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African wildlife conservation and the evolution of hunting institutions

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Abstract

Hunting regulation presents a significant challenge for contemporary global conservation governance. Motivated by various incentives, hunters may act legally or illegally, for or against the interests of conservation. Hunter incentives are shaped by the interactions between unevenly evolving formal and informal institutions, embedded in socio-ecological systems. To work effectively for conservation, regulatory interventions must take these evolving institutional interactions into account. Drawing on analytical tools from evolutionary institutional economics, this article examines the trajectory of African hunting regulation and its consequences. Concepts of institutional dynamics, fit, scale, and interplay are applied to case studies of rhinoceros and lion hunting to highlight issues of significance to conservation outcomes. These include important links between different forms of hunting and dynamic interplay with institutions of trade. The case studies reveal that inappropriate formal regulatory approaches may be undermined by adaptive informal market responses. Poorly regulated hunting may lead to calls for stricter regulations or bans, but such legal restrictions may in turn perversely lead to more intensified and organised illegal hunting activity, further undermining conservation objectives. I conclude by offering insights and recommendations to guide more effective future regulatory interventions and priorities for further research. Specifically, I advocate approaches that move beyond simplistic regulatory interventions toward more complex, but supportive, institutional arrangements that align formal and informal institutions through inclusive stakeholder engagement.

1. Introduction

The high-profile death of Cecil the lion has reinvigorated debates over the role of hunting and hunters in conservation. The combination of this event, a controversial auctioned black rhinoceros hunt in Namibia, and recent public and media outcry has generated renewed calls for increased regulation, supported and advocated by NGO campaigns (Di Minin *et al* 2016a). These calls have prompted policymakers from the USA and other Western countries to impose tighter restrictions or even complete bans on certain forms of recreational hunting (Goode 2015, Grijalva 2016), and have raised the profile of hunting in recent academic literature. Conservation scientists have expressed concerns that hunting constitutes a threat to African

wildlife populations, notably megafauna, especially in tropical regions (Bennett *et al* 2002, Ripple *et al* 2016a, 2016b, Benítez-López *et al* 2017).

However, not all hunting is inimical to conservation. Appropriately managed at sustainable harvest levels, hunting may support efforts to conserve biodiversity, yielding potentially significant positive environmental and socio-economic benefits, both direct and indirect (Brown and Williams 2003, Leader-Williams 2009). Examples of such benefits include protein and revenues from animal products and hunting fees, which underpin the livelihoods of rural communities, provide essential income to landowners and conservation agencies, and support the maintenance of wildlife habitat in areas that would otherwise be converted to agricultural use. In extensive African

wildland regions that are ill-suited to alternative uses such as ecotourism, hunting can and does provide critical economic support to sustain conservation management (Lindsey *et al* 2006).

Nonetheless, the Cecil incident has highlighted that hunting regulation is a complicated matter. Public calls to restrict recreational hunting are motivated in part by emotional responses and ethical concerns relating to the welfare of non-human animals, against which conventional economic and consequentialist arguments may be regarded as less persuasive (Nelson *et al* 2016, Macdonald *et al* 2016a). Recent discussions on the acceptability of trophy hunting as a conservation tool have become highly polarized (Muposhi *et al* 2016). Influential international environmental groups increasingly oppose all forms of hunting and actively challenge arguments that support it¹.

Given these conflicting world views and changing socio-ecological contexts in Africa, what are the implications for future hunting regulation and associated conservation impacts? Related to this question, Macdonald *et al* (2016b) ask whether existing models of conservation financing that depend on lion trophy hunting revenues can be replaced effectively by a global conservation governance regime that does not. Others question whether hunting bans will protect wildlife and wildlands or simply devalue them and lead to their demise. This article proposes that the answers to such questions are illuminated by analysing the nature of evolving and interacting institutions, informed by contemporary institutional and governance theory.

Building on this notion, and embedded in a complex adaptive socio-ecological systems framework, this contribution explores the interplay between regulatory institutions of African conservation governance and the consequent incentives of hunters to comply with them. It posits that the effectiveness of regulations depends on the socio-ecological context in which they are established². To explore this proposition and gain deeper insights into the effectiveness of various regulatory measures, I draw on two case studies, namely rhino hunting and lion hunting, in an Africa-wide context. My analysis introduces institutional perspectives by employing principles identified in the emerging field of evolutionary institutional economics (Potts 2007, Beinhocker 2007).

¹ For example, assessments of the economic and conservation contributions of trophy hunting by conservation scientists (Lindsey *et al* 2007) and consultants representing the hunting lobby (Southwick 2015) have been publicly contested by other economic consultants hired by protectionist groups (Campbell 2013, Murray 2017).

² Conventionally, conservation regulations are set by government agencies, aimed at private actors, and may relate to a species, a geographic area, or both. Hunting is regulated by issuance of licenses, quota-setting, seasonal or other time-based limits, specification of allowable techniques or equipment, area-based restrictions on access and activity, and outright bans.

2. Hunting and institutions

Hunting may have either a positive or negative influence on African wildlife conservation, depending on the formal and informal institutions that shape the incentives of hunters within socio-ecological systems. To effectively promote conservation, regulatory interventions—a form of institutional change—should take full account of the incentives that drive human behaviour within these systems (Milner-Gulland 2012). Accordingly, I examine human behavioural motives for hunting and how these may be influenced by regulations and other institutions over time.

