

Review Paper

ECOLOGICAL, PHYSIOLOGICAL, GENETIC TRADE-OFFS AND SOCIO-ECONOMIC IMPLICATIONS OF TROPHY HUNTING AS A CONSERVATION TOOL: A NARRATIVE REVIEW

Victor K. Muposhi^{1*}, Edson Gandiwa¹, Stanley M. Makuza² and Paul Bartels³

¹School of Wildlife, Ecology and Conservation, ²School of Agricultural Sciences and Technology, Chinhoyi University of Technology, School of Wildlife, Private Bag 7724, Chinhoyi, Zimbabwe

³Department of Nature Conservation, Tshwane University of Technology, Staatsartillerie St, Pretoria, 0183, South Africa

* Corresponding author; Email: vkmposhi@gmail.com

ABSTRACT

Although the contribution of trophy hunting as a conservation tool is widely recognised, there is perpetual debate and polarization on its sustainability. This review integrates five themes mostly considered in isolation, as independent research fields in wildlife conservation: (1) trophy quality and population ecology of hunted species, (2) behavioural ecology of hunted populations and associated avoidance mechanisms, (3) physiological stress in hunted populations, (4) genetic variability and desirable traits, and (5) socio-economic imperatives in wildlife conservation. We searched for articles on search engines using specific key words and found 350 articles from which 175 were used for this review under five key themes. Population and trophy quality trends of commonly hunted species seem to be declining in some countries. Elevated hunting pressure is reported to influence the flight and foraging behaviour of wildlife thus compromising fitness of hunted species. Selective harvesting through trophy hunted is attributed to the decline in desirable phenotypic traits and increased physiological stress in most hunted species. Though it provides financial resources need for conservation in some countries, trophy hunting works well in areas where animal populations are healthy and not threatened by illegal harvesting and other disturbances. There remains much polarity on the sustainability of trophy hunting in modern-day conservation. More research need to be conducted across the five themes examined in this review for broader analytical analysis and comparison purposes. A new research agenda is needed regarding wildlife sustainable use principles and their sustainability and acceptability in modern-day conservation.

Key words: Wildlife harvesting, wildlife behaviour, landscape of fear, conservation physiology, genetic diversity, trophy hunting bans.

INTRODUCTION

Human societies have depended on the utilisation of wildlife for most of their existence (Ingold *et al.*, 1991; Muboko and Murindagomo, 2014). Extractive exploitation of wildlife still remains the foundation of human survival in much of the developing world and to some extent indirectly by the developed world in various capacities (Leader-Williams and Hutton, 2005; Nasi *et al.*, 2008; Ochieng *et al.*, 2015). However, as a response to the overwhelming exploitation of wildlife species through hunting activities by humans in the 19th century, some mindful hunters promoted various conservation initiatives to promote the protection of the remaining wildlife populations (Adams, 2013). Accordingly, during the early 20th century, hunters played a key role in the establishment of protected areas in various countries and the subsequent institutionalisation of trophy hunting as a conservation tool using the principle of sustainable use (Mahoney, 2009; Mahoney and Jackson III, 2013), supported with proto-ecological motivations and considerations which is now known as

ecological theory (Milner-Gulland *et al.*, 2009; Treves, 2009).

Trophy hunting, is used to describe hunting by paying tourists, typically with the objective of selecting individuals with exceptional physical attributes (e.g., large horns, tusks, body size, mane or skull length) and usually in the company of a professional hunting guide (Lindsey *et al.*, 2007c). Trophy hunting promotes the off-take of older males or individuals that would have crossed the line to post-reproductive stage (Baker, 1997; Damm, 2008). Through a quota system approach, trophy hunting, promotes sustainable off-takes by removing a fraction of natural population growth rates which arguably falls within the compensatory mortality range and has a negligible impact on overall population sizes (Cooley *et al.*, 2009; Morrill, 1993). In human-dominated landscapes, humans will continue utilizing wildlife resources especially in areas where wildlife exists and thus sustainable use and incentive-driven conservation has to be at the centre of conservation initiatives (Hutton and Leader-Williams, 2003; Robinson and Bennett, 2004). Consequently, trophy hunting has been

institutionalised and has evolved since the early 20th century and is currently practiced worldwide in most continents for example, America (Heffelfinger *et al.*, 2013); Europe (Milner *et al.*, 2006; Sharp and Wollscheid, 2009); Australia (Albrecht *et al.*, 2009; Thiriet, 2009); Asia (Harris *et al.*, 2013); Africa (Damm, 2008; Lindsey *et al.*, 2006; Loveridge *et al.*, 2006).

