephants and lions) are also the most desired for non-consumptive tourism (Di Minin et al. 2013). The contribution of charismatic species to a country's economy, together with their ecological significance, make them vitally important species to conserve (Richardson & Loomis 2009). Game ranching has become established in other southern African countries; including Botswana, Namibia, Zambia and Zimbabwe (Bond et al. 2004; Lindsey et al. 2009b). In addition, we highlight an issue limited not only to Africa, as European countries (e.g., Spain) have also demonstrated decreased tolerance towards large carnivores following the adoption of intensive game management practices (López-Bao et al. 2015). Threatened species within these countries require extensive rangelands to maintain large and biologically viable populations (Graham et al. 2009). The adoption of game ranching is largely perceived to be a compatible land-use option for the protection of these threatened species (Cousins et al. 2008). However, the increased use of predator-proof fencing and legal destruction of wildlife in Limpopo, suggests that game ranching practices have become less compatible with species conservation.

Given the scale of decentralization and the widespread adoption of game ranching, together with the economic instability faced by countries within southern Africa, further research is required to quantify the extent to which ecologically important species are persecuted as a result of intensive game ranching practices. In South Africa, game ranching trends are currently accelerating, with high-value species being sold at record prices (e.g., sable antelope bull and kudu bull sold for ZAR 27 million (US$ 1.9 million) and ZAR 9.4 million (US$ 0.7 million) in 2015, respectively; www.vleissentraal.co.za; date accessed: 29 September 2015). By

bestowing custodial rights of wildlife to individual property owners, legislative policies encouraged innovation among the private and communal sectors that has ultimately inflicted a significant cost to wildlife conservation. Given these findings, devolution-based natural resource management likely requires increased centralized regulation to limit, or better control, the widespread adoption of intensive game ranching practices and their negative consequences on large scale conservation objectives. Increased centralized regulation likely provides a more scientifically-justified, holistic approach to land management and conservation, but may also present significant disadvantages. Limiting the use of wildlife may diminish their value and make them an intolerable financial burden (Murombedzi 2003), whilst centralized governance may disempower individuals and communities (Carruthers 2008), leading to non-compliance in conservation objectives and a general distrust towards governing authorities. The solution to the conservation issue we highlight therefore requires adept consideration of all stakeholders within a transparent and science-based framework.

Table 1. Model descriptions and output. Model outputs include β values, standard errors (SE), t-values and significance values (P-value; α at 0.05) for the intercept and coefficients, and the likelihood ratio test statistic (χ^2) and significance value (P-value; α at 0.05) testing each model against their null counterpart.

	Model description*	$\beta_{intercept}$	$SE_{intercept}$	t-value	P-value$_{intercept}$	$\beta_{coefficient}$	$SE_{coefficient}$	t-value	P-value$_{coefficient}$	χ^2	P-value$_{likelihood}$ [‡]
a)	Average price of all game by year[†]	-678.31	69.61	-9.74	≤ 0.001	0.34	0.03	9.93	≤ 0.001	1.75e+11	≤ 0.001
b)	Annual turnover of all game by year[†]	-1.048e+03	1.04e+02	-10.05	≤ 0.001	0.53	0.052	10.25	≤ 0.001	6.45e+17	≤ 0.001
c)	Number high-value game sold by year[†]	-258.21	34.53	-7.48	≤ 0.001	0.13	0.02	7.68	≤ 0.001	1.18e+06	≤ 0.001
d)	Average price of high-value game by year[†]	-681.32	69.39	-9.82	≤ 0.001	0.35	0.03	10.00	≤ 0.001	1.69e+11	≤ 0.001
e)	Number common game sold by year[†]	121.19	39.16	3.09	0.02	-0.06	0.02	-2.86	0.02	2.38e+07	0.005
f)	Number of ranchers breeding high-value game by year[†]	-2.69e+02	7.54	-35.67	≤ 0.001	0.14	0.004	36.20	≤ 0.001	2757.8	≤ 0.001
g)	Number of ranchers using predator-proof fencing by year[†]	-272.13	21.79	-12.48	≤ 0.001	0.14	0.01	12.64	≤ 0.001	999.31	≤ 0.001
h)	Permit applications by game ranchers for nuisance wildlife by year	-1.972e+04	6356.8	-3.10	0.02	9.86	3.17	3.11	0.01	8011.7	0.002
i)	Permit applications by non-game ranchers for nuisance wildlife by year	-2462.73	1597.66	-1.54	0.16	1.23	0.79	1.55	0.16	124.88	0.12
j)	Permit applications by game ranchers for non-nuisance wildlife by year	-1.684e+04	8076.55	-2.09	0.07	8.42	4.02	2.09	0.07	5854.8	0.04
k)	Relationship between nuisance wildlife permit applications and the adoption of high-value game breeding	23.49	8.00	2.94	0.02	0.29	0.09	2.89	0.02	1414.7	0.004
l)	Relationship between nuisance wildlife permit applications and the adoption of predator-proof fencing	15.76	5.37	2.93	0.02	0.16	0.07	2.38	0.05	431.85	0.02