2.1. Hunting

Hunting is the active pursuit and harvest of wild animals. Loveridge *et al* (2006) identify three different types of hunters, based on motivation: (i) subsistence hunters, who seek to acquire food and other useful products for themselves and their immediate families; (ii) market or commercial hunters, who seek to acquire animal products to sell for profit; and (iii) recreational hunters, who enjoy the practice of hunting as a sport or leisure activity, albeit harvesting products such as meat or trophies. Fischer *et al* (2013a, 2013b) provide more detailed models of hunting motivations and functions, further identifying (iv) hunting for socio-cultural reasons and (v) perceived managerial needs to selectively control animal numbers or eliminate designated problem animals (i.e. culling). These analyses also reveal that motives for hunting are often mixed, confounding simple typologies. Hunting may also take place either legally or illegally. The latter practice, commonly termed ‘poaching’, is typically linked with rural poverty (Duffy *et al* 2016, Knapp *et al* 2017).

Within the conservation literature, there are three distinct focal points of discussion relating to hunting and appropriate policy responses. First is the so-called bushmeat crisis (Milner-Gulland and Bennett 2003, Bennett *et al* 2007), which is driven by expanding nutritional demands of human populations and changes in scale of hunting for meat from subsistence to commercial levels (Fa and Brown 2009, Brashares *et al* 2011, Lindsey *et al* 2013). Second is the transnational commercial poaching crisis, typically labelled as the ‘illegal wildlife trade’, which concerns market hunting to harvest valuable products such as elephant ivory, rhino horn and pangolin scales (Warchol 2004, Challender and MacMillan 2014).

The third focal area concerns recreational hunting, including trophy hunting, which is extensively discussed and debated in the literature (e.g. Dickson *et al* 2009). Some analysts argue that trophy hunting plays a vital supportive role in African wildlife conservation and caution against bans and excessive restrictions; others disagree (Naidoo *et al* 2016, Jacquet and Delon 2016, Ripple *et al* 2016c, Di Minin *et al* 2016b). Muposhi *et al* (2017, 2016) comprehensively

review trophy hunting as a conservation tool, detailing problems with illegal hunting, inadequate monitoring systems and hunting bans. They argue that recreational hunting retains potential to incentivize conservation and contribute to rural development, but that more research is needed at local, regional and international levels to inform policy.

Contemporary opposition to hunting, especially trophy hunting, is also motivated by ethical concerns related to animal welfare, animal rights, aesthetics and objections against wildlife commodification (Varner 1998, 2011, King 2005, 't Sas-Rolfes 2016). These concerns underpin an emerging compassionate conservation movement that emphasizes protection of individual animals in addition to species (Vucetich and Nelson 2013, Ramp and Bekoff 2015), but which is not universally accepted by conservationists (Nelson *et al* 2016). Moral philosophers note that there are multiple ways to address ethical issues (moral pluralism), that ethical codes vary with culture and context (moral relativism), and that it is problematic to legally enforce ethical principles that are not universally shared (Brennan 2011, Rachels 1993, 2004). Accordingly, ethical approaches may influence public opinion and the positions of specific interest groups, but may not provide a firm basis for universally applicable hunting regulation. However, ethical codes clearly underpin varying informal institutions.

2.2. Institutions

Separate strands of institutional thought within the fields of political science and economics are starting to converge under the influence of evolutionary theory, increasingly recognizing institutions as both structures and processes (Hodgson 2007, Lewis and Steinmo 2012, Potts 2007). Consistent with contemporary approaches, North (1991, p. 97) defines institutions as 'the humanly devised constraints that structure political, economic and social interaction', noting that they 'consist of both informal constraints (sanctions, taboos, customs, traditions, and codes of conduct), and formal rules (constitutions, laws, property rights)'. An evolutionary institutional economics approach examines and elucidates the dynamic interactions between these various institutions and the behaviour of humans motivated by economic incentives, and is grounded in seminal work by North (1990), Ostrom (1990) and Williamson (2000)³. This work is extended by richer theories of institutional links to socio-ecological systems and polycentric forms of environmental governance (Ostrom *et al* 2002, Ostrom 2005; 2010, Young *et al* 2006, Paavola 2007), and illuminated by the important concepts of institu-

tional interplay, fit, scale, and dynamics (Young 2002, 2010).

The core insight to be gleaned from this literature is that setting effective regulation is a complex undertaking. Allocations of rights profoundly influence human behaviour, and regulations do not always guide behaviour in simple and direct ways. Regulators and lobbyists should consider the interplay between institutions at multiple scales and across geographies, and be mindful of how formal institutions interact with informal institutions—i.e. whether rights and regulations are inclusive or serve the vested interests of a minority or elite group. Failure to do so may result in significant second-order effects and unintended consequences that undermine the original intent of the regulations and create collateral and possibly even larger long-term problems. This last point, already well known to economists (Acemoglu 2006, Bastiat 1850), highlights the importance of understanding and anticipating institutional dynamics, and generally supports bottom-up approaches to regulation that involve all relevant stakeholders rather than top-down approaches that do not.

