Key factors and related principles in conservation of large African carnivores

H. E. K. WINTERBACH*

Centre for Wildlife Management, University of Pretoria, Private Bag X20 Hatfield, Pretoria 0028, South Africa. E-mail: tauconsultants@gmail.com

C. W. WINTERBACH

Centre for Wildlife Management, University of Pretoria, Private Bag X20 Hatfield, Pretoria 0028, South Africa. E-mail: tauconsultants@gmail.com

M. J. SOMERS

Centre for Wildlife Management, University of Pretoria, Private Bag X20 Hatfield, Pretoria 0028, South Africa. E-mail: mjs@up.ac.za

M. W. HAYWARD

Australian Wildlife Conservancy, P.O. Box 432, Nichol's Point, Victoria 3501, Austra-lia. E-mail: matt@australianwildlife.org

* Correspondence author.

ABSTRACT

1. Large carnivores are a critical component of Africa's biodiversity and their conservation requires a clear understanding of interactions between large carnivores and people.

2. Reviewing existing literature, we identified 14 key factors that influence large African carnivore conservation, which include ecological (interspecific competition,

ranging behaviour, ecological resilience, prey availability, livestock predation, disease, and population viability), socio-economic (people's attitudes and behaviours, and human costs and benefits of coexistence with large carnivores), and political (conservation policy development and implementation, conservation strategies, and land use zoning).

3. We presented these key factors in a model illustrating the levels of impact on large African carnivore conservation.

4. We identified the key principle that underpins each factor and its implications for both large carnivore conservation and human-carnivore conflict.

5. This literature review provides a synthesis of the key factors and related principles in large African carnivore conservation, and highlights the importance of site- and species-specific context in conservation policy and implementation formulated through an inter-disciplinary and adaptive approach.

KEYWORDS: hyaena, cheetah, leopard, lion, African wild dog, human-carnivore conflict

INTRODUCTION

Despite conservation efforts, large carnivore numbers continue to decline globally (Anonymous 2010a). Significant failures have occurred, notably the extinction of three tiger (*Panthera tigris*) subspecies within the past 50 years (Weber & Rabinowitz 1996). The large African carnivore guild is made up of seven species (Dalerum et al. 2008) with declining populations with the following statuses: African wild dogs (*Lycaon pictus*) are Endangered; cheetahs (*Acinonyx jubatus*) and lions (*P. leo*) are

Vulnerable; leopards (*P. pardus*) and striped hyaenas (*H. hyaena*) are Near Threatened; brown hyaenas (*Hyaena brunnea*) are Lower Risk, Near Threatened, and spotted hyaenas (*Crocuta crocuta*) are Least Concern (Anonymous 2010a). Being endemic to Africa, however, the spotted hyaena is given the third highest conservation priority in Africa, following that of the endangered Ethiopian wolf (*Canis simensis*) and African wild dog (Mills et al. 2001). We excluded the striped hyaena from this review since it is considered the northern equivalent of the brown hyaena (Estes 1995).

The difficulty with conservation of large carnivores is that they inflict considerable socio-economic costs on people (Treves & Karanth 2003, Thirgood et al. 2005) and human-carnivore conflict is the main cause of large carnivore population declines (Woodroffe et al. 2005b).

Nonetheless, a growing number of cases show that large carnivore conservation can be successful if the approach is coordinated on international, regional, national, and local levels, and effectively addresses both ecological and human aspects involved (Weber & Rabinowitz 1996, Marker 2008, Gusset et al. 2008b, Balme et al. 2009).

The aim of this paper is to review the literature on conservation of large African carnivores and identify and synthesize the key factors, associated principles, and implications for conservation and human-carnivore conflict. This synthesis is essential to guide objectives and policies for successful long-term conservation of large African carnivores, and crucial for biologists, sociologists, bureaucrats and politicians that are responsible for balancing the needs of people with the conservation of large carnivores.

1. KEY ECOLOGICAL FACTORS AND PRINCIPLES

1.1 Biodiversity Conservation

Key Principle: Africa's large carnivore guild *per se* is a critical component of biodiversity (Mills 2005, Woodroffe & Ginsberg 2005) because each species has a different prey spectrum (Hayward & Kerley 2008) whose diverse impacts increase resilience of ecosystems (Miller et al. 2001, Worm & Duffy 2003).

Conservation Implication: Conservation of intact guilds is a higher priority than conservation of single large carnivore species (Woodroffe & Ginsberg 2005).

Human-carnivore Conflict Implications: 1) A wider range of conflict mitigation strategies are required to conserve a large carnivore guild than are required to conserve any single species. 2) The loss of large carnivores in an ecosystem can result in mesopredator release of smaller carnivore species which may introduce, exacerbate, or alter the scope of local human-carnivore conflict (Treves & Naughton-Treves 2005, Gusset et al. 2009).

Discussion: Quantitative data supporting large African carnivores as keystone species are lacking (Dalerum et al. 2008), but many agree that predation shapes large-mammal food webs and the diverse, highly flexible interactions between predator and prey are vital components of biodiversity (Mills 2005, Dalerum et al. 2008, Owen-Smith & Mills 2008). Species in the large African guild have different preferred prey or prey weight ranges (Hayward & Kerley 2008). In addition, herbivores can distinguish among potential predators and use spatial avoidance of risky habitats as an antipredator strategy (Thaker et al. 2011). Thus, one carnivore species cannot act as a substitute for another in the diverse trophic processes in African ecosystems (Woodroffe & Ginsberg 2005).

A loss of large carnivores in an ecosystem can allow smaller predators to undergo an ecological release (Palomares & Caro 1999, Crooks 2002). On South African farmlands, after the extirpation of large carnivores, populations of black-backed jackal (*Canis mesomelas*) and caracal (*Caracal caracal*) increased such that they became major threats to livestock (Beinart 1998, Stadler 2006). In areas not suitable for conservation of intact large carnivore guilds, the consequences of conserving an incomplete guild, such as potential mesopredator release, should therefore be addressed in the conservation strategies of these areas.

Conserving an intact guild complicates human-carnivore conflict since the behaviour of carnivore species differ and conflict mitigation will necessitate a species specific approach.

1.2 Interspecific Competition among Large Carnivores

Key Principle: Interspecific competition can exert a strong influence on large carnivore distribution and density (Creel et al. 2001, Johnson & VanDerWal 2009) and can increase the local extinction risk of subordinate competitors (Hayward & Kerley 2008).

Conservation Implications: 1) Densities of subordinate competitors tend to be low in areas with high densities of dominant competitors, thus habitat- and species-level approaches are needed to conserve intact guilds of large African carnivores (Creel et al. 2001). 2) Species-specific conservation efforts beyond protected areas (national parks and game reserves) become important if high levels of interspecific competition inside protected areas hamper conservation of subordinate competitor populations (Marker & Dickman 2004, Hayward & Kerley 2008).

Human-carnivore Conflict Implication: Unprotected areas with low densities of dominant competitors can provide refuge areas to subordinate competitors if conflict with people can be reduced.

Discussion: In Africa, lions and spotted hyaenas are dominant competitors that restrict the distribution and density of cheetahs, African wild dogs, and brown hyaenas (Mills 1982, Laurenson et al. 1995, Creel & Creel 1996, Durant 2000b). Interspecific competition also occurs between lions and spotted hyaenas but the intensity depends on prey availability (Hayward 2006, Watts & Holekamp 2009). Leopards are generally least affected by interspecific competition because their behavioural and dietary flexibility enables them to co-exist with other large predators (Karanth & Sunquist 2000, Marker & Dickman 2005).

Cheetahs, African wild dogs, and brown hyaenas avoid their dominant competitors by ranging widely and using areas where few lions and spotted hyaenas occur (Mills & Gorman 1997, Durant 2000a, Creel et al. 2001). Thus, in areas where the aim is to conserve these three species as part of the carnivore guild, it is important to have a mosaic of high and low densities of dominant competitors. A mosaic can be achieved by either maintaining the *status quo* in areas with naturally low numbers of lions or spotted hyaenas or by actively managing for lower numbers of dominant competitors (Van Dyk & Slotow 2003, Lindsey et al. 2004b) by manipulating prey availability (Hayward et al. 2007a) or by a managed reduction of dominant competitors. Interspecific competition is the main reason why cheetahs cannot be conserved in many protected areas across their range in Africa, since these areas tend to have high ungulate densities that support high densities of lions and spotted hyaenas (Durant 1998, Marker & Dickman 2004). Farmlands, however, where densities of dominant

competitors tend to be low and small to medium-sized wild game still occur in sufficient numbers, can form critical conservation habitats for cheetahs (Marker & Dickman 2004) and African wild dogs (Woodroffe et al. 2007b). Mitigation of human-carnivore conflict will be critical to conservation efforts in these areas.

1.3 Carnivore Range

Key Principle: The wide-ranging behaviour of large carnivores increases their potential contact with people and thus their exposure to conflict.

Conservation Implications: 1) The furthest ranging carnivores determine the minimum size of conservation areas (protected areas and any other government, communal or private land where wildlife is the main form of land use and is partially protected) needed to protect the guild and a few large conservation areas are better than many small ones (Woodroffe 2001). 2) Where protected areas are too small to contain the movements of the large carnivores they aim to protect, the effective conservation area needs to be increased, or conservation fences can be constructed to reduce the ranging behaviour of large carnivores.

Human-carnivore Conflict Implications: 1) Species-specific conflict mitigation strategies are required for large carnivores that range beyond protected areas in the absence of conservation fences. 2) Non-lethal conflict mitigation is a priority where human-caused mortalities negatively impact on the viability of large carnivore populations, and the importance of non-lethal conflict mitigation increases with proximity to protected areas.

Discussion: Resource distribution, and in particular prey availability, is the primary factor that determines the ranging behaviour of large carnivores (Gittleman & Harvey

1982, Van Orsdol et al. 1985, Grant et al. 2005, Hayward et al. 2009), followed by interspecific competition that strongly contributes to the ranging behaviour of subordinate competitors (Creel 2001, Durant 1998). Home range size and ranging behaviour thus differ both among carnivores and among habitats (Hemson 2003, Hayward et al. 2009, Valeix et al. 2010). Among carnivores, for example, lion home ranges cover 144±5km², spotted hyaenas 91±10km², and a solitary leopard 38km² in the Addo Elephant National Park, South Africa (Hayward et al. 2009). Among habitats, spotted hyaena ranges vary from 13km² where there is sufficient sedentary prey to over 1000km² in areas with low prey density (Trinkel et al. 2006). They also undertake long extra-territorial trips to reach migratory prey (Höner et al. 2005).

The smaller a protected area is in relation to the home ranges, the greater the proportion of the population that will range beyond the boundary and come into contact with people. Resultant conflict can lead to high mortality of carnivores that create population sinks around the boundary (Davidson et al. 2011). This edge effect is a major threat to carnivore populations inside protected areas worldwide (Woodroffe 2001). An edge effect can also be created by unsustainable off-take close to protected areas (Loveridge et al. 2007). Where the extent and impact of edge effects threaten the conservation of protected populations, creating conservation buffer zones with non-lethal conflict strategies and managing human activities around protected area boundaries are essential (Balme et al. 2010).

An alternative strategy to reducing conflict around protected areas is the incorporation of conservation fences. Fencing for conservation is designed to separate biodiversity from the factors threatening it and are some substantial risks (notably genetic isolation and spatial limitation) (Hayward and Kerley 2009, de Tores and Marlow 2012,

Hayward and Somers 2012), however metapopulation management has been largely successful in ameliorating these risks in South Africa (Davies-Mostert et al. 2009, Gusset et al. 2009, Marnewick et al. 2009, Lindsey et al. 2011), where conservation fencing is required wherever large, dangerous wildlife occur (Hayward 2012, Slotow 2012). Even the risk of inbreeding in isolated protected areas has been solved via metapopulation management (Kettles and Slotow 2009, Trinkel et al. 2010).