* Analyses comprise generalised linear models from a Gaussian error distribution

[†] Modelled using a log link function

[‡] A significant result (i.e., ≤ 0.05) suggests rejection of the null model

Figure 1. Location of the study area situated between northern South Africa, Botswana, Zimbabwe, and Mozambique. White circles and grey crosses represent permit applications for nuisance wildlife and non-nuisance wildlife, respectively. Inset represents the location of the study area within Africa.
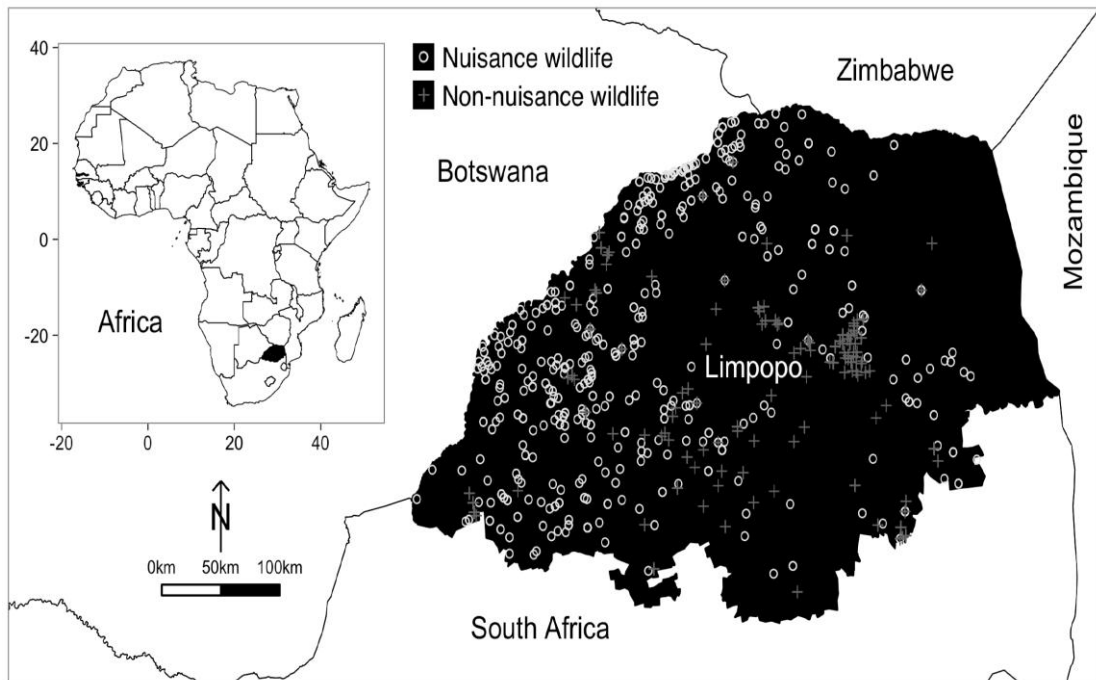