These paradigm shifts are evident in more recent direct applications of institutional and governance theory to African conservation and natural resource management (see Child *et al* 2008, Barnes and Child 2014, Muchapondwa and Stage 2015) and even specifically to hunting (Fischer *et al* 2013b). Much of this line of inquiry is nascent and unacknowledged in mainstream conservation science literature. Nonetheless, at least some conservationists recognize the significance of social values and role of political ecology (Jepson and Canney 2003, Adams and Hutton 2007). Accordingly, some academics and practitioners also seek to incorporate social development goals into African conservation policy, invoking the principle of sustainable use of natural resources (Prins *et al* 2000, Child 2004, McShane *et al* 2011), while others acknowledge that social values cannot be readily changed for the sake of conservation (Manfredo *et al* 2017).

Muposhi *et al* (2016) shed light specifically on African hunting institutions, following a detailed historical review in Zimbabwe. They affirm that hunting has deep traditional roots in human civilization and that many indigenous African communities sustainably regulated their hunting activities by way of customary frameworks (demarcation of sacred areas, use of totems, and other social norms) throughout pre-colonial history. These institutions were largely displaced during the colonial era and ultimately superseded by the establishment of state protected areas and strictly regulated recreational hunting in designated areas, with access often limited to paying outside visitors.

Social scientists have recently provided insights into underlying social tensions, the significance of power relationships, and mismatch between formal and

³ This approach also draws upon the property rights analyses developed by Coase (1960) and Demsetz (1967), which have been specifically applied to wildlife law by Lueck (1989, 1995).

informal institutions in other African countries where both legal and illegal hunting is prevalent⁴. These studies highlight that many institutional arrangements for African wildlife conservation and commercial hunting remain inherently socially unstable and that significant reforms may be needed to ensure future sustainability. Much of this instability, it is argued, is linked to a history of dispossession—widespread instances of local communities losing their customary rights to land and wildlife use—and apparent strong desires to reappropriate such rights from the government agencies, national elites, foreign investors, and foreign consumers who currently claim them. Trickle-down economic benefits from existing commercial hunting enterprises are frequently seen as inadequate, and more fundamental devolution of power or transfers of rights may be sought to address perceived past injustices, failing which conservation efforts may be impaired.

As Muchapondwa and Stage (2015) have thus noted, addressing elite capture, stakeholder disengagement and distributional issues remain key issues for African wildlife conservation governance. In the realm of hunting, two additional issues emerge. The first pertains to an alternative method of producing hunting stock: intensive and selective breeding, which has been enabled by the development of wildlife market institutions and raises new concerns for conservationists. The second relates to complex interdependent interactions between hunting and wildlife trade regulation, and the conservation consequences thereof. Both issues are highlighted in the following two case studies.

3. Case studies

To gain a deeper understanding of institutional dynamics and interplay in relation to contemporary African hunting regulation, I consider rhinos and lions as illustrative subjects. The details of these case studies were obtained by research and participant observation, the latter through direct engagement of the author with policy analysis and consultation on both topics. Given sensitivities related to these cases, not all relevant supporting data are available in the public domain, especially not in peer-reviewed literature; accordingly, most of the facts are presented generally and qualitatively rather than specifically and quantitatively. This section deals only with key aspects relevant to the research approach. Further background information is provided in supplementary appendices A and B available at stacks.iop.org/ERL/12/115007/mmedia.

The two cases share a few significant characteristics. Both rhinos and lions play key functional

ecological roles and are popular icons among trophy hunters, eco-tourists, the wildlife media, conservationists and animal welfare activists alike. Because they are potentially dangerous to humans, neither are compatible with human settlement outside of more remote rural areas, and they may be targeted for removal as problem animals.

Previously widely hunted for sport under open access regimes during colonial times, rhinos and lions are now largely restricted to protected or managed areas in which hunting is either forbidden or tightly regulated. Both also have a unique history in South Africa, where the development of market institutions such as private property rights and live animal trade has engendered novel commercial breeding practices. This has resulted in more rapid population recovery rates, but also led to tensions between private owners and the state, the former having successfully overturned in the courts government attempts to restrict activities for both animals (domestic rhino horn trade and 'put-and-take' lion hunting).

In both cases, four distinct informal institutional constellations are apparent: (i) rural African people who share their environment with these animals and have developed customary attitudes toward them, (ii) pragmatic conservationists and private landowners who embrace hunting and other forms of sustainable use, (iii) modern (typically urban) compassionate conservationists who reject sustainable use and support bans, and (iv) traditional markets for rhino and lion body parts (used for medicinal and ornamental purposes, often linked to culture or prestige). These informal institutions interact with formal institutions of wildlife protection and management. Whilst these vary between jurisdictions, they typically follow a standard regulatory model⁵, as exemplified by the Convention on International Trade in Endangered Species (CITES), of which all relevant countries are signatories. To the extent that they vary, some countries claim state ownership of wildlife, whereas others treat it as *res nullius* (unowned property), with some enabling the devolution of use rights to local authorities. South Africa is the most extreme outlier, enabling full private ownership rights over certain wild animals.