1.4 Ecological Resilience

Key Principle: Large carnivores have different levels of ecological resilience to human-caused habitat fragmentation (Purvis et al. 2001, Woodroffe 2001, Crooks 2002).

Conservation Implications: 1) The site-specific ecological resilience of each large carnivore populations needs to be determined. 2) Large carnivores with low ecological resilience have a high risk of local extinction, and their conservation requires larger contiguous habitats with lower negative human impacts than do more resilient species.

Human-carnivore Conflict Implication: Effective legal protection and the reduction of human-caused mortality is a priority for large carnivore populations with low ecological resilience.

Discussion: Ecological resilience is influenced by biological traits such as body size, resource specialization, social structure, fecundity, and behaviour (Purvis et al. 2001, Crooks 2002). The strongest effect, though, is the impact of human persecution on carnivore populations (Linnell et al. 2001, Woodroffe 2001, Gusset et al. 2008a).

The two species of large African carnivores that appear to have the lowest resilience to human-caused habitat fragmentation are African wild dogs and lions. Wild dogs have a highly specialized social structure with cooperative breeding (Creel et al. 2007). They also are highly visible as diurnal pack hunters that, in most populations, specialize on medium-sized prey (Hayward & Kerley 2008). Interspecific competition, especially inside protected areas, combined with human conflicts lead to precipitous declines of their populations and keep African wild dogs across their range at very low densities in shrinking, isolated groups that are highly prone to local extinctions (Creel et al. 2007). Wild dogs are habitat generalists that can move over vast distances between resources, tend to avoid human habitations, and can subsist on small prey (Woodroffe et al. 2007b). Therefore, farmlands have a high potential as conservation areas for them and may provide vital corridors (Woodroffe 2010). Conversely, lions are hunter-scavengers, have a high population growth rate comparative to other large carnivores, and can persist in relatively small areas (Druce et al. 2004, Kettles & Slotow 2009). Yet, they are the least successful large carnivore outside conservation areas (Woodroffe 2001) and their densities decrease with distance from conservation areas (Ogutu et al. 2005, Schiess-Meier et al. 2007). This is mainly because lions are the carnivore that kills most people in Africa (Sillero-Zubiri & Laurenson 2001) and in many areas they are the principal predator of large livestock (Anonymous 2006), resulting in nearly ubiquitous lethal human-lion conflict (Frank et al. 2006). Even in Masailand in East Africa, which is home to the largest contiguous lion population in Africa, lions outside protected areas are in imminent danger of being extirpated by pastoralists (Anonymous 2006, Frank et al. 2006).

Consequently, survival of lion populations is increasingly dependent on conservation areas (Woodroffe 2001).

Cheetahs share the same threats with African wild dogs in terms of low densities, interspecific competition, and conflict with people (Anonymous 2007). Their ecological resilience, however, is increased by traits such as their mostly solitary behaviour, high mobility, habitat flexibility (Bissett & Bernard 2007), having a diverse prey base (Hayward et al. 2006b), and ability to reproduce rapidly from an early age (Kelly et al. 1998). In Namibia and Botswana where the largest continuous cheetah population in Africa occurs, more cheetahs persist on farmlands than inside protected areas (Klein 2007, Marker et al. 2007). Nevertheless, conflict with farmers remains the biggest threat to cheetahs across their range (Purchase et al. 2007) and training farmers in integrated livestock-wildlife management practices combined with non-lethal conflict mitigation are crucial to cheetah conservation (Marker et al. 2008).

Leopards and spotted hyaenas have a high ecological resilience and occur widely in human-altered landscapes: they are predominantly nocturnal with broad diet ranges and exhibit great behavioural flexibility that enables them to hunt or scavenge individually and to alter their behavioural response to human activity (Boydston et al. 2003, Hayward 2006, Hayward et al. 2006a, Kolowski et al. 2007).

Brown hyaenas generally seem to benefit, at least to some extent, from living in proximity to people and continue to occur in stable viable populations throughout southern Africa (Maude & Mills 2005). They are predominantly scavengers with a wide-ranging diet (Mills & Hofer 1998), and livestock carcasses can form a reliable and abundant food source in agricultural areas (Maude & Mills 2005). Since brown hyaenas are almost entirely nocturnal, very secretive, rarely vocalize and are usually

difficult to find, persecution by people has little effect on their overall population size (Mills 1990). Farmer education on foraging behaviour of brown hyaenas is important for changing perceptions regarding the threat that brown hyaenas pose to livestock to minimise conflict.

1.5 Prey Availability

Key Principle: Prey availability governs the movements, abundance, and population viability of large carnivores (Karanth & Stith 1999, Fuller & Sievert 2001, Hayward et al. 2007b).

Conservation Implications: 1) The availability of appropriate-sized prey plays a major role in determining the suitability of an area for the conservation of large carnivores (Fuller & Sievert 2001, Lindsey et al. 2004b, Hayward & Kerley 2008). 2) Prey availability can be used to predict carrying capacities for large carnivores in restricted areas where management is necessary to prevent overpopulation of carnivores and unsustainable impacts on prey (Hayward et al. 2007b).

Human-carnivore Conflict Implication: Changes in wild prey availability can be used to predict trends in livestock depredation, enabling managers to implement timely conflict mitigation measures.

Discussion: Strong linear relationships exist between the density of African large carnivores and the biomass of their natural prey (Hayward et al. 2007b). Whereas high levels of human-related mortality and interspecific competition can exert a strong influence on carnivore densities and distribution (Hayward & Kerley 2008, Burton et al. 2010), prey availability is probably the primary natural determinant (Fuller & Sievert 2001). Prey availability affects large carnivore reproduction and recruitment

(Fuller & Sievert 2001), foraging behaviour (Hanby et al. 1995, Höner et al. 2005, Balme et al. 2007) and movements (Hayward et al. 2009).

Coexistence among large African carnivores despite a high level of dietary overlap is facilitated by spatial partitioning (Mills & Gorman 1997, Bissett & Bernard 2007), temporal partitioning in hunting activity (Hayward & Slotow 2009), and selection for different age classes of the same prey species (Mills 1990).

Seasonal changes in wild prey abundance often influence human-carnivore conflict (Fuller & Sievert 2001, Frank et al. 2005). Lions in Botswana's Makgadikgadi move closer to human habitation and livestock grazing areas when their migratory wild prey is scarce (Hemson 2003). It is essential to understand the effect of changes in prey availability on the foraging behaviour of large carnivores to plan and prioritize conflict mitigation when and where conflict is likely to increase, thus allowing for more efficient allocation of limited resources.

1.6 Livestock Predation

Key Principle: Livestock predation by large carnivores is the most widespread cause of conflict and retaliatory killing by people is one of the most serious threats to carnivore survival (Thirgood et al. 2005, Woodroffe et al. 2005b).

Conservation Implication: Minimizing livestock predation by large carnivores is a key conservation priority.

Human-carnivore Conflict Implication: Understanding livestock predation by large carnivores is vital to implement socially just, practical, and cost-effective conflict mitigation (Karlsson & Johansson 2010).

Discussion: The frequency of predation on livestock by large carnivores depends on a range of biological and human factors (Stahl et al. 2001, Woodroffe & Frank 2005, Kolowski & Holekamp 2006), as these examples illustrate. Density and distribution of carnivore species: lions are often the main culprits in livestock depredation (Ogada et al. 2003, Patterson et al. 2004, Lagendijk & Gusset 2008) though the frequency of attacks may decrease with distance from protected areas (Schiess-Meier et al. 2007, Van Bommel et al. 2007). Leopard attacks, in Botswana's Khutse District at least, are independent of distance from the nearest protected area (Schiess-Meier et al. 2007) indicating that leopards there are resident and lions transient. Spotted hyaenas at high densities can cause more stock losses than lions and leopards combined (Kolowski & Holekamp 2006). Livestock prey preferences: lions can kill any livestock and are the only carnivore that regularly kill adult cattle, horses and donkeys (Butler 2000, Ogada et al. 2003, Schiess-Meier et al. 2007). Leopards, spotted hyaenas, cheetahs and African wild dogs tend to kill goats and sheep (Marker 1999, Mizutani 1999, Woodroffe et al. 2005a, Kolowski & Holekamp 2006), and occasionally take calves and foals (Hofer 1998, Rasmussen 1999, Butler 2000, Ogada et al. 2003, Schiess-Meier et al. 2007). African wild dogs, however, may kill adult cattle (J. Horgan *pers. comm.*) although it is an uncommon occurrence. Timing and location of livestock predation: lions, leopards and spotted hyaenas tend to attack livestock in enclosures at night (Ogada et al. 2003, Patterson et al. 2004, Holmern et al. 2007), whereas cheetahs and African wild dogs mainly predate on stock grazing during the day (Ogada et al. 2003, Woodroffe et al. 2005a) reflecting their activity patterns (Hayward & Slotow 2009). An occasional brown hyaena has been observed digging underneath traditional kraals and killing goats (D.R. Mills pers. obs). Behaviour of individuals: in

Africa, habitual killers of livestock have been identified in lions (Stander 1990, Funston 2001, Bauer & De Iongh 2005, Woodroffe & Frank 2005), leopards (Mizutani 1993) and cheetahs (Marker et al. 2003a). Translocating habitual stock-raiding lions back into protected areas has failed to keep them from returning to kill livestock, and lethal removal of the individuals is recommended to avoid the spread of such behaviours (Funston 2001, Frank et al. 2006). Seasonal variation: livestock predation is linked to variations in wild prey availability and can peak anytime through the year (Butler 2000, Hemson 2003, Patterson et al. 2004, Schiess-Meier et al. 2007), depending on the distribution and movement of prey (Van Bommel et al. 2007). Habitat differences: livestock attacks by leopards and lions are more likely in dense bush that provides better cover for ambush than in open habitats (Woodroffe et al. 2007a). Wild prey availability: large carnivores will take wild prey in preference to livestock and will subsist mainly on wild prey even when livestock is more abundant (Mizutani 1999, Hemson 2003, Marker et al. 2003c, Frank et al. 2006, Ogara et al. 2010). In an area of 5700km² of communal and private land in Kenya's Laikipia District, livestock predation by African wild dogs costs residents around US$3.40/wild dog/year where wild prey occur, but where wild prey is seriously depleted the costs rise to US$389/wild dog/per year (Woodroffe et al. 2005a). Maintaining wild prey populations outside protected areas as part of integrated livestock-wildlife management practices can divert carnivore pressure away from domestic livestock (Mizutani 1999, De Azevedo & Murray 2007) and may provide an incentive for communities to protect their local wildlife (Cozza et al. 1996). Husbandry practices: herding, enclosure design and deterrents can reduce depredation levels, but the most effective practices vary between carnivores and areas (Woodroffe

& Frank 2005, Frank et al. 2006, Woodroffe et al. 2007a, Balme et al. 2009). For example, domestic dogs (*Canis familiaris*) are effective in deterring cheetahs and African wild dogs (Marker et al. 2005) and domestic dogs with a gathering of people often discourage lions from attacking livestock in enclosures (Ogada et al. 2003). However, dogs are generally ineffective in deterring leopards and spotted hyaenas (Kolowski & Holekamp 2006). Bush-fenced enclosures are more effective in excluding leopards than poled-fenced enclosures that provide good footholds for climbing, but pole fences are effective against spotted hyaenas (Kolowski & Holekamp 2006). Confining livestock in enclosures may cause surplus killing because livestock cannot escape and their panicked movements repeatedly stimulate a carnivore's killing instinct (Nowell & Jackson 1996, Ogada et al. 2003, Patterson et al. 2004). In Botswana, two lions killed 43 goats, and a leopard killed 36 goats in one night (Hemson 2003, D.P. Mills pers. obs), and in South Africa, one leopard killed 51 sheep and lambs in one incident (Stuart 1986).