Figure 2. High-value game breeding and its economic contribution to Limpopo's economy. (a) Average price (ZAR) of high-value game, categorized by sex (higher price of females emphasizes the importance of breeding), and (b) high-value game breeding's percentage contribution to agricultural gross domestic product in Limpopo Province, South Africa from 2003–2012 (Grey shading represents 95% CI; pre-recession years represented by white bars and post-recession years represented by grey bars).
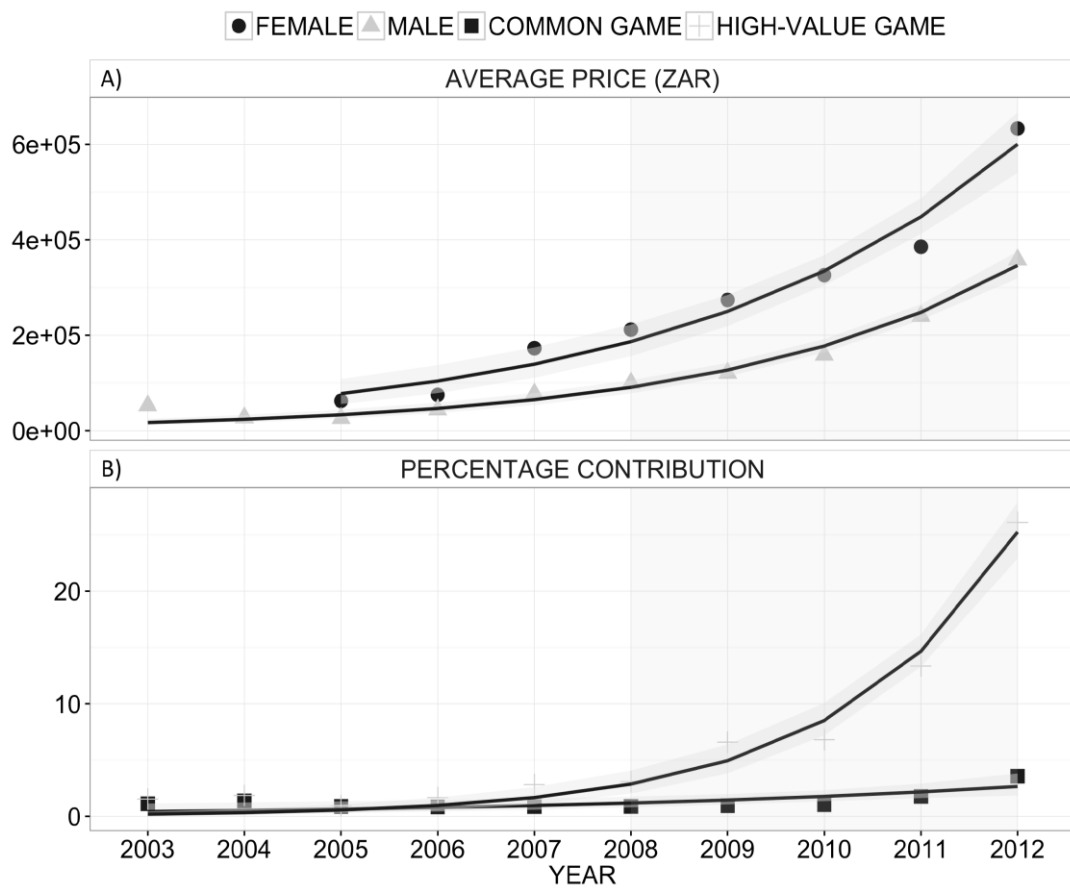
Figure 3. Growth in Limpopo's game ranching industry. Game auction data for high-value