3.1. Rhino hunting

Populations of both African rhino species were abundant and widespread prior to the 19th century arrival of significant numbers of European colonial settlers with guns (Martin and Martin 1983). Treating wildlife as an open access resource, early settlers hunted rhinos extensively for sport, harvesting their meat for food and their horns for trade, sometimes co-opting local Africans as collaborators. Following drastic declines in African big

⁴ This research comprises case studies in Botswana, Namibia, South Africa, and Tanzania, and details evolving interactions between traditional local hunters and outsiders during both colonial and post-colonial times (Gressier 2014, Bollig and Olwage 2016, Brandt 2016, Goodrich 2016, Hübschle 2016, Widlok 2016, Wright 2016).

⁵ This standard regulatory model typically involves a designated government authority that applies permits, quotas, term limits or complete bans on activities such as hunting, transport and trade of wild animals and their products.

game numbers, elite Western lobby groups inspired by hunters initiated the international conservation movement in the early 20th century (Jepson and Whittaker 2002). Rhinos benefited from the consequent creation of protected areas and game laws; sport and meat hunting largely ceased. However, rhino horn continued to be valued in Asian markets, inducing illegal market hunting. This prompted a 1977 international rhino horn trade ban under CITES. Initially considered a failure, the CITES trade ban finally appeared to contain poaching levels by 1995, by which time significant consumer countries had acceded to the convention and banned domestic trade.

South Africa's rhino populations, close to extinction by 1900, recovered impressively during the second half of the 20th century. To achieve this, South Africa adopted a formal institutional model, grounded in sustainable use principles, that enabled both state and private land-owning entities secure and beneficial property rights over individual animals, further allowing regulated commercial trophy hunting and market trade in live animals and their products ('t Sas-Rolfes 1990). This arrangement enabled both private and public operations to gain additional conservation finance, generated widespread economic benefits, and facilitated significant expansion of rhino range. This contrasted sharply with most other African countries, which maintained strict regulations and hunting bans, but mostly lost their wild populations during this time.

Following resurgent demand and associated rising market prices for rhino horn, from 2003 visiting Asian nationals started masquerading as trophy hunters to exploit the only legal means to export horns out of South Africa. The South African government responded by imposing tighter restrictions on a range of rhino-related activities, including hunting, and a moratorium on the domestic trade in rhino horn. Some wildlife industry participants responded to these restrictions by engaging in illegal practices, and the period 2007–2014 was characterised by a dramatic increase in rhino poaching and spread of related illegal activity across the country and internationally. This period is remarkable for the adaptability and ingenuity displayed by illegal market actors in response to evolving formal attempts to thwart their activities. The illegal market drew in many people, from impoverished rural locals to transnational organised crime syndicates, and involved numerous cases of corruption (Hübschle 2017).

From 2015, rhino poaching levels appeared to stabilize, but this was achieved only with substantial investment in militarized security measures, and poaching pressure remained high. Social scientists warned that this approach alienated local communities, was neither financially nor socially sustainable, and could result in deleterious long term consequences for wildlife conservation (Annecke and Masubelele 2016, Duffy 2015). Private owners, who harboured a growing portion of the rhino population (more than

a third by 2017), mostly supported legalizing the horn trade, hoping to reinforce the successful 20th century sustainable use approach (Rubino and Pienaar 2017). However, an increasing number of privately-owned rhinos were being selectively bred under semi-extensive conditions, outside their core historical range, raising concerns about their long-term conservation role. Although private breeders eventually succeeded in rescinding the domestic trade moratorium, prospects of lifting the international CITES ban remained poor, preventing easy access to Asian consumer markets. NGOs mostly opposed legalizing rhino horn trade and objected to the emergence of rhino farming, with many also campaigning against continued trophy hunting.

3.2. Lion hunting

Once widespread throughout Africa, lion populations have declined due to encroaching human agriculture and settlement, to the point where their future elicits great concern among conservationists (Bauer *et al* 2015). Lions are killed for sport by (mostly foreign) trophy hunters and for socio-cultural and retaliatory reasons by local Africans such as Maasai warriors (Hazzah *et al* 2009). In recent decades, lion trophy hunting has become increasingly regulated, if not banned altogether, in most African countries. The Cecil incident highlighted the occurrence of regulatory infractions, prompting conservation biologists to emphasize that exceeding established quotas may have serious negative impacts on lion population dynamics (Loveridge *et al* 2016).

As with rhinos, the South African institutional environment enabled the development of a commercial lion breeding and hunting industry. Initially intending to supply zoos and safari-parks, captive lion breeders started supplying 'put-and-take' trophy hunting ventures, which galvanized protests from animal welfare activists. Already firmly established by 2007, this industry also started supplying lion skeletons, as a by-product from trophy hunts, to Asian export markets. Following evidence that lion bones were being used as substitutes for tiger bones in traditional Asian medicines, conservationists raised concerns that such trade could stimulate commercial poaching of wild lions, but found no evidence that this was happening in South Africa (Williams *et al* 2015).

Following Cecil's death and a coordinated campaign against commercial captive breeding, activist NGOs persuaded several Western governments to implement trophy import bans. Most notable among these was a 2016 US ban on the import of trophies from captive-bred South African lions. This ban had a potentially significant impact on the economic viability of both lion breeding and trophy hunting, given that more than 95% of lions hunted in South Africa at the time were captive bred. A further NGO-led attempt to ban all international commercial lion trade under CITES failed. Instead, South Africa's government negotiated to maintain an annual legal lion skeleton

export quota, supplied from captive bred lions only. No other international trade in wild lion body parts, aside from some hunter trophies, was permitted.