All the above examples demonstrate the importance of understanding, on a local level, the factors that influence livestock predation. Realistic site- and species-specific strategies are needed to reduce the vulnerability of livestock to large carnivore predation, and livestock losses can be reduced by conflict mitigation and better husbandry practices (Ogada et al. 2003, Woodroffe et al. 2007a, Balme et al. 2009, Stein et al. 2010). However, conflict will always occur where people, livestock and carnivores co-exist and conflict mitigation will remain an ongoing process. It is also important to put conflict in perspective; farmers may perceive large carnivore depredation to be the main problem even though the major source of livestock losses

is due to poor management and disease (Mizutani 1999, Rasmussen 1999, Dar et al. 2009).

Another source of human-carnivore conflict is large carnivore predation of commercially farmed game (Sillero-Zubiri & Laurenson 2001, Marker et al. 2003b, Selebatso et al. 2008). It is difficult to mitigate this type of conflict since free-ranging farmed game cannot easily be protected against carnivores. The establishment of conservancies where such economic losses are shared among several farms or allowing consumptive use of carnivores on game farms are two solutions to provide incentives for farmers to tolerate some large carnivores on their game farms (Linnell et al. 2005, Marker 2008).

1.7 Wildlife Disease

Key Principle: Disease outbreaks can devastate small, localized large carnivore populations (Macdonald 1993, Funk et al. 2001, Cleaveland et al. 2002, Dybas 2009).

Conservation Implications: 1) Disease management is especially important in small populations of large carnivores (Woodroffe et al. 2004). 2) Translocation of large carnivores may pose a serious risk of disease transmission into naïve populations (Hofmeyr et al. 2000).

Human-carnivore Conflict Implication: Large carnivore populations can act as sources of disease that threaten human health and livestock and therefore exacerbate conflict with people (Macdonald 1993, Funk et al. 2001, Butler et al. 2004, Hugh-Jones & Blackburn 2009).

Discussion: Pathogens can be viewed as keystone species (Power et al. 1996) that impact directly and indirectly on other organisms (Peterson 1999, Mouritsen & Poulin

2002). Carnivore population declines from disease normally result from a "spill over" of generalist pathogens from common species (Cleaveland et al. 2002).

The greatest disease concerns in large African carnivore populations are canine distemper and rabies (Butler et al. 2004, Laurenson et al. 2004, Dybas 2009). Alone, canine distemper is not a serious threat to large populations of lions, for example, but in the Serengeti in 1994, simultaneous outbreaks of canine distemper and babesiosis - a tick-borne blood parasite called *Babesia* that infects Cape buffalo (*Syncerus caffer*) - killed more than 1000 lions (Dybas 2009).

Generally, the primary reservoir that maintains rabies cycles are domestic dogs and most likely were the sources of rabies that decimated populations of both African wild dogs and Ethiopian wolves (Gascoyne et al. 1993, Sillero-Zubiri et al. 1996, Cleaveland et al. 2002, Butler et al. 2004, Dybas 2009). In central Namibia, the primary reservoir of rabies is black-backed jackals (Courtin et al. 2000). Striped jackals (*Canis adustus*) can also be common vector (Butler et al. 2004).

Rabies is a serious problem in Africa where around 25000 people die from the disease each year (Dybas 2009). Habitat loss and fragmentation increase contact between large carnivores, people and domestic dogs and result in higher risk for disease transmission (Scott 1988, Saunders et al. 1991, Forman 1995). Large African carnivores contribute sporadically to the circulation of rabies as non-maintenance populations (Lembo et al. 2008) and rabid carnivores can fatally attack people and livestock (Shah & Jaswal 1976).

Epidemiological data is lacking to develop appropriate disease management strategies in carnivore populations (Funk et al. 2001, Cleaveland et al. 2002, Laurenson et al. 2004). Current options for controlling disease are: 1) do nothing, 2) reduce disease in

reservoir species through vaccination, culling and sterilization, 3) reduce the disease in host species through vaccination and treatment, and 4) prevent contact between target species and reservoir species through barriers or restraining the movements of the domestic reservoir (Laurenson et al. 1997, Hudson et al. 2002, Woodroffe et al. 2004, Rhyan & Spraker 2010). Scientific research should be combined with monitoring to evaluate disease management options, identify limitations, and develop effective adaptive strategies (Funk et al. 2001).

1.8 Carnivore Population Viability

Key Principle: The effective size of a carnivore population has a strong influence on its long-term viability.

Conservation Implications: 1) Maintaining large carnivore populations at sizes large enough to ensure viability in the long term improves their resilience to environmental variations and stochastic events. 2) Monitoring the factors that impact on population size is essential (Beissinger & Westphal 1998, Balme et al. 2009, Caro et al. 2009, Kettles & Slotow 2009).

Human-carnivore Conflict Implication: High levels of human-caused mortality may disrupt the social systems of large carnivores to the extent that it impacts negatively on population size (Packer & Pusey 1984, Whitman et al. 2004, Balme et al. 2009).

Discussion: Habitat loss and human-caused mortality are two key factors that affect viability of large carnivore populations. Habitat loss results in small, fragmented carnivore populations, which increases their vulnerability to local extinctions due to events such as overexploitation, environmental and demographic stochasticity, and

catastrophes (Woodroffe 2001). It also increases risk of disease through increased potential contact between carnivores and domestic animals (Funk et al. 2001, Cleaveland et al. 2002, Woodroffe et al. 2004) and may lead to a decrease in genetic heterogeneity, which is a major threat to long-term viability for most mammalian taxa occurring at small to moderate population sizes (i.e. less than a few thousand individuals; O'Brien et al. 1985, Packer et al. 1991, Roelke et al. 1993, O'Grady et al. 2006, Traill et al. 2010). Population links via transfrontier parks, conservancies, and corridors that allow the free movement of migrants and increase effective population sizes are vital to prevent inbreeding depression (Schwartz & Mills 2005). Small, geographically isolated sub-populations can be managed as one large meta-population by artificially maintaining population links (Lindsey et al. 2004a).

Population viability may also be jeopardized when high levels of human-caused mortality in large carnivore populations with specialized breeding systems leads to social disruptions such as increased intraspecific fighting, infanticide, and lower fecundity (Courchamp & Macdonald 2001, Whitman et al. 2007, Balme et al. 2009). It is, therefore, important to understand the interaction between human-caused mortality and behavioural ecology of large carnivores (Balme et al. 2009, Caro et al. 2009).

Methods are needed to reliably estimate population demographics, and data should be collected to understand the site-specific ecology and population dynamics of large carnivores. Long term monitoring is necessary to assess risks to large carnivore populations, determine potential management options, and to evaluate the impact of conservation actions to facilitate informed decisions using adaptive management (Johnson et al. 2001, Sutherland et al. 2004).

2. KEY SOCIO-ECONOMIC FACTORS AND PRINCIPLES

2.1 People's Attitudes and Behaviour toward Large Carnivores

Key Principle: Positive attitudes of people toward conservation are important but attitude does not necessarily translate into tolerance for large carnivores, and it is the behaviour of people that ultimately determines the local extinction risks of large carnivores (Woodroffe 2000, Linnell et al. 2001, Loveridge 2005).

Conservation Implication: Conservation of large carnivores depends on the long-term change of people's behaviour from antagonistic to supportive (Marker & Dickman 2004).

Human-carnivore Conflict Implication: A clear understanding of the reasons for people's unwillingness to support conservation efforts (Waylen et al. 2010) and their intolerance towards large carnivores are central to developing conflict mitigation strategies that facilitate positive change in human behaviour (Mattson et al. 2006).

Discussion: People's attitudes toward wildlife are generally determined by basic wildlife values (e.g. aesthetic, cultural, symbolic, utilitarian); perception of species; and education, knowledge, and understanding of wildlife conservation issues (Kellert et al. 1996, Hutton & Leader-Williams 2003, Marshall et al. 2007, Bath et al. 2008). Rural people typically view wildlife in terms of its resource value (e.g. meat or economic value) (Lamarque et al. 2009). When wildlife has no tangible value, negative attitudes become strongly associated with real or perceived losses, such as loss of agricultural land, prevention of natural resource use, and damage to livelihoods (Mbaiwa et al. 2008, Lamarque et al. 2009).

People's behaviour, on the other hand, is largely determined by a combination of personal situational factors (e.g. self-sufficiency, resources, skills, wealth),

psychological factors (e.g. motivation, character), and value-based factors (moral and social norms) (Barr 2003). A combination of attitudinal and behavioural factors will determine if and how people choose to conserve, exploit, or eradicate natural resources (Caro 1999, Anonymous 2000, Lagendijk & Gusset 2008).

People who rely on livestock for their livelihood are the least inclined to tolerate large carnivores (Mishra 1997, Patterson et al. 2004, Frank et al. 2005). Livestock is a source of food, clothing and income. It also constitutes people's savings and social standing in a community, and the emotional value of livestock is commonly more important than its monetary value (Loveridge 2005). People continue to kill predators even without suffering direct losses (Marker at al. 2003c), based on their perceptions and knowledge of large carnivores as a potential threat to safety and livelihoods.

Rural people often fail to support wildlife conservation because: a) protected areas have little direct value to any but a privileged few (Hutton & Leader-Williams 2003, Baldus 2006), b) wildlife and conservation may be a symbol of government control (Wilshusen et al. 2002), c) wildlife that are perceived as threats are protected outside protected areas (Stander 1991), and d) human-carnivore conflict strategies are unacceptable to the people who are affected (Cozza et al. 1996). People's behaviour is also strongly affected by the way wildlife authorities deal with carnivore control (Loveridge 2005, Lagendijk & Gusset 2008, Balme et al. 2009).

Human behaviour can change and the challenge is to understand the psychological and sociological factors behind current behaviour and what is needed to effect change (Clayton & Myers 2009). Conservation education programmes are an integral part of large carnivore conservation, but active programmes must be continuous to have a lasting impact on people's attitudes (Gusset et al. 2008a, Marker 2008). Knowledge

alone does not generally affect human behaviour (Barr 2003, Selebatso et al. 2008, Kaplan & Kaplan 2009) and local conservation efforts must be based on a clear understanding of the social, economic, and cultural situations and adapt accordingly (Barr 2003, Clayton & Myers 2009, Waylen et al. 2010).

2.2 Large Carnivore Costs

Key Principle: People who co-exist with free-ranging large carnivores bear the brunt of conservation costs.

Conservation Implication: Conservation will fail where large carnivores continue to inflict heavy costs on rural people (Stander 1991, Gazzola et al. 2008).

Human-carnivore Conflict Implications: 1) Costs people have to bear where large carnivores occur must be accurately determined and effectively addressed in conflict mitigation strategies to be effective. 2) The conservation needs of large carnivores must justify the costs of conservation and the costs of people co-existing with these predators.

Discussion: For people, co-existence with large carnivores may result in direct costs (e.g. actual losses suffered), indirect costs (e.g. fear, time, effort to prevent damage by wildlife), and opportunity costs (e.g. acquiring potential incomes are prevented by the presence of wildlife) (Thirgood et al. 2005).

In Tanzania and Mozambique, lions kill around 50 to 70 people per year (Packer et al. 2005, Lamarque et al. 2009). Loss of human lives affects not only the victims, but also has grave psychological and economic consequences for families and communities (Lamarque et al. 2009). Generally, most lion attacks are by healthy animals, and occur when rural people are farming, protecting livestock and crops

against wildlife, using natural resources, and sleeping (Treves & Naughton-Treves 1999, Baldus 2006, Lamarque et al. 2009).