game, common game, and all game breeds combined from 2003–2012; categorized into (a) total head of game sold, (b) average price of game (ZAR), and (c) total annual turnover (ZAR), for Limpopo Province, South Africa (Grey shading represents 95% CI; pre-recession years represented by white bars and post-recession years represented by grey bars).
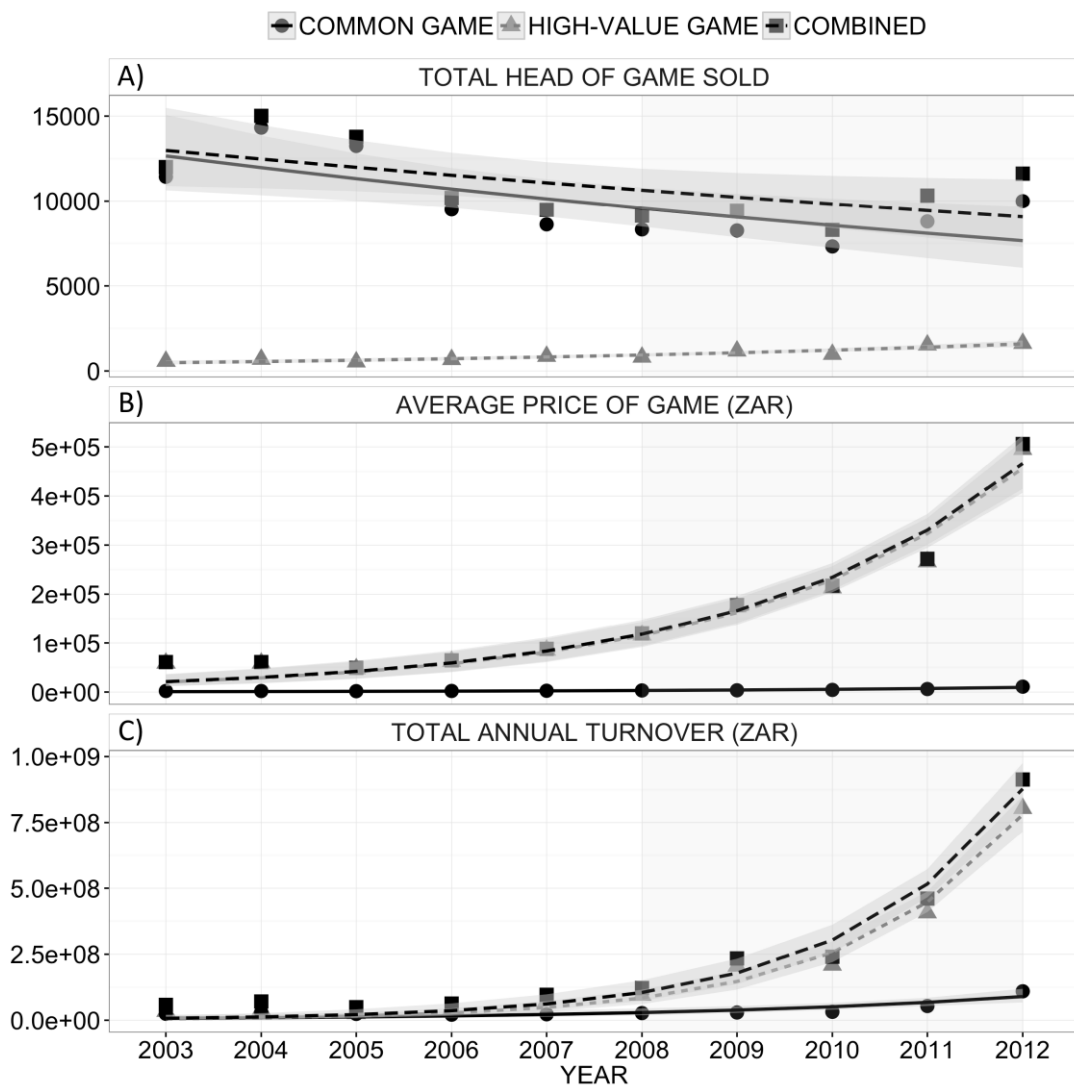
Figure 4. High-value game breeding and the adoption of predator-proof fencing.
Cumulative proportion of game ranches (a) breeding high-value game, and (b) using predator-proof fencing to protect their