The South African government undertook to review its export quota annually, applying an adaptive management approach subject to the results of research on the conservation impact of wild lions. Although captive-bred lions are considered unsuitable for reintroduction into the wild (Hunter *et al* 2013) and therefore considered by the US government to have no conservation value, they may play a vital (as yet poorly understood) buffer role for wild populations (Lindsey *et al* 2012). Experience from the rhino case suggests that reactive attempts to stifle legal commercial activity may have unintended consequences that are ultimately detrimental for conservation. A comparative institutional analysis suggests that a complete ban on lion hunting since 1977 in Kenya failed to prevent the decline of wild populations in that country (Nelson *et al* 2013). By contrast, in 2015 South Africa appeared to be the only country in which all wild lion populations were increasing (Bauer *et al* 2015).

4. Discussion

The rhino and lion hunting case studies affirm that hunting regulation is not a simple matter. In these cases, hunting motivations vary from recreation (trophy hunters) to profit (poachers), modulated by informal institutions. The varying socio-cultural attitudes of local African people interact with those of pragmatic conservationists, animal product consumers and protectionist proponents of bans on hunting and trade. Formal institutions at global scale, such as CITES, do not easily accommodate these partly conflicting informal institutions, the influence of which varies regionally and changes over time. For example, pragmatic conservation has tended to dominate policy in Southern African countries since the 1960s, whereas Kenya's policies have been increasingly dominated by protectionist thinking since the 1977 bans on hunting and international rhino horn trade. Significantly, Kenya supports a regulatory approach that is more closely aligned with influential international NGOs and governments of western countries that tend to dominate CITES policy decisions.

In a similar analysis of elephant hunting, Carruthers (2010) affirms the rising influence of emotional animal welfare concerns on policy toward elephant conservation and management. These concerns reflect evolving social norms: dynamic informal institutions that may over time engender formal institutions. There is clear evidence of a growing social movement that opposes all forms of wildlife hunting, especially of charismatic and threatened African megafauna, on ethical grounds. This movement consistently lobbies for tighter regulations and outright bans to supplement existing legislation and treaties such as the US Endangered Species Act

and CITES, and appears to be gaining traction in countries that have traditionally embraced sustainable use policies.

To the extent that the anti-hunting movement succeeds in eliminating legal markets, it may inadvertently foster the growth of illegal markets, with potentially undesirable consequences for conservation. For example, if local rural people who benefit economically from trophy hunting lose their vital income source following a hunting ban, they may be tempted to hunt illegally to supply animal product markets. This case reflects such dynamic interplay between regulatory and market institutions. Market institutions, both legal and illegal, provide support to existing cultural preferences and mediate conflicts between competing consumer demands, albeit not necessarily in ways that align with public policy goals. For example, private rhino and lion breeders in South Africa cater variously to demands from eco-tourists, trophy hunters and consumers of body parts, providing relevant products to each, even if illegally.

The case studies demonstrate the significance of property rights and prices as components of market institutions. Secure property rights that provide revenue-earning potential appear to be correlated with conservation success, whereas insecure or heavily restricted rights appear to discourage conservation: contrast the fate of rhinos on private conservation land in South Africa with those on state land in most other African countries. However, the cases also reveal that if property rights for valuable animals are not easily secured in the wild, private owners may attempt husbandry under more intensive and less humane conditions, thus moving away from desirable conservation and social objectives. Market prices—legal and illegal—serve as indicators of consumer preferences and their responses to changing conditions, providing potentially useful information about relative scarcity over time (Hayek 1945), which may stimulate and guide private entrepreneurial action. Rising black market prices for harvested wildlife products signal strong incentives for intensified poaching and supporting illegal activity, as revealed by the rhino case, and provide a cautionary signal in the case of lion bone trade.

5. Conclusion

Evolutionary economic analysis suggests that strict regulations and complete bans on hunting and trade will fail in the absence of appropriately aligned formal and informal institutions, and possibly even result in perverse effects for conservation. Kenya's long-standing hunting and trade bans, strongly supported by international NGOs, have failed to prevent substantial wildlife losses and may have even facilitated them in the face of strong incentives to convert wildlife habitat to conventional agricultural uses (Norton-Griffiths 2010, Ogutu *et al* 2016). This stands in stark contrast

with southern African countries that have employed the sustainable use approach: by enabling regulated and culturally appropriate commercial wildlife harvesting with meaningful benefits flowing to relevant local people, they have witnessed impressive expansion of managed wildlife habitats (Child *et al* 2012, Child and Child 2015).

With economic development as a political imperative (Kinzig and McShane 2015) and ongoing shortfalls in global conservation funding (McCarthy *et al* 2012), institutions that raise the economic profitability of legal ownership and management of living wild animals relative to the profitability of illegal harvesting—and channel the benefits to relevant private actors and local communities—seem most likely to succeed in Africa. In this regard, appropriately governed and managed commercial hunting activities may still play a pioneering developmental role in regions that are less suited to other forms of land use, such as conventional agriculture or ecotourism (Child 2000). Conversely, if the growing international anti-hunting lobby succeeds in further restricting existing sustainable commercial hunting activities without providing alternative and culturally appropriate sources of income for relevant local people, conservation is likely to suffer.