The most common economic cost inflicted by large carnivores is livestock predation (Thirgood et al. 2005). The loss of an animal includes the additional loss of revenue through by-products such as milk, cheese, wool, and offspring (Mertens & Promberger 2001). For large commercial operations, annual economic losses relative to total stock value are likely to be low. For example, a conservancy adjacent to Tsavo East National Park, Kenya, loses 2.6% of its herd's total economic value to wildlife attacks (mainly lions, and elephants); and the ranches are prepared to tolerate a population of approximately 26 adult lions whose diet consist 5.9% of livestock and which cost the ranches US$290 per lion per year (Patterson et al. 2004). For rural people, livestock losses to large carnivores are often small compared to losses to disease or theft (Cozza et al. 1996, Mizutani 1999, Patterson et al. 2004, Graham et al. 2005, Schiess-Meier et al. 2007), but even small levels of depredation can be devastating (Mizutani 1993, Oli et al. 1994, Mishra 1997, Rasmussen 1999, Mech et al. 2000, Gusset et al. 2008a, Dar et al. 2009). Livestock owners in seven villages adjacent to the Serengeti National Park, Tanzania, lose on average 19.2% of their annual cash income due to livestock predation, mainly by spotted hyaenas (Holmern et al. 2007).

As long as people believe that they are bearing the brunt of carnivore conservation costs without any benefits to themselves, the future of large carnivores remains in serious jeopardy.

2.3 Large Carnivore Benefits

Key Principle: The incentive for people to co-exist with large carnivores depends on whether the benefits of coexistence offset the costs.

Conservation Implication: Making large carnivores valuable to people outside protected areas is an essential conservation goal (Lewis & Alpert 1997, Marker & Dickman 2004, Lindsey et al. 2005, Loveridge 2005, Anonymous 2006, Stein et al. 2010).

Human-carnivore Conflict Implication: Providing tangible long-term and sustainable net benefits to people who tolerate large carnivores should be included in conflict mitigation strategies.

Discussion: Large carnivores can provide both direct and indirect benefits to many rural communities. Tanzanian crop farmers, for example, have a high tolerance for lions where they perceive that lions benefit them by controlling bush pigs (*Potamochoerus larvatus*) that destroy their crops (Packer et al. 2006).

The main direct benefit, and probably the most desired, widely attainable and long-term sustainable goal is economic gains through wildlife-based tourism, which have additional benefits such as employment, skills development, value-added income, and social services (Gössling 1999, Hutton & Leader-Williams 2003, Lindsey et al. 2007, Hoole 2010, Mbaiwa & Stronza 2010). In Africa, wildlife tourism is a fast-growing industry and large carnivores are a priority on most visitors' list of animals to see (Macdonald & Sillero-Zubiri 2002, Gusset et al. 2008a). Botswana's travel and tourism industry, for instance, is expected to generate US$1.3 billion and 25700 jobs in 2010 (Anonymous 2010b). To be attractive to rural people, wildlife conservation must generate tangible net benefits to these people, include them in resource

ownership and management decisions, provide a clear link between the benefits gained from wildlife and the need to conserve it, and in terms of large carnivores specifically, provide equitable benefits (Sillero-Zubiri & Laurenson 2001, Scanlon & Kull 2009). An honest accounting by the wildlife tourism industry should exist to determine its negative impacts on people and environments (Isaacs 2000) and address factors that inhibit the tourism industry from fulfilling its conservation goals.

The Namibian conservancy model is proving increasingly successful in providing a mutually-beneficial coexistence between farmers and large carnivores. Community conservancies provide people with ownership and user rights of their wildlife, the independence to live traditional lifestyles, the potential to obtain food and cash income from consumptive use, direct economic gains from wildlife tourism, and indirect benefits from employment and capacity building (Anonymous 2008). Successful conservancies promote an integrated livestock-carnivore management approach with education and training in effective livestock and range management techniques, and carnivore identification, behaviour, and conservation. The result is effective conflict mitigation combined with large carnivores having an economic value. The outcome is a changed perception of large carnivores and support for their conservation (Marker 2008). In addition, the marketing of "predator-friendly beef" where Namibian farmers with ecologically sound husbandry practices receive a premium price for their products encourages them to tolerate predators (Marker 2003). This provides both a direct monetary benefit to farmers and actively involves them in large carnivore conservation.

Compensation for livestock losses is designed to offset damage caused by carnivores. Unfortunately, government-based compensation schemes often fail, largely because of

bureaucratic delays in investigating cases and compensation payments (Nyhus et al. 2005, Ogra & Badola 2008, Gusset et al. 2009, Lamarque et al. 2009). Potentially more effective are approaches that are decentralized and include performance-based schemes dependant on appropriate livestock husbandry practices (Dyar & Wagner 2003, Hemson 2003, Swenson & Andrén 2005), insurance for livestock in which owners pay a premium to cover losses (Kasaona 2009) and privately funded compensation schemes (Maclennan et al. 2009), all of which operate on a local level and are strictly governed. Financial compensation is seldom enough to positively change people's behaviour towards large carnivores in the long term because it does not cover the social and cultural impacts of livestock depredation (Wilshusen et al. 2002). It is also expensive to maintain and when such an incentive is stopped, motivation for behavioural change diminishes (Clayton & Myers 2009).

A variety of opportunities are possible for people to benefit from coexisting with large carnivores. For these opportunities to result in positive change in human behaviour, site-specific analyses are necessary to determine the most suitable benefits people can derive from large carnivores. In addition, accurate evaluations are needed to determine the impact of these benefits on human behaviour.

3. KEY POLITICAL FACTORS AND PRINCIPLES

3.1 Conservation Policy Development and Implementation

Key Principle: Large carnivore conservation policies must be based on problem definitions that deal with the ecological, social, and political processes involved (Clark et al. 1996) and should convert promptly into adaptive strategies and actions (Reyers et al. 2010).

Conservation Implication: Stakeholders need to commit to a process of collaborative problem definition to formulate policy development and implementation (Seidensticker et al. 1999, Woodroffe 2000, Hutton & Leader-Williams 2003, Treves & Karanth 2003, Loveridge 2005, Selebatso et al. 2008).

Human-carnivore Conflict Implication: Failure to develop interdisciplinary and adaptive large African problem definitions to guide conservation policies will lead to a lack of support or resistance from people to conservation efforts (Mattson et al. 2006, Gusset et al. 2009).

Discussion: The traditional approach to development of conservation policies defines problems mainly from an exclusive "people first" or "wildlife first" standpoint, both of which are inadequate when applied to the complex conservation challenge posed by large carnivores (Ascher & Healy 1990, Clark et al. 1996). Needed instead, are conservation policies that provide for the ecological and social scales (Cumming et al. 2006); international, such as the Convention on International Trade in Endangered Species (CITES); regional, such as the Regional Conservation Strategy for Lions in Eastern and Southern Africa (Anonymous 2006); national, such as each country's wildlife legislation; and local, where policies make provision for the implementation of adaptive strategies (Clayton & Myers 2009). The implementation of policy at different ecological and social scales is dependent on matching it with the appropriate hierarchical level in institutions that have the power, mandate, and resources to action (Cumming et al. 2006).

The foundation of policy development is problem definition; it ultimately guides and shapes actions chosen to provide solutions (Laswell 1971, Dery 1984, Weiss 1989, Clark et al. 2001). The process of defining problems includes identifying differences

of perspectives and points of shared aims among stakeholders and ultimately reaching consensus on the true problems (Clark et al. 1996). This enables decision makers to form policies and design problem-solving strategies that are in concurrence with governments and their international and national responsibilities, with interest groups, and with the people whose lives and livelihoods are affected by conservation actions. The competing interests of concerned stakeholders make this a complex process.

In the case of large carnivore conservation, the main stakeholders are political decision makers, conservationists, and people living with free-ranging large carnivores. In addition, it is vital to include social scientists and conservation psychologists in the collective process (Mascia et al. 2003) to facilitate collaboration among stakeholders with conflicting interests. Unfortunately, there remains a lack of a cohesive approach despite the considerable knowledge available (Clayton & Myers 2009, Kaplan & Kaplan 2009, Reyers et al. 2010, Waylen et al. 2010).

The conversion of conservation policies into action remains inadequate (Reyers et al. 2010). In terms of large carnivore conservation, part of the problem is poorly designed policies and the corporate culture of bureaucracies that tend not to perform well with the complex, urgent, and often novel nature of the conservation challenge (Clark et al. 1989, Finlayson & McMahon 1994). Non-governmental organizations on the other hand, tend to have the capacity, skills, and resources for speedy assistance, rapid assessment programs, and innovative conservation actions and can play an important role in the implementation of conservation plans (Mascia et al. 2003, Slotow & Hunter 2009).

To be effective, large carnivore conservation policies and action plans must be based on scientific research, continuous monitoring and evaluation in terms of desired

outcomes, and adaptive strategies that are evidence-based (Gusset et al. 2008b). The decision-making processes must be flexible and result in prompt, practical actions (Clark & Brunner 1996, Primm & Clark 1996, Clark et al. 2001, Sutherland et al. 2004, Karanth & Chellam 2009).

3.2 Conservation Strategies

Key Principle: Governments and people decide the ultimate fate of large carnivores.

Conservation Implication: Large carnivore conservation requires an approach that balances the need for legal protection of large carnivores with the use of natural resources by rural people for their livelihoods (Hutton & Leader-Williams 2003, Abensperg-Traun 2009, Andrew-Essien & Bisong 2009).

Human-carnivore Conflict Implication: Conflict mitigation is vital to reduce human-caused mortality of large carnivores and should be part of governments' conservation goals to enable the coexistence between people and large carnivores.

Discussion: Two contrasting approaches to biodiversity conservation have emerged: the protectionist approach (conservation through enforced laws) and the people-oriented approach (integrated conservation and sustainable use). Protectionists maintain that protected areas form the last safeguard of biodiversity against human encroachment, that sustainable development is unattainable and top-down approaches to conservation are preferable (Oates 1999, Rabinowitz 1999, Terborgh 1999). Although maintaining protected areas is an essential requirement for conservation and are primary refuges for many large carnivores worldwide (Mills 1991, Karanth & Chellam 2009), protected areas and legal protection in the law books, both on international and national levels, has thus far failed to prevent declines in large

carnivore populations; in Africa, the endangered African wild dog and cheetah are good examples (Weber & Rabinowitz 1996, Marker & Dickman 2004). The protectionist approach underplays the complex socio-economic and political realities involved in conservation, and fail to account for the consequences of the approach - that it is operationally unrealistic and morally questionable (Wilshusen et al. 2002). In Africa, it is the people living outside protected areas that decide the ultimate fate of wide-ranging large carnivores (Woodroffe 2001, Ogada et al. 2003, Marker & Dickman 2004, Frank et al. 2006). Simply put, the reason is two-fold: 1) top-down conservation approaches generally lead to rural people feeling marginalized and resentful towards protected areas because of the loss of land and livelihoods (Andrew-Essien & Bisong 2009), and 2) the failure of governments to adequately address human-carnivore conflicts puts the onus on rural people to protect their livelihoods, often through illegal activities, deepening their antagonism toward conservation in general. Most human-carnivore conflict in Africa occurs along protected area boundaries (Loveridge 2005) and, unless the support of rural people is garnered, the negative impact of conflict on many large carnivore populations means that conservation will at best be nominal even inside protected areas (Woodroffe 2001). Integrated conservation and sustainable use are successful in many cases (Sillero-Zubiri & Laurenson 2001, Balme et al. 2009, Child 2009, Mbaiwa & Stronza 2010). Sustainable use can play a complementary role as one component of a broader landscape conservation strategy, and is an economical and political option to make large tracts of land viable for wildlife as the primary land use (Wilshusen et al. 2002, Langholz & Kerley 2006, Sachedina & Nelson 2010). Unfortunately, people-oriented approaches often flounder not because of any fundamental incompatibility with

biodiversity conservation and human development, but rather through shortcomings in its implementation (Wilshusen et al. 2002, Abensperg-Traun 2009).