There is widespread recognition on the potential and significance of trophy hunting as a conservation tool (Baker, 1997; Damm, 2008; Lindsey *et al.*, 2007a). Researchers acknowledge the contribution of trophy hunting towards sustainable development in biodiversity rich countries (Balduş, 2008; Fischer *et al.*, 2013). More importantly, trophy hunting is considered the most profitable form of consumptive wildlife utilization, and represents a large and growing industry spreading over 23 sub-Saharan African countries (Lindsey, 2008). However, there is perpetual debate, polarisation and lack of consensus among conservation Non-Governmental Organizations, some African governments, animal rights and welfare groups over the acceptability and effectiveness of trophy hunting as a conservation tool (Loveridge *et al.*, 2006; Mayaka *et al.*, 2004; Sorensen, 2015). This polarisation seems to be exacerbated by a lack of reliable data on the impact of trophy hunting on wildlife species, given that most information on African trophy hunting occurs in unpublished grey literature (Lindsey *et al.*, 2007c), and framing of trophy hunting issues in the mass media and social media platforms seem to be emotive and lacks parity (Gandiwa *et al.*, 2014; Sorensen, 2015).

Nonetheless, at a broader scale, insufficient governance and institutional failure of regulatory authorities trophy hunting issues (Damm, 2008; Lindsey *et al.*, 2007c; Palazy *et al.*, 2011) may result in the population decline of hunted species and loss of some desirable traits such as the trophy size or quality (Crosmarý *et al.*, 2015c). Moreover, the selective nature of trophy hunting may be detrimental to the viability of harvested populations by interfering with the behaviour (de Boer *et al.*, 2004; Muposhi *et al.*, 2016a; Setsaas *et al.*, 2007), physiological (Maréchal *et al.*, 2011; Romero and Butler, 2007), genetic and evolutionary (Allendorf *et al.*, 2008; Allendorf and Hard, 2009) adaptations of target species. Most of the research related to trophy hunting in mammals and its associated trade-offs is conducted in isolation hence making it difficult to promote effective adaptive management. Accordingly, this review focuses on this topical and emotive subject in modern-day conservation, to advance holistic and pragmatic policy measures in wildlife conservation in relation to sustainable utilization and development.

METHODS

A review of literature was made consulting 175 articles under the five themes outlined below on the basis of their contextual relevancy. The five themes include; (1) trophy quality and population ecology of hunted species, (2) behavioural ecology of hunted populations and associated avoidance mechanisms, (3) physiological stress in hunted populations and ecological traps, (4) genetic variability and desirable traits, and (5) socio-economic imperatives in wildlife conservation policy measures. The findings were thereafter presented in the five themes and further integrated into a conceptual framework based on the review.

RESULTS AND DISCUSSION

Trophy quality and population ecology of hunted wildlife species: Most hunters have certain expectations on the choice of individual selected, e.g., presence of animals with exceptional phenotypic traits such as large trophies (Festa-Bianchet, 2007). Accordingly, the sustainability of trophy hunting may be compromised when populations of preferred species with the desirable traits shrink in numbers and extent of occurrence (Nuzzo and Traill, 2013; Palazy *et al.*, 2012). Temporal and spatial trophy quality changes may have adverse effects on the sustainability of the hunting industry (von Brandis and Reilly, 2007). Declines in trophy quality of preferred wildlife species have been reported in sub-Saharan Africa (Crosmarý *et al.*, 2013; Loveridge *et al.*, 2009; Nuzzo and Traill, 2013; von Brandis and Reilly, 2008; Wilfred, 2012). Nonetheless, Wilfred (2012) argues that negative trends in trophy quality will certainly illicit similar trends in the economy since the trophy hunting market aligns itself with those countries producing superior trophy animals. Thus, the decrease in trophy quality may jeopardize the conservation potential of hunting areas, which would be a major concern in southern Africa where hunting zones represent over half of the total area of protected lands (von Brandis and Reilly, 2007).

Few attempts have been made in southern Africa to chronicle such trends other than those found in grey literature. As such, Loveridge *et al.* (2009) argues that it is imperative to ensure that monitoring of the population size, trends in trophy quality and hunting success in most preferred and common trophy species is done even though it may be expensive, time consuming and may require extensive expertise. Monitoring of trophy sizes offers an understanding of the short and long-term changes in populations and trophy quality parameters (e.g., horn or tusk size) of hunted species (Milner-Gulland and Rowcliffe, 2007; Wilfred, 2012). There is need to probe into whether trophy size matter for hunters or it is the overall experience these hunters rather than the

ultimate traits of the target species. It is likely that with the evolution of hunters and trophy hunting as a sport, the size of the trophy may not matter due to different satisfaction needs by the hunters (Holbrook and McSwain, 1991). It is believed that with time, the total hunting experience would outweigh the need for shooting the target species (Holbrook and McSwain, 1991; Voeller, 2005), and as such the trophy quality may not matter.