This research suggests that future changes to hunting regulation should take greater account of institutional dynamics and interplay across different scales, sectors and geographies. Regulators should consider how informal institutions might shape the incentives and consequent responses of relevant stakeholders, all of whom should ideally be involved in the formulation of inclusive formal institutions that acknowledge hunter motivations. Although more complex, such arrangements are likely to be more socially sustainable and beneficial for conservation. Finally, the rhino and lion hunting case studies suggest further avenues for future research: (i) more specific investigations of the role of property rights, prices and benefit flows in shaping adaptive responses to regulatory change, and (ii) more penetrating comparative institutional analyses of conservation performance between different jurisdictions, relating this to hunting, trade and market metrics.

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SUPPLEMENTARY INFORMATION

Appendix A: Rhino case study

The world's five rhino species (two of which occur in Africa) include some of the most endangered large mammals on earth, with two Asian species on the brink of extinction and several identified sub-species having already become extinct in recent decades. Traditionally, humans hunted rhinos for meat and other body parts. Following the arrival of colonial settlers and guns in Africa, rhinos were extensively hunted for sport, resulting in a significant loss of range through parts of the continent (Martin and Martin, 1983). During the early twentieth century, rhino hunting rates slowed with the establishment of state protected areas and restrictions on recreational hunting, but during the latter half of the twentieth century a new wave of illegal rhino hunting (poaching) emerged, driven by expanding consumer demand for harvested rhino horns. Rhino horn is considered a valuable commodity in parts of Asia, where it has a tradition of both ornamental and medicinal uses, typically accompanied by a sense of prestige.

Concerned by rapidly declining rhino numbers in the early 1970s, a coalition of governments moved to ban the international trade in rhino horn, listing all rhino species on Appendix I of the United Nations Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) by 1977. Initially, the trade ban was followed by an exponential increase in the market price of horn, which likely stimulated further illegal activity and saw the spread of rhino poaching across most of Africa (Leader-Williams, 2003). It was only in the early 1990s, after key rhino horn consumer countries yielded to specific political pressure from the United States and enacted laws against domestic trade, that poaching subsided. However, by this time remnant rhino populations survived in only a handful of range states, most significantly in South Africa, the only country to have largely avoided this more recent crisis.

South Africa had already lost almost all wild populations of its two indigenous rhino species by the start of the twentieth century; only one small population of southern white rhinos survived in a single protected area and black rhino numbers were similarly low. However, in the late 1950s conservationists initiated a bold plan to dramatically expand rhino populations by translocating them to new areas, including privately owned land (Milliken and Shaw, 2012). The late 1960s saw the first legal recreational white rhino hunt on private land and a market for rhino trophy hunting grew steadily from that time.

Initially, private landowners did not engage seriously in rhino breeding. Research revealed concerns about weak property rights over the animals, which were classified as *res nullius* under the South African common law, meaning that they were unowned until killed, captured or domesticated. Accordingly, private landowners had strong incentives to have rhinos shot and sold as trophies as soon as possible after taking possession and releasing them on their properties. However, this situation changed after new legislation, the 1991 Theft of Game Act, explicitly recognized private ownership of commercially valuable animals in extensive fenced areas, stimulating the growth of a competitive live sales market, accompanied by exponentially rising market prices (’t Sas-Rolfes, 1990). This legislation also fuelled rapid general growth of

private conservation and wildlife ranching activity in South Africa and furthermore benefitted public parks agencies, which gained a valuable source of income from the sale of live animals.

Many private landowners now embraced rhino breeding and began to play a significant role in their conservation: South African rhino numbers rose significantly as they were being depleted throughout the rest of Africa. In 1994, recognizing the success of South Africa's sustainable use approach to rhino conservation, the world's governments agreed to down-list the country's population of southern white rhinos to CITES Appendix II, thereby allowing limited international trade in live animals and trophies. They did not extend this concession to rhino horn, although trade remained legal within South Africa.

Records reveal that from the year 2003 nationals from Vietnam started to visit South Africa for the ostensible purpose of rhino trophy hunting. However, Vietnam has no tradition of trophy hunting and it became apparent that these visitors sought to circumvent CITES restrictions by taking advantage of the trophy export concession to specifically obtain rhino horns. Once it became obvious to South African wildlife ranchers that rhino horn demand had resurged in Asia, some facilitated increased supply of horn via this so-called 'pseudo-trophy hunting' route and others sold accumulated stocks of horn to traders who apparently exported them illegally. Once conservationists and regulators became aware of these schemes, the South African government responded by enacting a series of strict regulations, requiring permits for a range of activities relating to the possession, management and movement of both live rhinos and their body parts and applying certain norms and standards to the hunting industry. It further announced a moratorium on all domestic trade in rhino horn.