game in Limpopo Province, South Africa from 2003–2012 (Grey shading represents 95% CI; pre-recession years represented by white bars and post-recession years represented by grey bars).
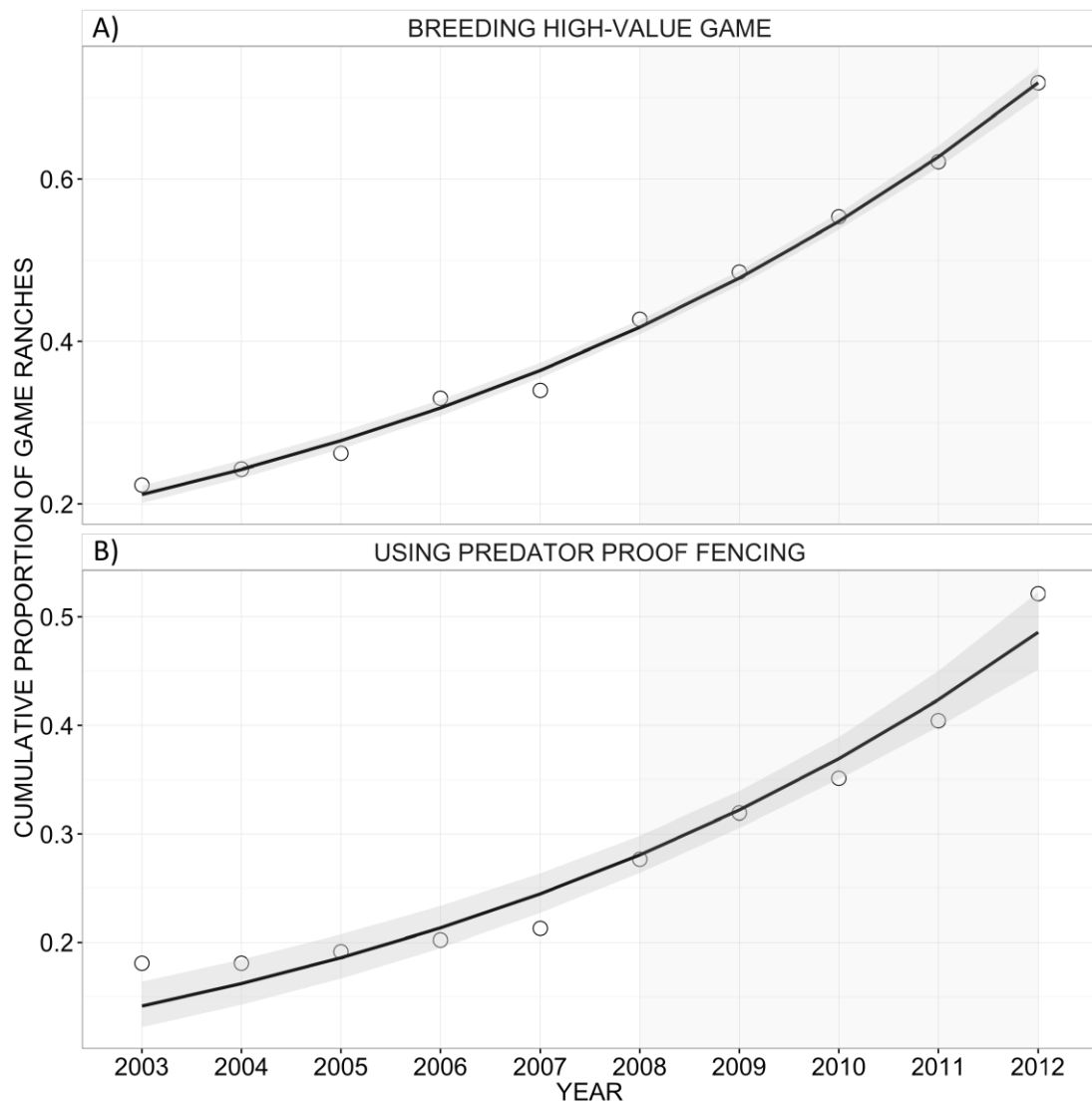
Figure 5. Legal destruction of nuisance wildlife and the adoption of game breeding practices. (a) Breeding of high-value game, and (b) using predator-proof fencing (Grey shading represents 95% CI; outlier represents the economic recession of 2008).
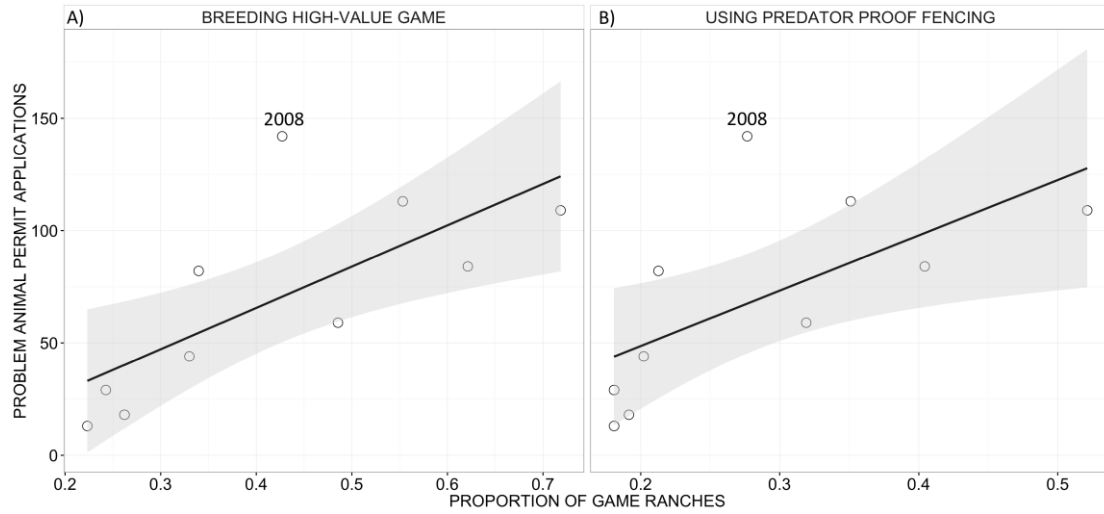
SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's website:

Supporting Information S1. Game breeding fashions. Game ranchers across Limpopo Province, South Africa breed (a) high-value game breeds such as sable antelope *Hippotragus niger*, and (b) common game breeds such as greater kudu *Tragelaphus strepsiceros*. Naturally rare game (e.g., sable antelope) are regarded as 'glamour' breeds, which fetch high prices at auction and as hunting trophies. Across southern Africa there has been a surge in the breeding of aberrant colour variants (Lindsey et al. 2009b) (also known as 'designer' breeds), which are selected through intensive breeding of related individuals with the purpose of expressing recessive morphological traits (e.g., black impala *Aepyceros melampus*). Designer breeds fetch exorbitantly high prices at auction, but are seldom hunted due to their high price. *Images courtesy of Charles James Sharp.*

Supporting Information S2. Details of game ranch survey.

Supporting Information S3. Datasets

Supporting Information S4. South African gross domestic product (GDP). Using quarterly intervals from 2003–2012 (ZAR; Vertical grey bar represents the onset of the economic recession).

Supporting Information S5. Percentage change in gross domestic product (GDP).

Gross domestic product by industry for South Africa from 2003–2012 (Vertical grey bar represents the onset of the economic recession).

Supporting Information S6. Legal destruction of free-ranging wildlife. Problem animal permit applications for (a) nuisance wildlife on game ranches, (b) nuisance wildlife on non-game ranches, and (3) non-nuisance wildlife on game ranches across Limpopo Province, South Africa from 2003–2012 (Grey shading represents 95% CI; pre-recession years represented by white bars and post-recession years represented by grey bars).

Supporting Information S7. Leopard population trends in Limpopo. Camera-trapping protocol, and Bayesian spatially-explicit capture-recapture models used to assess leopard population trends during and after the study period.

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