Consequently, the exclusive reliance on either legal protection or a universal application of sustainable use, will inevitably fail to protect biodiversity (Hutton & Leader-Williams 2003). Conservation, irrespective of geography or taxa, depends on the ability of governments to integrate the needs of biodiversity conservation with the needs of people (Abensperg-Traun 2009, Andrew-Essien & Bisong 2009). Legitimate and enforceable integrated conservation strategies are needed that are ecologically sound, pragmatically feasible, and socially just (Wilshusen et al. 2002). In addition, due to its complex nature, such strategies should be implemented, facilitated, and monitored on an interdisciplinary basis (Reid et al. 2009), using already-successful models as guidelines and providing relevant information to the literature to increase the long-term success of this approach.

3.3 Land Use Zoning

Key Principle: Zoning is an important land use management tool that complements the conservation mission of protected areas and can be vital for some wide-ranging large carnivore populations.

Conservation Implications: 1) Land use zones with wildlife conservation as one of their primary goals can be used to enlarge conservation areas beyond protected areas that are too small to contain the movements of the carnivores they aim to protect. 2) Wildlife conservation zones can provide important dispersal corridors.

Human-carnivore Conflict Implication: The expansion of wildlife-conservation zones around small protected areas can move the interface of human-carnivore

conflict away from protected area boundaries, thereby increasing the protection of source populations of large carnivores (Linnell et al. 2005, Loveridge 2005).

Discussion: The existing conservation network in Africa covers the distribution of large mammals relatively well and contributes significantly to biodiversity conservation (Fjeldså et al. 2004). However, wide-ranging large carnivores need larger areas than other terrestrial species and edge effects around protected areas make this network on its own inadequate to conserve many large carnivore populations (Weber & Rabinowitz 1996, Loveridge et al. 2001). Edge effects are especially severe where the primary land use bordering a protected area is livestock and human-carnivore conflict is rampant (Loveridge 2005, Schiess-Meier et al. 2007, Van Bommel et al. 2007). Additional conservation zones, if appropriately managed, can act as buffer zones where the edge effect around the protected area boundary is reduced and the threat for local extinctions of source populations lowered. Conservation zones can support a variety of land uses such as wildlife management (with wildlife use), forest management, and integrated livestock-wildlife management. In Botswana, most community and state wildlife management areas (WMAs) are adjacent to protected areas and contribute an additional 20% to the 17% of land designated for wildlife conservation (Mogae (Hon) 1997). Some WMAs with naturally low densities of lions and spotted hyaenas provide important refuge areas for cheetahs and African wild dogs. Livestock areas can also be potential conservation zones (e.g. the Namibian community conservancy model; Marker 2008). These conservancies employ integrated livestock-wildlife land management that leads to improved land productivity, higher wildlife densities, increased connectivity between areas for wildlife movements, and increasing viability of Namibia's protected area

network (Weaver & Skyer 2003). They also play a crucial role in conservation of cheetahs (Marker et al. 2007). Both the WMA and conservancy models prove successful in changing land use patterns in some of Africa's arid and semi-arid communal areas towards more environmentally appropriate and improved livelihoods (Weaver & Skyer 2003, Mbaiwa & Stronza 2010).

A pragmatic and morally defendable approach to large carnivore conservation outside conservation areas is important. Not all areas are suitable and not all carnivore species can be conserved as viable populations outside conservation areas. Therefore, legal protection of these populations will most likely only result in their continued persecution by people and lead to public resentment and alienation of support for other conservation projects (Stander 1991). The question that needs to be asked is … in which areas is it operationally realistic and morally defendable to expect the conservation of large carnivores (Loveridge 2005)?

If the importance of people's livelihoods is recognized, then a sensible way of zoning will include areas with complete protection of large carnivores, areas where people and large carnivores can co-exist, and areas where large carnivores are not tolerated (Linnell et al. 2005, Loveridge 2005). Thus, in areas where it is impossible to offset the human cost of coexisting with large carnivores by acceptable benefits, then human interests should be given preference and these carnivores should be controlled in the most humane and cost-effective ways possible (Anderson & Pariela 2005, Treves & Naughton-Treves 2005).

4. CONCLUSION

The 14 key factors identified in this review as features of large African carnivore conservation reflect the breadth and scope of the systems that collectively lead to their successful conservation. The key factors can be illustrated as a rainbow of layers in a model, one over the other (Figure 1). The immediate factors have the most direct impact on large carnivore conservation and the factors further away from the centre, although of equal importance, have a more gradual impact. The innermost layers represent priority ecological requirements that have the potential to promote or hinder the persistence of large carnivores. These ecological requirements are dependent on the following layer, the socio-economic key factors, which represent the value that people living in proximity place on large carnivores. The outermost layer contains the overarching political conditions that ultimately set the scene for activities that support large carnivore conservation.

All key factors are interrelated and the importance of individual factors will depend on the species of large carnivore in a site-specific context. Activities designed to improve large carnivore conservation are likely to be less effective if they focus on one key factor without complementary action to influence a linked factor in another layer. The conservation and human-carnivore implications guide the implementation of the key principles in large carnivore conservation policies, conservation strategies, and actions.

Although this review focused on the large African carnivore guild, the model, key principles, and conservation and human-carnivore conflict implications should generally be relevant to large carnivore conservation worldwide.

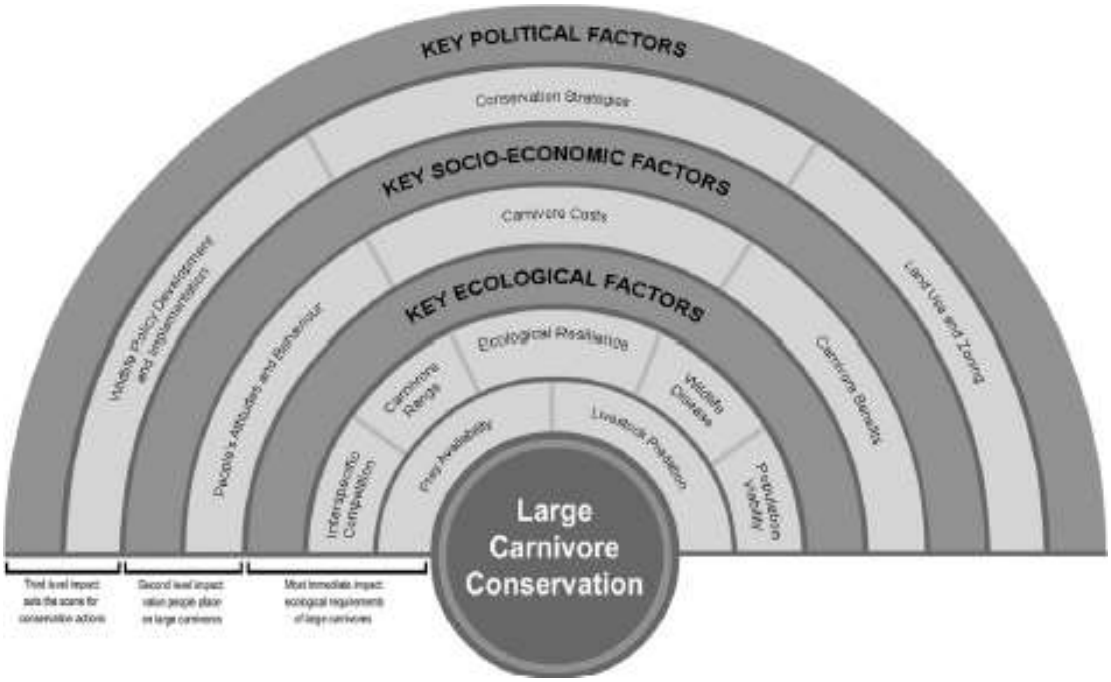

Figure 1. A model of the key ecological, socio-economic and political factors and associated levels of impact on the long-term conservation of African large carnivores.

ACKNOWLEDGEMENTS

Thanks to Peter J. Apps, Glyn Maude, Jesse M. Kalwij, Scott Hygnstrom, and Helen Apps for their valuable contributions. This manuscript was partly funded by the Botswana Wildlife Management Association, Maun, Botswana, and made possible by the Department of Wildlife and National Parks, Ministry of Environment, Wildlife and Tourism, Gaborone, Botswana.

REFERENCES

Abensperg-Traun M (2009) CITES. Sustainable use of wild species and incentive-driven conservation in developing countries, with an emphasis on southern Africa. *Biological Conservation* 142: 948-963.

Anderson JL, Pariela F (2005) *Strategies to Mitigate Human-wildlife Conflict in Moçambique*. Unpublished report, National Directorate of Forests and Wildlife, Moçambique.

Andrew-Essien E, Bisong F (2009) Conflicts, conservation and natural resource use in protected area systems: an analysis of recurrent issues. *European Journal of Scientific Research* 25: 118-129.

Anonymous (2000) *Community Based Conservation Experience in Tanzania: An Assessment of Lessons Learned*. Unpublished report, International Resources Group, Washington DC, USA.

Anonymous (2006) Regional Conservation Strategy for the Lion *Panthera leo* in Eastern and Southern Africa. http://www.catsorg.org/

Anonymous (2007) *Regional Conservation Strategy for the Cheetah and African Wild Dog in Southern Africa*. Unpublished report, IUCN Cat Specialist Group, Gland, Switzerland, IUCN.

Anonymous (2008) Achieving Sustainability: Conservancy Based Natural Resource Management Programme - North East and North West Namibia. http://www.irdnc.org.na/

Anonymous (2010a) The IUCN Red List of Threatened Species. http://www.iucnredlist.org/

Anonymous (2010b) Travel & Tourism Economy GDP. http://www.wttc.org/

Ascher W, Healy RG (1990) *Natural Resource Policymaking in Developing Countries*. Duke University Press, London, UK.

Baldus RD (2006) A man-eating lion (*Panthera leo*) from Tanzania with a toothache. *European Journal of Wildlife Research* 52: 59-62.

Balme G, Hunter L, Slotow R (2007) Feeding habitat selection by hunting leopards *Panthera pardus* in a woodland savanna: prey catchability versus abundance. *Animal Behaviour* 74: 589-598.

Balme GA, Slotow R, Hunter LTB (2009) Impact of conservation interventions on the dynamics and persistence of a persecuted leopard (*Panthera pardus*) population. *Biological Conservation* 142: 2681-2690.

Balme GA, Slotow R, Hunter LTB (2010) Edge effects and the impact of non-protected areas in carnivore conservation: leopards in the Phinda-Mkuze Complex, South Africa. *Animal Conservation* 13: 315-323.

Barr S (2003) Strategies for sustainability: citizens and responsible environmental behaviour. *Area* 35: 227-240.

Bath A, Olszanska A, Okarma H (2008) From a human dimensions perspective, the unknown large carnivore: public attitudes toward Eurasian lynx in Poland. *Human Dimensions of Wildlife* 13: 31-46.

Bauer H, De Iongh HH (2005) Lion (*Panthera leo*) home ranges and livestock conflicts in Waza National Park, Cameroon. *African Journal of Ecology* 43: 208-214.

Beinart W (1998) The night of the jackal: sheep, pastures and predators in the Cape. *Past & Present* 158: 172-206.

Beissinger SR, Westphal MI (1998) On the use of demographic models of population viability in endangered species management. *Journal of Wildlife Management* 62: 821-841.

Bissett C, Bernard TF (2007) Habitat selection and feeding ecology of the cheetah (*Acinonyx jubatus*) in thicket vegetation: is the cheetah a savanna specialist? *Journal of Zoology* 271: 310-317.

Boydston EE, Kapheim KM, Watts HE, Szykman M, Holekamp KE (2003) Altered behaviour in spotted hyenas associated with increased human activity. *Animal Conservation* 6: 207-219.