Fenberg and Kaustuv (2008) outline some ecological impacts of trophy hunting in wildlife species such as: (1) changes in body size, (2) growth and survival of offspring, mortality rates, (3) reproductive investment, (4) growth size and age (size) at maturity, and (5) changes in the sex ratio of harvested populations. The effect of size-selective harvesting on the body size and phenotypic traits in wildlife species has been observed in bighorn (*Ovis canadensis*) male population due to hunting of trophy rams (Coltman *et al.*, 2003). Similarly, Ginsberg and Milner-Gulland (1994) argue that harvested ungulate populations invariably have mortality patterns that deviate significantly from those in non-hunted populations.

A continual decline in the population size of wildlife species in most African countries have been reported with human activities such as trophy hunting and illegal hunting being attributed as the main causes (Ogutu *et al.*, 2011; Ripple *et al.*, 2015). For instance, declines in wild animal populations as a result of unsustainable exploitation have been observed in Africa, e.g., Umfuruzi Park, Zimbabwe where hunting was at one time suspended as a result of population decline (Muposhi *et al.*, 2014a; Muposhi *et al.*, 2014b). However, declines in species density elsewhere, have been linked to other factors other than trophy hunting, e.g., droughts (Ogutu *et al.*, 2008; Ogutu and Owen-Smith, 2003), habitat change and illegal harvesting among others (Gandiwa, 2013; Muboko *et al.*, 2014; Ottichilo *et al.*, 2000). Nonetheless, there remain high densities of wildlife species in some hunting areas of Zimbabwe, South Africa and Botswana (Dunham, 2012; Lindsey *et al.*, 2009). Similar trends where wildlife densities remained stable in southern African countries were also observed by Craigie *et al.* (2010). However, in cases where off-take rates are low and conservative and rigorously managed, trophy hunting areas maybe valuable conservation zones wildlife species (Crosmar *et al.*, 2015a).

Behavioural ecology of hunted populations and associated avoidance mechanisms: Human recreation in natural areas have been observed to increase the level of disturbance to wildlife (Maréchal *et al.*, 2011; Stankowich, 2008). Integrating an understanding of behaviour into wildlife conservation is becoming more important (Anthony and Blumstein, 2000). Improving the

knowledge of how and to what extent the impact of anthropogenic disturbance (e.g. trophy hunting) has on the welfare and behaviour of wildlife in natural ecosystems may provide valuable information to managers and planners in conservation (Tingvold *et al.*, 2013).

Trophy hunting, like predation, tends to alter wildlife behaviour by influencing the perceived risk (Muposhi *et al.*, 2016a) thus shaping the landscape of fear for most wildlife species (Ciuti *et al.*, 2012; Coleman and Hill, 2014; Rösner *et al.*, 2014). Kilgo *et al.* (1998) observed that hunted deer evaded roads and increased nocturnal behaviour as an avoidance mechanism that has much implications on photographic tourism. Similarly, sable antelope (*Hippotragus niger*) has also been observed to avoid would be suitable habitat patches with high hunting pressure in favour of habitats areas as an avoidance strategy (Ndaimani *et al.*, 2013). Instances where animals shift their habitat in response to hunting have been noted in impala (*Aepyceros melampus*) (Setsaas *et al.*, 2007) and wildebeest (*Connochaetes taurinus*) (Tambling and Du Toit, 2005). This hunting aversion strategy may also come as a cost and eventually become an indirect source of stress to individuals subjected to high hunting pressure (Verdade, 1996). However, this coping strategy may result in ecological traps as individuals may prefer to use poor habitats (i.e., habitats with lower feed quality (Kilgo *et al.*, 1998)) over the most suitable ones due to hunting disturbance aversion (Abrams *et al.*, 2012; Battin, 2004; Robertson and Hutto, 2006).