The imposition of these regulations coincided with a rapid and substantial increase in both trophy prices and illegal activity and a second international rhino poaching crisis has erupted since 2007 (Rademeyer, 2012). Although it is difficult, if not impossible, to ascertain a direct causal effect, one can at least hypothesize that the imposition of onerous restrictions and attempted closure of the trophy export loophole yielded perverse results. Many wildlife ranchers, clearly discontent with the new levels of restrictions, found themselves with significantly constrained property rights, whereas their vulnerability to dangerous poaching attacks rose drastically. Numerous privately-owned rhinos were thus effectively converted from assets into liabilities and this was reflected in declining real live prices at wildlife stock auctions.

Private rhino owners and others in the wildlife ranching industry reacted to the restrictions and poaching crisis in various ways. Some are known to have turned to illegal activity, either ignoring the new regulations or actively participating in poaching and trade, sometimes even staging fake poaching incidents on their properties. Most others increased their investment in security, employing a wide range of measures that included innovations such as periodic removal ('dehorning', which is non-lethal and relatively harmless) and subsequent secure storage of removed horns or contamination of horns still attached to living animals. Others arranged to move their animals to safer locations, some attempting to negotiate long-term lease agreements with landholders in other countries, and others moving their animals to more

intensively managed (higher density) enclosures where they could be more easily monitored and protected. Finally, others divested themselves of rhinos by selling them – survey results indicate that the extent of privately protected rhino habitat shrunk by up to 10% between 2008 and 2015.

In its attempt to prevent pseudo-trophy hunting, the South African government ceased issuing hunting permits to Vietnamese nationals. This was followed by a surge of interest from citizens of other countries, notably the Czech Republic, which was then revealed to be acting as a conduit to the Vietnam market. After further tightening of hunting regulation in 2012 through additional norms and standards, which included provisions for micro-chipping and DNA-profiling all horns from hunted rhinos, the interest in rhino trophy hunting appeared to wane somewhat, but by this time poaching had become widespread and firmly established, with large numbers of incursions into state protected areas such as the Kruger National Park, which is home to the world's largest free-ranging rhino population.

Eager to find a solution to the poaching problem, the South African government investigated a range of potential policy options, including the possible submission of a proposal to the 2016 CITES Conference of Parties (CoP) to re-establish an international commercial trade in rhino horn, supplied from existing legal stockpiles and established private breeding operations that practiced routine dehorning. The government eventually decided against such a submission, but during this time two South African private rhino owners instituted a court action against it, challenging the moratorium on domestic trade. The private owners won the case, following which the South African government unsuccessfully attempted to appeal the decision, which was finally and decisively upheld by the South African Constitutional Court in early 2017. By this time, the Environment Minister had published draft legislation to regulate domestic rhino horn trade, including clear guidelines on the circumstances under which limited exports of horn for personal use would be permitted. By mid 2017 private rhino owners were exploring potential auctions and other methods to legally trade rhino horns within South Africa, within what remained a highly restrictive regulatory framework.

After dramatic annual increases from 2007 to 2014, South African rhino poaching levels appeared to stabilize in the subsequent two years. However, the socio-economic costs of rhino poaching – including the considerable losses of human and rhino lives, and substantial raised costs of law enforcement – continued to weigh heavily on the country, with many observers concerned that the situation was unsustainable for both state conservation agencies and private owners, most of whose resources were stretched by drastically higher security costs. Social scientists expressed further concern at the social consequences of increasingly militarized approaches to poaching prevention (Anneck and Masubelele, 2016; Duffy, 2015; Hübschle, 2016) and conservationists expressed concern over collateral potential biodiversity loss due to the diversion of critically limited financial resources for conservation management. Anti-hunting activists continued to lobby for bans on rhino trophy hunting, focusing their attention on importing countries.

Appendix B: Lion case study

Prior to the twenty-first century, African lions were considered relatively common and did not feature as an ‘endangered species’. Traditionally hunted by some indigenous African tribes, notably the Maasai (Hazzah et al., 2009), lions also became popular with colonial sport hunters as one of the ‘Big Five’ most dangerous animals to pursue during the nineteenth and twentieth centuries. As apex predators, lions do not co-exist comfortably with humans in higher density agricultural and settled areas, and human-lion conflict has challenged conservation throughout history, often providing a case for hunting as a form of pest control (as retaliation for livestock and occasional human attacks and deaths). The twentieth century also saw the establishment of regulated commercial recreational lion trophy hunting practices in several African countries.

The conservation status of African lions has recently emerged as an issue of significant concern, following revelations that populations are declining in most parts of the continent other than within intensively managed areas in some southern African countries (Bauer et al., 2015). South Africa is the most notable exception, with all its wild populations believed to be increasing. Significantly, South Africa is also the only country with a large captive lion population, estimated at some 5,800 animals in 2013, and growing (Williams et al., 2015). In most other African countries, the decline of wild lion populations and concerns about effective governance have led conservation scientists to question to what extent recreational trophy hunting practices can be sustained. Accordingly, the issue of lion trophy hunting has attracted a large volume of recent discussion in the academic literature (Loveridge et al., 2007, 2016; Croes et al., 2011; Davidson et al., 2011), consistent with broader concerns over carnivore hunting associated with the possible negative synergistic effects of predator persecution by farmers (Treves, 2009; Packer et al., 2009).