Burton AC, Buedi EB, Balangtaa C, Kpelle DG, Sam MK, Brashares JS (2010) The decline of lions in Ghana's Mole National Park. http://www.wiley.com/

Butler JRA (2000) The economic costs of wildlife predation on livestock in Gokwe communal land, Zimbabwe. *African Journal of Ecology* 38: 23-30.

Butler JRA, Du Toit JT, Bingham J (2004) Free-ranging domestic dogs (*Canis familiaris*) as predators and prey in rural Zimbabwe: threats of competition and disease to large wild carnivores. *Biological Conservation* 115: 369-378.

Caro T (1999) The behaviour-conservation interface. *Tree* 14: 366-369.

Caro TM, Young CR, Cauldwell AE, Brown DDE (2009) Animal breeding systems and big game hunting: models and application. *Biological Conservation* 142: 909-929.

Child B (2009) Community conservation in southern Africa: right-based natural resource management. In: Suich H, Child B, Spenceley A (eds) *Evolution and Innovation in Wildlife Conservation. Parks and Game Ranches to Transfrontier Conservation Areas*, 187-200. Earthscan, London, UK.

Clark TW, Crete R, Cada J (1989) Designing and managing successful endangered species recovery programs. *Environmental Management* 13: 159-170.

Clark TW, Brunner RD (1996) Making partnerships work in endangered species conservation: an introduction to the decision process. *Endangered Species Update* 13: 1-5.

Clark TW, Curlee AP, Reading RP (1996) Crafting effective solutions to the large carnivore conservation problem. *Conservation Biology* 10: 940-948.

Clark TW, Mattson DJ, Reading RP, Miller BJ (2001) Interdisciplinary problem solving in carnivore conservation: an introduction. In: Gittleman JL, Funk SM, Macdonald DW,

Wayne RK (eds) *Carnivore Conservation*, 223-240. Cambridge University Press, Cambridge, UK.

Clayton S, Myers G (2009) *Conservation Psychology. Understanding and promoting human care for Nature*. Wiley-Blackwell, West Sussex, UK.

Cleaveland S, Hess GR, Dobson AP, Laurenson MK, McCallum HI, Roberts MG, Woodroffe R (2002) The role of pathogens in biological conservation. In: Hudson PJ, Rizzoli A, Grenfell BT, Heesterbeek H, Dobson AP (eds) *The Ecology of Wildlife Diseases*, 139-150. Oxford University Press, Oxford, UK.

Courchamp F, Macdonald DW (2001) Crucial importance of pack size in the African wild dog *Lycaon pictus*. *Animal Conservation* 4: 169-174.

Courtin F, Carpenter TE, Paskin RD, Chomel BB (2000) Temporal patterns of domestic and wildlife rabies in central Namibia stock-ranching area, 1986-1996. *Preventive Veterinary Medicine* 43: 13-28.

Cozza K, Fico R, Battistini M, Rogers E (1996) The damage-conservation interface illustrated by predation on domestic livestock in central Italy. *Biological Conservation* 78: 329-336.

Creel S (2001) Four factors modifying the effect of competition on carnivore population dynamics as illustrated by African wild dogs. *Conservation Biology* 15: 271-274.

Creel S, Creel NM (1996) Limitation of African wild dogs by competition with larger carnivores. *Conservation Biology* 10: 526-538.

Creel S, Spong G, Creel NM (2001) Interspecific competition and the population biology of extinction-prone carnivores. In: Gittleman JL, Funk SM, Macdonald DW, Wayne RK (eds) *Carnivore Conservation*, 35-60. Cambridge University Press, Cambridge, UK.

Creel S, Mills MGL, McNutt JW (2007) African wild dogs. Demography and population dynamics of African wild dogs in three critical populations. In: Macdonald DW, Sillero-Zubiri C (eds) *Biology and Conservation of Wild Canids*, 337-352. Oxford University Press, Oxford, UK.

Crooks KR (2002) Relative sensitivities of mammalian carnivores to habitat fragmentation. *Conservation Biology* 16: 488-502.

Cumming GS, Cumming DHM, Redman CL (2006) Scale mismatches in social-ecological systems: causes, consequences, and solutions. *Ecology and Society* 11(1): 14. http://www.ecologyandsociety.org/

Dalerum F, Somers MJ, Kunkel KE, Cameron EZ (2008) The potential for large carnivores to act as biodiversity surrogates in southern Africa. *Biodiversity Conservation* 17: 2939-2949.

Dar NI, Minhas RA, Zaman Q, Linkie M (2009) Predicting the patterns, perceptions and causes of human-carnivore conflict in and around Machiara National Park, Pakistan. *Biological Conservation* 142: 2076-2082.

Davidson Z, Valeix M, Loveridge AJ, Madzikanda H, MacDonald DW (2011) Socio-spatial behaviour of an African lion population following perturbation by sport hunting. *Biological Conservation* **144**, 114-121.

Davies-Mostert HT, Mills MGL, MacDonald DW (2009) South Africa's wild dog *Lycaon pictus* meta-population management programme. In: Hayward MW, Somers MJ (eds) *The Reintroduction of Top-order Predators*, 10-42. Blackwell Publishing, Oxford, UK.

De Azevedo FCC, Murray DI (2007) Evaluation of potential factors predisposing livestock to predation by jaguars. *Journal of Wildlife Management* 71: 2379-2386.

Dery D (1984) *Problem Definition in Policy Analysis*. University Press of Kansas, Kansas, USA.

de Tores PJ, Marlow NJ (2012) A review of the relative merits of predator exclusion fencing and repeated 1080 fox baiting for protection of native fauna: five case studies from Western Australia. In: Somers MJ, Hayward MW (eds) *Fencing for Conservation*, in press. Springer-US, New York, USA.

Druce D, Genis H, Braak J, Greatwood S, Delsink A, Kettles R, Hunter L, Slotow R (2004) Population demography and spatial ecology of a reintroduced lion population in the Greater Makalali Conservancy, South Africa. *Koedoe* 47(1): 103-118.

Durant SM (1998) Competition refuges and coexistence: an example from Serengeti carnivores. *Journal of Animal Ecology* 67: 370-386.

Durant SM (2000a) Living with the enemy: avoidance of hyenas and lions by cheetahs in the Serengeti. *Behavioural Ecology* 11: 624-632.

Durant SM (2000b) Predator avoidance, breeding experience and reproductive success in endangered cheetahs, *Acinonyx jubatus*. *Animal Behaviour* 60: 121-130.

Dyar JA, Wagner J (2003) Uncertainty and species recovery program design. *Journal of Environmental Economics and Management* 45: 505-522.

Dybas CL (2009) Infectious diseases subdue Serengeti lions. *BioScience* 59: 8-13.

Estes RD (1995) *The behaviour guide to African mammals*. Russel Friedman Books CC, Halfway House, South Africa.

Finlayson B, McMahon T (1994) Funding and conduct of environmental research. In: Evans D, Yencken D (eds) *Restoring the Land: Environmental Values, Knowledge and Action*. Melbourne University Press, Melbourne, Australia.

Fjeldså J, Burgess ND, Blyth S, De Klerk H (2004) Where are the major gaps in the reserve network for Africa's mammals? *Oryx* 38: 17-25.

Forman RTT (1995) *Land Mosaics: the Ecology of Landscapes and Regions*. Cambridge University Press, Cambridge, UK.

Frank LG, Woodroffe R, Ogada MO (2005) People and predators in Laikipia District, Kenya. In: Woodroffe R, Thirgood S, Rabinowitz AR (eds) *People and Wildlife - Conflict or Coexistence?* 286-304. Cambridge University Press, Cambridge, UK.

Frank LG, Hemson G, Kushnir H, Packer C (2006) Lions, conflict and conservation in eastern and southern Africa. In: *Eastern and Southern African Lion Conservation Workshop*. IUCN/Cat Specialist Group, Johannesburg, South Africa.

Fuller TK, Sievert PR (2001) Carnivore demography and the consequences of changes in prey availability. In: Gittleman JL, Funk SM, Macdonald DW, Wayne RK (eds) *Carnivore Conservation*, 163-178. Cambridge University Press, Cambridge, UK.

Funk SM, Fiorello CV, Cleaveland S, Gompper ME (2001) The role of disease in carnivore ecology and conservation. In: Gittleman JL, Funk SM, Macdonald DW, Wayne RK (eds) *Carnivore Conservation*, 443-466. Cambridge University Press, Cambridge, UK.

Funston P J (2001) *Kalahari Transfrontier Lion Project: Population-Ecology and Long Term Monitoring of a Free-Ranging Population in an Arid Environment*. Unpublished report GT87, Endangered Wildlife Trust.

Gascoyne SC, Laurenson MK, Lelo S, Borner M (1993) Rabies in African wild dogs (*Lycaon pictus*) in the Serengeti region, Tanzania. *Journal of Wildlife Diseases* 29: 396-402.

Gazzola A, Capitani C, Mattioli L, Apollonio M (2008) Livestock damage and wolf presence. *Journal of Zoology* 274: 261-269.

Gittleman JL, Harvey PH (1982) Carnivore home-range size, metabolic needs and ecology. *Behavioral Ecology and Sociobiology* 10: 57-63.

Gössling S (1999) Ecotourism: a means to safeguard biodiversity and ecosystem functions? *Ecological Economics* 29: 303-320.

Graham K, Beckerman AP, Thirgood S (2005) Human-predator-prey conflicts: ecological correlates, prey losses and patterns of management. *Biological Conservation* 122: 159-171.

Grant J, Hopcraft C, Sinclair ARE, Packer C (2005) Planning for success: Serengeti lions seek prey accessibility rather than abundance. *Journal of Animal Ecology* 74: 559-566.

Gusset M, Jakoby O, Muller M, Somers MJ, Slotow R, Grimm V (2009) Dogs on the catwalk: modeling the re-introduction of endangered wild dogs in South Africa. *Biological Conservation* 142: 2774-2781.

Gusset M, Maddock AH, Gunther GJ, Szykman M, Slotow R, Walters M, Somers MJ (2008a) Conflicting human interests over the re-introduction of endangered wild dogs in South Africa. *Biodiversity Conservation* 17: 83-101.

Gusset M, Ryan SJ, Hofmeyr M, Van Dyk G, Davies-Mostert HT, Graf JA, Owen C, Szykman M, Macdonald DW, Monfort SL et al. (2008b) Efforts going to the dogs? Evaluating attempts to re-introduce endangered wild dogs in South Africa. *Journal of Applied Ecology* 45: 100-108.

Gusset M, Swarner MJ, Mponwane L, Keletile K, McNutt JW (2009) Human-wildlife conflict in northern Botswana: livestock predation by Endangered African wild dog *Lycaon pictus* and other carnivores. *Oryx* 43: 67-72.

Hanby JP, Bygott JD, Packer C (1995) Ecology, demography, and behaviour of lions in two contrasting habitats: Ngorongoro Crater and the Serengeti Plains. In: Sinclair ARE, Arcese P (eds) *Serengeti II: Dynamics, Management and Conservation of an Ecosystem*, 315-331. University of Chicago Press, Chicago, USA.

Hayward MW (2006) Prey preferences of the spotted hyaena (*Crocuta crocuta*) and degree of dietary overlap with the lion (*Panthera leo*). *Journal of Zoology* 270: 606-614.

Hayward MW (2012) Perspectives on fencing for conservation based on four case studies: marsupial conservation in Australian forests; bushmeat hunting in South Africa; large predator reintroduction in South Africa; and large mammal conservation in Poland. In: Somers MJ, Hayward MW (eds) *Fencing for Conservation*, in press. Springer-US, New York, USA.

Hayward MW, Hayward GJ, Druce DJ, Kerley GIH (2009) Do fences constrain predator movements on an evolutionary scale? Home range, food intake and movement patterns of large predators reintroduced to Addo Elephant National Park, South Africa. *Biodiversity and Conservation* 18: 887-904.