Trophy hunting may alter the flight behaviour wildlife species in some areas depending on the intensity and frequency of the hunting (de Boer *et al.*, 2004; Donadio and Buskirk, 2006). To assess the amount of perceived risk by wildlife species, several studies have used flight initiation distance (FID) as a proxy for fearfulness and anxiety as a result of human disturbances (Stankowich, 2008; Stankowich and Blumstein, 2005). Flight initiation distance is the distance at which an animal begins to flee from an approaching test-person, who in this case is perceived as a predation threat (Setsaas *et al.*, 2007). To maximise the chances of survival in the wild, individuals do vary the distance at which they begin to flight from an approaching disturbance or threat (Tarakini *et al.*, 2014). However, most of the studies on FID have explored the influence of environmental, predatory or prey condition-based factors (Stankowich and Blumstein, 2005). By influencing flight decisions of hunted wildlife species, trophy hunting is therefore thought to shape the landscape of fear in many human-mediated ecosystems (Muposhi *et al.*, 2016a; Rösner *et al.*, 2014). Here we consider the landscape of fear to represent the relative levels of 'predation' risk as peaks and valleys that reflect the level of fear a certain trophy species experiences in different parts of its habitat

(Laundré *et al.*, 2010). There is a general realization that our understanding of the relationship between trophy hunting and behaviour is limited (de Boer *et al.*, 2004). Incorporating behavioural studies in the development of management plans is therefore important in conservation

especially under closed environments or areas with poor dispersal options for wildlife species. We present a model showing the different factors that may shape the landscape of fear in a human-mediated ecosystem where trophy hunting is practiced (Figure 1).

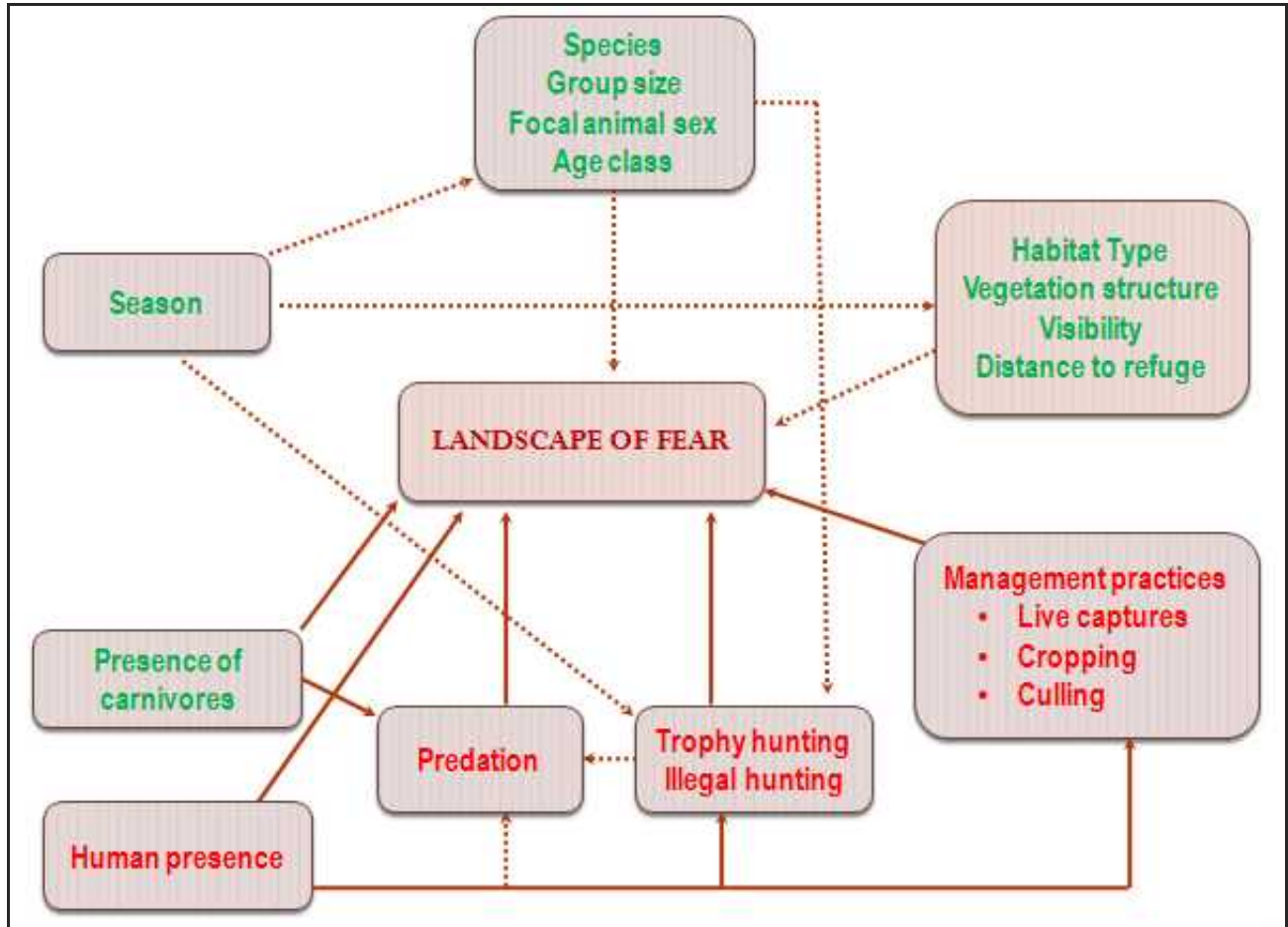


Figure 1. Conceptual model showing factors that may shape the landscape of fear in wildlife occurring in human-mediated ecosystems. Solid arrows show direct relationships whereas dotted arrows indicate indirect relationships.