South Africa’s (privately owned) captive lion population has grown in response to consumer market demands, starting out several decades ago as lion parks to cater to any tourists who were unable to view wild lions in state protected areas. Viewing from private vehicles within large enclosures was subsequently supplemented by cub petting, lion walking experiences, and the provision of captive-bred animals to even larger enclosed areas to be hunted for trophies. This last practice, labelled ‘put-and-take’ or ‘canned’ hunting, has attracted significant controversy in recent years. Initial attempts to restrict it through government regulations were thwarted after the South African Predator Breeders Association and two other appellants won a judgement in the Supreme Court of Appeal in late 2010.

Adding to the suite of captive-bred lion products, from around 2008, South African breeders started legally exporting bones from hunted and other deceased animals to buyers in Southeast Asia, where they are used as substitutes for tiger bone in traditional medicinal preparations such as wines and pastes. Tiger bone trade was officially outlawed in China in 1993 (along with domestic rhino horn trade), following which captive breeding operations proliferated. This prompted Chinese scientists and officials to recommend establishing a legal domestic tiger bone trade supplied from these tiger farms (Jiang et al., 2007), but this was strongly opposed by conservationists and activist NGOs, who succeeded in lobbying for a 2007 CITES decision calling for limits on commercial captive tiger breeding. Although domestic trade in tiger bone

remains officially illegal in all Asian countries, in practice the number of captive bred tigers has allegedly increased since then, along with consumption of various tiger products.

Many conservationists believe that the presence of tiger farms threatens wild tigers, by enabling product leakage, allegedly stimulating consumer demand and providing potential cover for laundering of wild tiger products (Gratwicke et al., 2008). Similar concerns started to surface over the role of captive lion breeding operations, further inspiring campaigns to outlaw them and the practice of canned hunting. Despite researchers warning that prohibition of captive lion hunting might have negative consequences for wild lion populations (Lindsey et al., 2012) activists succeeded in persuading the governments of Australia and France to ban the import of all lion trophies in 2015 and the following year the United States government announced a ban on trophies obtained from hunted captive lions, but not wild ones. The last measure is significant, as US hunters previously accounted for a great majority of South African lion hunts, of which more than 95% are of captive-bred animals, and South Africa in turn accounted for 80% of the Southern African (SADC) region's (wild and captive) lion trophy exports between 2005 and 2014 (Sinovas et al., 2016).

In 2016, activists also successfully orchestrated a motion of the International Union for the Conservation of Nature (IUCN) calling upon the South African government to outlaw canned hunting and tightly regulate the captive breeding of lions. However, at the subsequent CITES CoP an attempt to list the African lion on Appendix I was rejected – instead the parties to the convention agreed to prohibit the international trade of lion body parts (other than hunting trophies) from wild lions, but granted South Africa an annual export quota of lion bones to be supplied from captive breeding operations. Activist NGOs protested this decision and argued for a zero quota, but the South African government decided to set the quota for 2017 at 800 skeletons, based on an assessment of the market size in prior years. Noting the experience of their failed initial attempts to stifle illegal rhino horn exports, government officials favoured a more measured approach to regulating lion bone exports, i.e. monitoring legal market activity and applying principles of adaptive management.

Unlike rhinos, up to the year 2017 wild lion populations had not been subjected to large-scale commercial poaching for their harvestable products, although there had been a few isolated incidents of illegal killing of (mostly captive) lions, evidently to supply domestic African markets for traditional medicine. The full impact of the US trophy hunting ban remained to be seen, but captive breeders had responded in different ways, with some curtailing their operations and others adopting a range of adaptive strategies such as seeking new hunting clients and product markets or attempting to reposition their lions as wild. Early evidence suggests that at least some breeders attempted to increase their sales and exports of lion bones, raising concerns over disruptive collateral effects on that market. Some breeders also hoped for a reversal of US policy, following that country's political regime change in late 2016. However, activist NGOs continued to campaign for the prohibition of all types of lion trophy hunting and commercial captive breeding.

Aside from the concerns relating to captive lion breeding and its associated trophy market, conservationists continued to debate the role of wild lion hunting and how it should be regulated (Bouché et al., 2016; Bauer et al., 2017; de Longh, 2012; Joppa and Hutton, 2012; Miller et al., 2016). However, most researchers appeared to accept the potential for trophy hunting to generate important revenues for conservation, provided it is appropriately regulated and managed for sustainability (Creel et al., 2016; Edwards et al., 2014). Focusing on such governance issues, Nelson et al. (2013) conducted a comparative institutional analysis between several African countries and identified factors that promote sustainable lion hunting, notably devolution of rights and accrual of hunting revenues to local landholders. They found that a 1977 hunting ban in Kenya had not prevented the subsequent rapid decline of lion populations in that country, owing to other factors such as retaliatory killings in human-lion conflict, habitat loss and prey depletion.

In mid 2017, the son of Cecil, a lion named Xanda, was killed by another trophy hunter in Zimbabwe, provoking a further round of international public outrage, albeit not on the same scale as Cecil. Aside from the expected condemnation from animal welfare activists, this incident also prompted a previously more mainstream conservation organisation (with strong links to Kenya) to publicly announce a policy change (online) toward trophy hunting as a means of financing conservation, which it said it now no longer supported. However, a few days later the public posting was removed and replaced with a far more moderate statement. Notwithstanding this last development, there is clear evidence that the public anti-hunting constituency is growing, and that lions represent a focal point over which this issue will continue to be debated.

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