Hayward MW, Henschel P, O'Brien J, Hofmeyr M, Balme G, Kerley GIH (2006a) Prey preferences of the leopard (*Panthera pardus*). *Journal of Zoology* 270: 298-313.

Hayward MW, Hofmeyr M, O'Brien J, Kerley GIH (2006b) Prey preferences of the cheetah (*Acinonyx jubatus*) (Felidae: Carnivora): morphological limitations or the need to capture rapidly consumable prey before kleptoparasites arrive? *Journal of Zoology* 270: 615-627.

Hayward MW, Kerley GIH (2008) Prey preferences and dietary overlap amongst Africa's large predators. *South African Journal of Wildlife Research* 38: 93-108.

Hayward MW, Kerley GIH (2009) Fencing for conservation: restriction of evolutionary potential or a riposte to threatening processes? *Biological Conservation* 142: 1-13.

Hayward MW, O'Brien J, Hofmeyer M, Kerley GIH (2007a) Testing predictions of the prey of lion derived from modelled prey preferences. *Journal of Wildlife Management* 71: 1567-1575.

Hayward MW, O'Brien J, Kerley GIH (2007b) Carrying capacity of large African predators: predictions and tests. *Biological Conservation* 139: 219-229.

Hayward MW, Slotow R (2009) Temporal partitioning of activity in large African carnivores: tests of multiple hypotheses. *South African Journal of Wildlife Research* 39: 109-125.

Hayward MW, Somers MJ (2012) An introduction to fencing for conservation. In: Somers MJ, Hayward MW (eds) *Fencing for Conservation*, in press. Springer-US, New York, USA.

Hemson G (2003) *The Ecology and Conservation of Lions: Human-Wildlife Conflict in Semi-Arid Botswana*. PhD thesis, University of Oxford, Oxford, UK.

Hofer H (1998) Species accounts. Spotted hyaena *Crocuta crocuta*. In: Mills MGL, Hofer H (eds) *Hyaenas. Status Survey and Conservation Action Plan*, 29-38. IUCN/SSC Hyaena Specialist Group, Gland, Switzerland.

Hofmeyr M, Bingham J, Lane EP, Ide A, Nel L (2000) Rabies in African wild dogs (*Lycaon pictus*) in the Madikwe Game Reserve, South Africa. *The Veterinary Record* 146: 50-52.

Holmern T, Nyahongo J, Røskaft E (2007) Livestock loss caused by predators outside the Serengeti National Park, Tanzania. *Biological Conservation* 135: 518-526.

Höner OP, Wachter B, East ML, Runyoro VA, Hofer H (2005) The effect of prey abundance and foraging tactics on the population dynamics of a social, territorial carnivore, the spotted hyena. *Oikos* 108: 544-554.

Hoole AF (2010) Place - Power - Prognosis: Community-Based Conservation, Partnerships and Ecotourism Enterprise in Namibia. *International Journal of the Commons* 4(1): 78-99.

Hudson PJ, Rizzoli A, Grenfell BT, Heesterbeek H, Dobson AP (2002) *The Ecology of Wildlife Diseases*, 1-5. Oxford University Press, Oxford, UK.

Hugh-Jones M, Blackburn J (2009) The ecology of *Bacillus antracis*. *Molecular Aspects of Medicine* 30: 356-367.

Hutton JM, Leader-Williams N (2003) Sustainable use and incentive-driven conservation: realigning human and conservation interests. *Oryx* 37: 215-226.

Isaacs JC (2000) The limited potential of ecotourism to contribute to wildlife conservation. *Wildlife Society Bulletin* 28: 61-69.

Johnson WE, Eizirik E, Lento GM (2001) The control, exploitation, and conservation of carnivores. In: Gittleman JL, Funk SM, Macdonald DW, Wayne RK (eds) *Carnivore Conservation*, 189-218. Cambridge University Press, Cambridge, UK.

Johnson CN, VanDerWal J (2009) Evidence that dingoes limit abundance of a mesopredator in eastern Australian forests. *Journal of Applied Ecology* 46: 641-646.

Kaplan S, Kaplan R (2009) Creating a larger role for environmental psychology: the Reasonable Person Model framework. *Journal of Environmental Psychology* 29: 329-339.

Karanth KU, Chellam R (2009) Carnivore conservation at the crossroads. *Oryx* 43: 1-2.

Karanth KU, Stith BM (1999) Prey depletion as a critical determinant of tiger population viability. In: Seidensticker J, Christie S, Jackson P (eds) *Riding the Tiger. Tiger*

Conservation in Human-Dominated Landscapes, 100-113. Cambridge University Press and the Zoological Society of London, Cambridge, UK.

Karanth KU, Sunquist ME (2000) Behavioral correlates of predation by tiger (*Panthera tigris*), leopard (*Panthera pardus*) and dhole (*Cuon alpinus*) in Nagarahole, India. *Journal of Zoology* 250: 255-265.

Karlsson J, Johansson Ö (2010) Predictability of repeated carnivore attacks on livestock favours reactive use of mitigation measures. *Journal of Applied Ecology* 47: 166-171.

Kasaona MK (2009) *An Assessment of Community Understanding of the Human Animal Conservancy Self-Insurance Scheme and the Impact of Human-Wildlife Conflicts: a Case Study from the Kwandu Conservancy, North-East Namibia*. Unpublished report, University of Kwazulu-Natal, South Africa.

Kellert SR, Black M, Reid Rush C, Bath AJ (1996) Human culture and large carnivore conservation in North America. *Conservation Biology* 10: 977-990.

Kelly MJ, Laurenson MK, FitzGibbon CD, Collins DA, Durant SM, Frame GW, Bertram BCR, Caro TM (1998) Demography of the Serengeti cheetah (*Acinonyx jubatus*) population: the first 25 years. *Journal of Zoology* 244: 473-488.

Kettles R, Slotow R (2009) Management of free-ranging lions on an enclosed game reserve. *South African Journal of Wildlife Research* 39(1): 23-33.

Klein R (2007) Status report for cheetah in Botswana. In: Breitenmoser C, Breitenmoser U, Durant S (eds) *Status and Conservation Needs of Cheetahs in Southern Africa*, 14-21. IUCN/Cat Specialist Group, Gland, Switzerland.

Kolowski JM, Holekamp KE (2006) Spatial, temporal, and physical characteristics of livestock depredations by large carnivores along a Kenyan reserve border. *Biological Conservation* 128: 529-541.

Kolowski JM, Katan D, Theis KR, Holekamp KE (2007) Daily patterns of activity in the spotted hyena. *Journal of Mammalogy* 88: 1017-1028.

Lagendijk DDG, Gusset M (2008) Human-carnivore coexistence on communal land bordering the Greater Kruger area, South Africa. *Environmental Management* 42: 971-976.

Lamarque F, Anderson J, Fergusson R, Lagrange M, Osei-Owusu Y, Bakker L (2009) *Human-Wildlife Conflict in Africa. Causes, Consequences and Management Strategies*. Paper 157, Food and Agriculture Organization of the United Nations Forestry, Rome, Italy.

Langholz JA, Kerley GIH (2006) *Combining conservation and development on private lands: an assessment of ecotourism-based private game reserves in the Eastern Cape*. Centre for African Conservation Ecology. Nelson Mandela Metropolitan University, Port Elizabeth, South Africa.

Laswell H (1971) *A Pre-View of the Policy Sciences*. Elsevier, New York, USA.

Laurenson MK, Cleaveland S, Artois M, Woodroffe R (2004) Canids and disease. In: Sillero-Zubiri C, Macdonald DW (eds) *Wild Canids: Status Survey and Conservation Action Plan*, 246-256. IUCN Canid Specialist Group, Gland, Switzerland.

Laurenson K, Shiferaw F, Sillero-Zubiri C (1997) Disease, domestic dogs and the Ethiopian wolf: the current situation. In: Sillero-Zubiri C, Macdonald DW (eds) *The Ethiopian Wolf: Status Survey and Conservation Action Plan*, 32-40. IUCN Canid Specialist Group, Gland, Switzerland, and Cambridge, UK.

Laurenson MK, Wielebnowski N, Caro TM (1995) Extrinsic factors and juvenile mortality in cheetahs. *Conservation Biology* 9: 1329-1331.

Lembo T, Hampson K, Haydon DT, Craft M, Dobson A, Dushoff J, Ernest E, Hoare R, Kaare M, Mlengeya T et al. (2008) Exploring reservoir dynamics: a case study of rabies in the Serengeti ecosystem. *Journal of Applied Ecology* 45: 1246-1257.

Lewis DM, Alpert P (1997) Trophy hunting and wildlife conservation in Zambia. *Conservation Biology* 11: 59-68.

Lindsey P, Du Toit JT, Mills MGL (2004a) The distribution and population status of African wild dogs (*Lycaon pictus*) outside protected areas in South Africa. *South African Journal of Wildlife Research* 34: 143-151.

Lindsey PA, Du Toit JT, Mills MGL (2004b) Area and prey requirements of African wild dogs under varying habitat conditions: implications for reintroductions. *South African Journal of Wildlife Research* 34: 77-86.

Lindsey PA, Du Toit JT, Mills MGL (2005) Attitudes of ranchers towards African wild dogs *Lycaon pictus*: conservation implications on private land. *Biological Conservation* 125: 113-121.

Lindsey P, Roulet PA, Romañach SS (2007) Economic and conservation significance of the trophy hunting industry in sub-Saharan Africa. *Biological Conservation* 134: 455-469.

Lindsey PA, Tambling CJ, Brummer R, Davies-Mostert HT, Hayward MW, Marnewick KA, Parker DM (2011) Minimum prey and area requirements of cheetahs: implications for reintroductions and management of the species as a managed metapopulation. *Oryx* In press.

Linnell JD, Nilsen EB, Lande US, Herfindal I, Odden J, Skogen K, Andersen R, Breitenmoser U (2005) Zoning as a means of mitigating conflicts with large carnivores: principles and reality. In: Woodroffe R, Thirgood S, Rabinowitz AR (eds) *People and Wildlife - Conflict or Coexistence?* 162-175. Cambridge University Press, Cambridge, UK.

Linnell JDC, Swenson JE, Andersen R (2001) Predators and people: conservation of large carnivores is possible at high human densities if management policy is favourable. *Animal Conservation* 4: 345-349.

Loveridge AJ (2005) Conflict synthesis. In: Loveridge AJ, Lynam T, and Macdonald DW (eds) *Lion Conservation Research: from Conflict to Socioecology. Workshop 3&4,* 59-64. Wildlife Conservation Research Unit, University of Oxford, Oxford, UK.

Loveridge AJ, Lynam T, Macdonald DW (2001) *Lion Conservation Research Workshop 1: Survey Techniques*. Wildlife Conservation Research Unit, University of Oxford, Oxford, UK.

Loveridge AJ, Searle AW, Murindagomo F, Macdonald DW (2007) The impact of sport-hunting on the population dynamics of an African lion population in a protected area. *Biological Conservation* 134: 548-558.

Macdonald DW (1993) Rabies and wildlife: a conservation problem? *Onderstepoort Journal of Veterinary Research* 60: 351-355.

Macdonald DW, Sillero-Zubiri C (2002) Dimensions of the problem. In: Loveridge AJ, Lynam T, and Macdonald DW (eds) *Lion Conservation Research: Modelling Conflict. Workshop 2*, 1-8. Wildlife Conservation Research Unit, University of Oxford, Oxford, UK.

Maclennan SD, Groom RJ, Macdonald DW, Frank LG (2009) Evaluation of a compensation scheme to bring about pastoralist tolerance of lions. *Biological Conservation* 142: 2419-2427.

Marker L (1999) Reducing conflicts between Namibian farmers and cheetahs. In: *2nd International Wildlife Management Congress*, 184-187. The Wildlife Society, Bethesda, USA.