Physiological stress in hunted populations and ecological traps: Concern has been raised over human activities in conservation areas, that may impact negatively on animals at emotional level as well as the physiological level (Bekoff, 2008). Conservation physiology is an integrative scientific discipline applying physiological concepts, tool and knowledge to characterize biological diversity and its ecological implications, understanding and predicting how organisms, populations and ecosystems respond to environmental change and stressors and solving conservation problems across the range of taxa (Cooke *et al.*, 2013). The incorporation of physiology and ecology enable conservationists to understand the impacts of physiological effects related to anthropogenic

disturbances and environmental perturbations at the individual level (Metcalfé *et al.*, 2012). When the physiological knowledge is incorporated into ecological models, it can improve predictions of organism responses to environmental and human disturbances and provide tools to support management decisions (Cooke *et al.*, 2013; Metcalfé *et al.*, 2012). However, there are limited studies on the impact of tourism activities especially trophy hunting on both anxiety and physiological stress of wildlife subjected to elevated hunting levels (Maréchal *et al.*, 2011).

Although trophy hunting related disturbances may represent a form of selective force in natural populations (Reeder and Kramer, 2005), most wildlife species have evolved a suite of behavioural and

physiological strategies to cope with such disturbances (Baker *et al.*, 2013). Wildlife species are known to cope with disturbances (e.g., presence of humans, noise from rifles) by mounting a stress response through by activating the hypothalamus-pituitary-adrenal axis and releasing glucocorticoid (GC) stress hormones such as cortisol and corticosterone (Romero, 2004; Setchell *et al.*, 2010). Nevertheless, chronic stress and the corresponding elevated GC concentrations due to high hunting pressure may have deleterious effects on fitness and survival of targeted wildlife species (Sheriff *et al.*, 2009). Repeated and frequent exposure to trophy hunting may cause prolonged stress and elevated GC concentrations in affected species. The cascading effects of elevated GC concentrations may lead to inhibition of growth, reproductive and immune system and alteration of animal behaviour (Romero, 2004). Setchell *et al.* (2010) noted that in some wildlife species, high GC concentrations may cause suppressed immunity system leading to elevated gastrointestinal parasitic infections. We argue that the amplitude and duration of stress responses as a result of trophy related disturbances may often correlate with the overall health of targeted species. Therefore, individual physiological responses to mild disturbances can be equally critical to the long-term survival of species (French *et al.*, 2010).

Studies on stress physiology have concentrated on the influence of habitat disturbances (Ahlering *et al.*, 2011; Deng *et al.*, 2014; Tingvold *et al.*, 2013), habitat quality (Creel *et al.*, 2013; Dantzer *et al.*, 2011), tourism (Maréchal *et al.*, 2011), logging and hunting (Rimbach *et al.*, 2013), translocation (Jachowski *et al.*, 2013), climate change (Chown *et al.*, 2010; Fuller *et al.*, 2010) and other environmental stressors (Kight and Swaddle, 2011; Laske *et al.*, 2011) among others. There are few studies done on stress physiology related to trophy hunting except for a few studies that report on poaching, social and ecological pressure on African elephant (Ahlering *et al.*, 2011; Foley *et al.*, 2001; Gobush *et al.*, 2008). There is need for research on the possible physiological effects of trophy hunting on wildlife species and their persistence in natural ecosystems. To inform adaptive management initiatives in wildlife conservation programs, researches that seek to integrate the physiological mechanisms and behaviour responses into ecological models is critical (Metcalf *et al.*, 2012).

Genetic variability and desirable traits: Trophy hunters invariably exhibit some preference towards the choice of animal to harvest at any given time (Myserud *et al.*, 2006). Trophy hunting can be considered as an artificial selection approach where the natural selection, historically imposed by predation would have been modified or magnified in natural ecosystems (Allendorf and Hard, 2009). Nonetheless, predation does select individuals with weaker survival capabilities (except for a

few ambush predators) whereas trophy hunters opt for those individuals in a population with superior and more desirable traits than others. Artificial selection through trophy hunting is therefore likely a pervasive force, whose potential genetic and evolutionary changes has far reaching conservation implications (Festa-Bianchet, 2003; Schneiders *et al.*, 2012).

Genetic variation is considered an important factor in the long-term persistence of a population, especially in the ability of the population to respond to environmental change (Spielman *et al.*, 2004). Allendorf *et al.* (2008) suggests that it is crucial to incorporate genetic considerations in wildlife management plans for harvested populations because hunting has the potential to cause three types of genetic changes, i.e., (1) alteration of population subdivisions, (2) loss of genetic variation and, (3) selective genetic changes. Usually traits associated with fitness are correlated with genetic variation, such as growth and development, fertility, survival, disease resistance and metabolic efficiency (DeYoung and Honeycutt, 2005). These factors have an impact on the sustainability of wildlife conservation programs in human mediated ecosystems. Regrettably, few studies have been conducted in most human-mediated tropical ecosystems which are endowed with much diversity and are preferred hunting destinations of trophy hunters.

Most studies on genetic and evolutionary impacts of selective harvesting have been done in fishes and a few wild ungulates as reviewed by Fenberg and Kaustuv (2008). However, it is important to take some cues from fisheries research and apply some of the molecular techniques in mammalian species exposed to hunting for management purposes (DeYoung and Brennan, 2005). This would be possible because the application of genetic analysis is becoming increasingly feasible and cost effective primarily due to recent advances in the number and types of genetic markers available, development of sophisticated data analysis methods, and increased automation of laboratory instrumentation (DeYoung and Honeycutt, 2005). With such advances in molecular ecology, it is possible to explore the evolutionary and or genetic changes associated with trophy hunting of wildlife species over time for management purposes.

Socio-economic imperatives in wildlife conservation policy measures: The sustainability of trophy hunting as a conservation tool has of recent years challenged the global community from moral, ethical and ecological perspective (Macdonald *et al.*, 2016; Nelson *et al.*, 2016; Ripple *et al.*, 2016). Despite the polarity and lack of consensus among stakeholders, some researchers argues that if trophy hunting is given its rightful place in conservation; it may not compromise the population viability of a targeted wildlife population (Crosmary *et*

al., 2015b; Damm, 2015; Di Minin *et al.*, 2016b; Lindsey *et al.*, 2016). Proposed trophy hunting bans by some countries may result in the loss of wildlife habitats due to the reduction of competitiveness of wildlife based land uses relative to ecologically unfavourable alternatives such as livestock and cropping (Di Minin *et al.*, 2016a; Lindsey *et al.*, 2012; McShane *et al.*, 2011). We argue that the use of mutual gains concept in addressing contested and highly polarised conservation issues like trophy hunting becomes important (Dallimer and Strange, 2015; Fay, 2007). To achieve desired conservation outcomes, there is dire need to combining socio-ecological, and ecological approaches to understanding how people and wildlife are linked and the associated challenges in modern day conservation (Carter *et al.*, 2014).

Trophy hunting is a common practice in several African countries because they are known for: (a) the prevalence of wildlife utilization, (b) a well established hunting industry and (c) an extraordinary alpha and gamma diversity of suitable and target wildlife species for trophy hunters. Countries like Namibia, Zambia and Zimbabwe have used trophy hunting to achieve the objectives of community based natural resources management through the Communal Areas Management Programme for Indigenous Resources (CAMPFIRE), Communal Wildlife Conservancies and Administrative Management Design for Game Areas (ADMADE) (Bond, 2001; Gibson and Marks, 1995; Lewis and Alpert, 1997; Weaver and Skyer, 2003), respectively. For example, in Zimbabwe, CAMPFIRE is known to have generated over US\$20 million of transfers to the participating communities during 1989-2001, of which 89% of which came from trophy hunting (Frost and Bond, 2008). Consequently, trophy hunting has contributed to poverty alleviation, local empowerment and community development though more administrative and legal structures that underlie the country's political ecology need to be strengthened (Logan and Moseley, 2002; Thakadu *et al.*, 2005). On the contrast, in protected areas, i.e., where there is no trophy hunting, incidences of illegal hunting have been persistent at the detriment of the species under conservation such as elephants (Gandiwa *et al.*, 2013; Muboko *et al.*, 2016; Muboko *et al.*, 2014).

A ban in trophy hunting would therefore result in the collapse of a well developed industry and revenue stream (Lindsey *et al.*, 2007a) that would be difficult to replace. A loss of income and revenue from trophy hunting and the promotion of photographic tourism as an option would not be sustainable in most African countries. Most African protected areas are thought to be not functioning efficiently and are underperforming in ecological, economic and social terms because sometimes numbers of photographic tourists are low (Hamilton *et al.*, 2007). Because of poor conservation funding issues,

trade bans or enlisting species as endangered will not stop these species from declining because the greatest threat to species persistence has been poaching, habitat loss and human-wildlife conflicts (Di Minin *et al.*, 2016a; Trethowan *et al.*, 2011) and not sustainable utilization through trophy hunting.

Alternative sources of income through photographic tourism have been applied in other countries such as Botswana (Coria and Calfucura, 2012; Mbaiwa, 2015). However, such alternatives are suitable in countries with political stability whose perceived risk by tourists is low (Lepp *et al.*, 2011; Lindsey *et al.*, 2007b; Sönmez and Graefe, 1998). Accordingly wildlife managers and conservationists should consider among other interventions but not limited to: (1) prioritizing funds for habitat management and protection, water provision, anti-poaching operations, (2) implementing age based regulations in sustainable off-takes programs, wildlife conservation and trophy hunting policy reviews and strengthening implementation initiatives, and (3) improving governance of trophy hunting in order to curb corruption and illegal trade of wildlife species and or products (Lindsey *et al.*, 2012).

However, the sustainability of trophy hunting industry may be hinged upon several other factors such as international legislation and local governance issues (Balme *et al.*, 2010; Peterson, 2014; Shanee, 2012); communication and branding aspects of hunting related issues (Campbell and Mackay, 2009; Damm, 2015); stakeholder and hunter perceptions, hunter attitudes and motivations (Mangun *et al.*, 2007; Miller, 2003); hunting ethics issues (Fox and Bekoff, 2011; Lunney, 2012; Paquet and Darimont, 2010); hunting leases and hunting fees (Mozumder *et al.*, 2007; Rhyne *et al.*, 2009), and marketing of permits and service (Little and Berrens, 2008) among others. Although these issues are being researched nowadays, we argue that they are being done in isolation without integrating and synthesizing them for the purposes of adaptive management.

Integration of factors affecting trophy hunting: We note that trophy hunting may have impacts on the ecology, physiology and genetic aspects of targeted wildlife species though the severity of these depends on the hunting pressure exposed to these species. In addition, in some cases, trophy hunting has been observed to cause a reduction in the trophy size of species over time. Some hunters prefer hunting destinations where there are species with exceptional trophy quality traits and high hunting success. We argue that low trophy quality may reduce the attractiveness of a trophy hunting destination resulting in loss of income and reduced funds for conservation and policy evolution and implementation. Here we present a conceptual framework that integrates the ecological, physiological, genetic and socio-economic

dimensions of trophy hunting as a conservation tool (Figure 2).

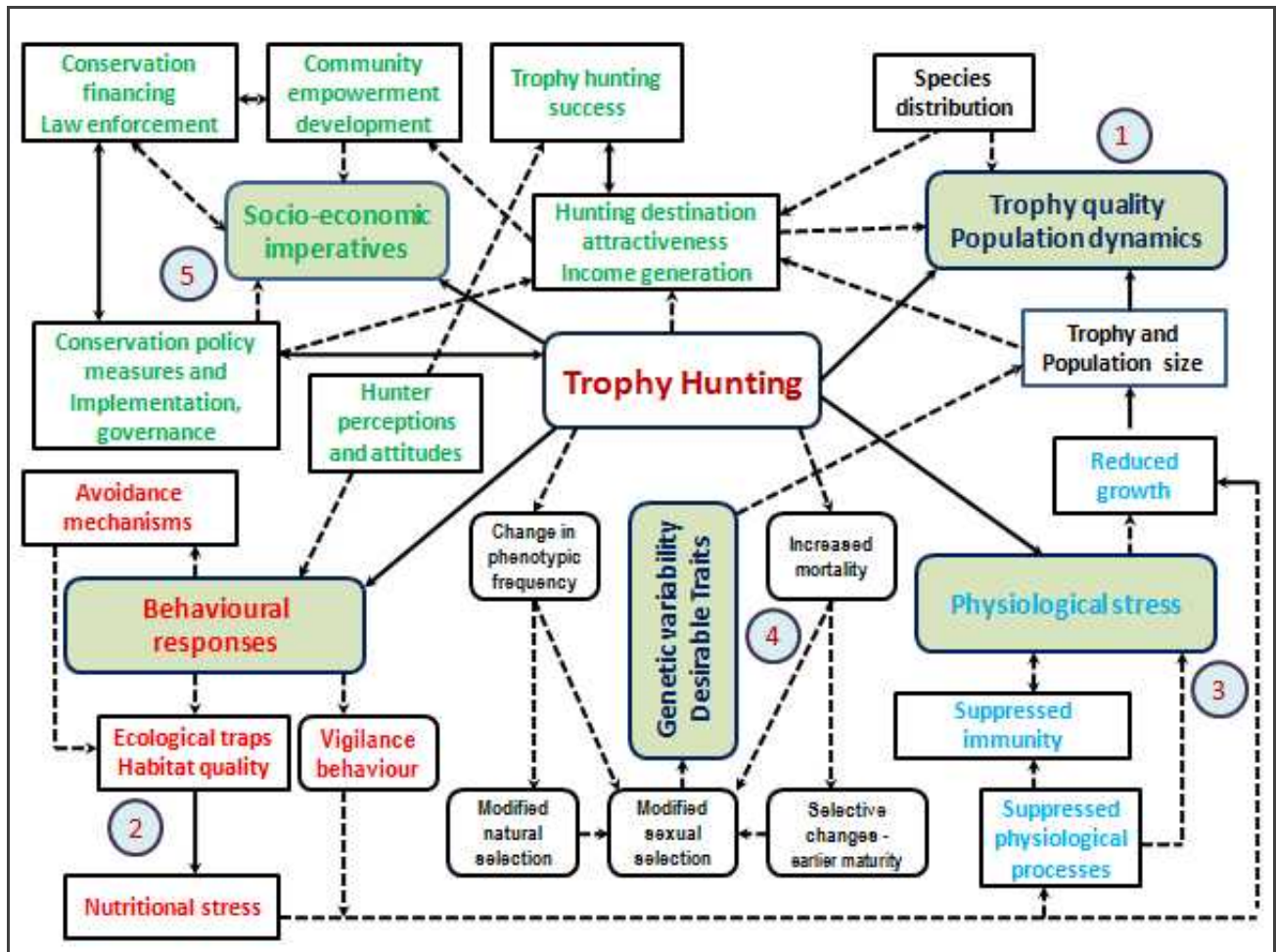


Figure 2: Conceptual framework for the integrated trophy hunting trade-offs: (1) trophy quality and population ecology of hunted species, (2) behavioural ecology of hunted populations and associated avoidance mechanisms, (3) physiological stress in hunted populations (4) genetic variability and desirable traits, and (5) socio-economic imperatives in wildlife conservation policy measures. Notes: Solid arrows indicate direct relationships; dotted arrows indicated indirect relationships between factors.

We believe that the nature and level of trophy hunting may directly or indirectly influence the behaviour of targeted species thereby shaping the landscape of fear for these species. Depending with the magnitude of behavioural plasticity and shifts in the habitat use as an avoidance mechanism, trophy hunting may cause ecological traps where individuals may utilize poor habitats which may result in nutritional stress. The direct effect of nutritional stress and the physiological stress emanating from the hunting pressure may reduce fitness of individuals hence may be more susceptible to parasitic infections. The cascading effects of all these may result in population decline of the affected species.

On the other hand, the selective nature of trophy hunting may result in the loss of genetic variability and low population growth of affected populations if there is

minimum management intervention. Trophy hunting may result in a decline in the trophy size and possible increase in hunting effort which may reduce the attractiveness of a hunting destination (Muposhi *et al* 2016b). These factors combined with trophy hunting restrictions may result in loss of income which may translate to poor conservation financing and a resultant loss of species due to habitat loss and illegal hunting. Accordingly, a concerted effort towards the integration of these impacts in wildlife research and management interventions is essential in the conservation of wildlife species and their habitats.

Conclusion: There is mounting evidence of a downward trend in trophy quality of commonly hunted wildlife species associated with a decline in population sizes in most southern African countries. Aspects on behavioural

change and the creation of ecological traps as a result of trophy hunting are however still less studied or documented. There is an increasing awareness on the need to incorporate stress physiology research aspects on trophy hunting activities albeit very little research on effect of trophy hunting on targeted species. Wildlife species develop behavioural mechanisms to evade trophy hunting disturbances and as such may reduce their reproductive success, suppress immunity and low population growth. Moreover, trophy hunting may induce nutritional stress and low fitness levels which may reduce resilience to parasitic infections and diseases over time if not managed properly. There is lack of integration of the five themes on trophy hunting as a conservation tool examined in this paper for broader analytical analysis and comparison purposes. It is recommended that conservationists should (1) consider the impacts of trophy hunting in entirety and endeavour to reduce their impact on wildlife species; (2) promote the enactment of progressive policies and action plans that promote innovation in the management of wildlife species e.g. establishing realistic and ecologically sound harvesting models and active monitoring of trophy hunts for sustainability.

Acknowledgments: We are grateful to Chinhoyi University of Technology for supporting this research. Comments from two anonymous reviewers are greatly acknowledged.

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