Marker L (2003) *Aspects of Cheetah (*Acinonyx jubatus*) Biology, Ecology and Conservation Strategies on Namibian Farmlands*. PhD thesis, University of Oxford, Oxford, UK.

Marker L (2008) Cheetah conservation strategies in Namibia - a model for the future. *African Wildlife Conference Proceedings*, 6-11. Zoo Dvur Kralove, Czech Republic.

Marker L, Dickman A (2004) Human aspects of cheetah conservation: lessons learned from the Namibian farmlands. *Human Dimensions of Wildlife* 9: 297-305.

Marker L, Dickman A (2005) Factors affecting leopard (*Panthera pardus*) spatial ecology, with particular reference to Namibian farmlands. South African *Journal of Wildlife Research* 35: 105-115.

Marker L, Dickman A, Schumann M (2005) Using livestock guarding dogs as a conflict resolution strategy on Namibian farms. *Carnivore Damage Prevention News*, 28-32.

Marker L, Dickman A, Wilkinson C, Schumann B, Fabiano E (2007) The Namibian cheetah: status report. In: Breitenmoser C, Breitenmoser U, Durant S (eds) *Status and Conservation Needs of Cheetahs in Southern Africa*, 1-13. IUCN/Cat Specialist Group, Gland, Switzerland.

Marker LL, Dickman AJ, Mills MGL, Jeo RM Macdonald DW (2008) Spatial ecology of cheetahs on north-central Namibian farmlands. *Journal of Zoology* 274: 226-238.

Marker LL, Dickman AJ, Mills MGL, Macdonald DW (2003a) Aspects of the management of cheetahs, *Acinonyx jubatus jubatus*, trapped on Namibian farmlands. *Biological Conservation* 114: 401-412.

Marker LL, Mills MGL, Macdonald DW (2003b) Factors influencing perceptions of conflict and tolerance toward cheetahs on Namibian farmlands. *Conservation Biology* 17: 1290-1298.

Marker LL, Muntifering JR, Dickman AJ, Mills MGL, Macdonald DW (2003c) Quantifying prey preferences of free-ranging Namibian cheetahs. South African *Journal of Wildlife Research* 33: 43-53.

Marnewick KA, Hayward MW, Cilliers D, Somers MJ (2009) Survival of cheetahs relocated from ranchland to fenced protected areas in South Africa. In: Hayward MW, Somers MJ (eds) *The Reintroduction of Top-order Predators*, 282-306. Blackwell Publishing, Oxford, UK.

Marshall K, White R, Fischer A (2007) Conflicts between humans over wildlife management: on the diversity of stakeholder attitudes and implications for conflict management. *Biodiversity Conservation* 16: 3129-3146.

Mascia MB, Brosius JP, Dobson TA, Forbes BC, Horowitz L, McKean MA, Turner NJ (2003) Conservation and the social sciences. *Conservation Biology* 17(3): 649-650.

Mattson DJ, Byrd KL, Rutherford MB, Brown SR, Clark TW (2006) Finding common ground in large carnivore conservation: mapping contending perspectives. *Environmental Science & Policy* 9: 392-405.

Maude G, Mills MGL (2005) The comparative feeding ecology of the brown hyaena in a cattle area and a national park in Botswana. *South African Journal of Wildlife Research* 35: 201-214.

Mbaiwa JE, Ngwenya BN, Kgathi DL (2008) Contending with unequal and privileged access to natural resources and land in the Okavango Delta, Botswana. Singapore *Journal of Tropical Geography* 29: 155-172.

Mbaiwa JE, Stronza AL (2010) The effects of tourism development on rural livelihoods in the Okavango Delta, Botswana. *Journal of Sustainable Tourism* 18: 635-656.

Mech LD, Harper EK, Meier TJ, Paul WJ (2000) Assessing factors that may predispose Minnesota farms to wolf depredations on cattle. *Wildlife Society Bulletin* 28: 623-629.

Mertens A, Promberger C (2001) Economic aspects of large carnivore-livestock conflicts in Romania. *Ursus* 12: 173-180.

Miller B, Dugelby B, Foremen D, Martinez del Río C, Noss R, Phillips M, Reading R, Soulé ME, Terborgh J, Willcox L (2001) The importance of large carnivores to healthy ecosystems. *Endangered Species Update* 18: 202-210.

Mills MGL (1982) Factors affecting the movement patterns of brown hyaenas, Hyaena brunnea, in the southern Kalahari. *South African Journal of Wildlife Research* 12: 111-117.

Mills MGL (1990) *Kalahari Hyenas: the Behavioural Ecology of Two Species*. Chapman & Hall, London, UK.

Mills MGL (1991) Conservation management of large carnivores in Africa. *Koedoe* 34: 81-90.

Mills MGL (2005) Large carnivores and biodiversity in African savanna ecosystems. In: Ray JC, Redford KH, Steneck RS, Berger J (eds) *Large Carnivores and the Conservation of Biodiversity*, 208-229. Island Press, Washington, USA.

Mills MGL, Freitag S, Van Jaarsveld AS (2001) Geographic priorities for carnivore conservation in Africa. In: Gittleman JL, Funk SM, Macdonald DW, Wayne RK (eds) *Carnivore Conservation*, 467-483. Cambridge University Press, Cambridge, UK.

Mills MGL, Gorman ML (1997) Factors affecting the density and distribution of wild dogs in the Kruger National Park. *Conservation Biology* 11: 1397-1406.

Mills MGL, Hofer H (1998) *Hyaenas - Status Survey and Conservation Action Plan*. IUCN / SSC Hyaena Specialist Group, Gland, Switzerland and Cambridge, UK.

Mishra C (1997) Livestock depredation by large carnivores in the Indian trans-Himalaya: conflict perceptions and conservation prospects. *Environmental Conservation* 24: 338-343.

Mizutani F (1993) Home range of leopards and their impact on livestock on Kenyan ranches. *Symposia of the Zoological Society of London* 65: 425-439.

Mizutani F (1999) Impact of leopards on a working ranch in Laikipia, Kenya. *African Journal of Ecology* 37: 211-225.

Mogae FG (Hon) (1997) Key note. In: *Proceedings of a National Conference on Conservation and Management of Wildlife in Botswana. Strategies for the Twenty First Century*, 3-6. Department of Wildlife and National Parks and Kalahari Conservation Society, Gaborone, Botswana.

Mouritsen KN, Poulin R (2002) Parasitism, community structure and biodiversity in intertidal ecosystems. *Parasitology* 124: 101-117.

Nowell K, Jackson P (1996) *Wild Cats: Status Survey and Conservation Action Plan*. IUCN, Gland, Switzerland.

Nyhus P, Osofsky S, Ferraro P, Madden F, Fischer H (2005) Bearing the costs oh human-wildlife: the challenges of compensation schemes. In: Woodroffe R, Thirgood S,

Rabinowitz AR (eds) *People and Wildlife - Conflict or Coexistence?* 107-121. Cambridge University Press, Cambridge, UK.

Oates JF (1999) *Myth and Reality in the Rain Forest: How Conservation Strategies are Failing in West Africa*. University of California Press, Berkley, USA.

O'Brien SJ, Roelke ME, Marker L, Newman A, Winkler CA, Meltzer D, Colly L, Evermann JF, Bush M, Wildt DE (1985) Genetic basis for species vulnerability in the cheetah. *Science* 227: 1428-1434.

Ogada MO, Woodroffe R, Oguge NO, Frank LG (2003) Limiting depredation by African carnivores: the role of livestock husbandry. *Conservation Biology* 17: 1521-1530.

Ogara WO, Gitahi NJ, Andanje SA, Oguge N, Nduati DW, Mainga AO (2010) Determination of carnivores prey base by scat analysis in Samburu community group ranches in Kenya. *African Journal of Environmental Science and Technology* 4: 540-546.

Ogra M, Badola R (2008) Compensating human-wildlife conflict in protected area communities: ground-level perspectives from Uttarakhand, India. *Human Ecology* 36: 717-729.

O'Grady JJ, Brook BW, Reed DH, Ballou JD, Tonkyn DW, Frankham R (2006) Realistic levels of inbreeding depression strongly affect extinction risk in wild populations. *Biological Conservation* 133: 42-51.

Ogutu JO, Bhola N, Reid R (2005) The effects of pastoralism and protection on the density and distribution of carnivores and their prey in the Mara ecosystem of Kenya. *Journal of Zoology* 265: 281-293.

Oli MK, Taylor IR, Rogers ME (1994) Snow leopard *Panthera unica* predation of livestock: an assessment of local perceptions in the Annapurna Conservation Area, Nepal. *Biological Conservation* 68: 63-68.

Owen-Smith N, Mills MGL (2008) Predator-prey size relationships in an African large-mammal food web. *Journal of Animal Ecology* 77: 173-183.

Packer C, Pusey AE (1984) Infanticide in carnivores. In: Hausfater G, Hrdy SB (eds) *Infanticide: comparative and evolutionary perspectives*, 31-42. Aldine, New York, USA.

Packer C, Ikanda D, Kissui B, Kushnir H (2006) The ecology of man-eating lions in Tanzania. *Nature & Faune* 21: 10-15.

Packer C, Ikanda D, Kissui B, Kushnir H (2005) *Lion attacks on the rise*. http://www.nature.com/

Packer C, Pusey AE, Rowley H, Gilbert DA, Martenson J, O'Brien SJ (1991) Case study of a population bottleneck: lions of the Ngorongoro Crater. *Conservation Biology* 5: 219-230.

Palomares F, Caro TM (1999) Interspecific killing among mammalian carnivores. *The American Naturalist* 153: 492-508.

Patterson BD, Kasiki SM, Selempo E, Kays RW (2004) Livestock predation by lions (*Panthera leo*) and other carnivores on ranches neighboring Tsavo National Parks, Kenya. *Biological Conservation* 119: 507-516.

Peterson RO (1999) Wolf-moose interaction on Isle Royale: the end of natural regulation? *Ecological Applications* 9: 10-16.

Power ME, Tilman D, Estes JA, Menge BA, Bond WJ, Mills LS, Daily G, Castilla JC, Lubchenco J, Paine RT (1996) Challenges in the quest for keystones. *BioScience* 46: 609-620.

Primm SA, Clark TW (1996) Making sense of the policy process for carnivore conservation. *Conservation Biology* 10: 1036-1045.

Purchase GK, Marker L, Marnewick K, Klein R, Williams S (2007) Regional assessment of the status, distribution and conservation needs of cheetahs in southern Africa. In: Breitenmoser C, Breitenmoser U, Durant S (eds) *Status and Conservation Needs of Cheetahs in Southern Africa*, 44-46. IUCN/Cat Specialist Group, Gland, Switzerland.

Purvis A, Mace G M, Gittleman JL (2001) Past and future carnivore extinctions: a phylogenetic perspective. In: Gittleman JL, Funk SM, Macdonald DW, Wayne RK (eds) *Carnivore Conservation*, 11-34. Cambridge University Press, Cambridge, UK.

Rabinowitz A (1999) Nature's last bastions: sustainable use of our tropical forests may be little more than wishful thinking. *Natural History* 108: 70-72.

Rasmussen GSA (1999) Livestock predation by the painted hunting dog *Lycaon pictus* in a cattle ranching region of Zimbabwe: a case study. *Biological Conservation* 88: 133-139.

Reid RS, Nkedianye D, Said MY, Kaelo D, Neselle M, Makui O, Onetu L, Kiruswa A, Ole Kamuaro N, Kristjanson P et al. (2009) *Evolution of Models to Support Community and Policy Action with Science: Balancing Pastoral Livelihoods and Wildlife Conservation in Savannas of East Africa*. http://www.pnas.org/

Reyers B, Roux DJ, Cowling RM, Ginsburg AE, Nel JL, O'Farrell P (2010) Conservation Planning as a transdisciplinary process. *Conservation Biology* 24(4): 957-965.

Rhyan JC Spraker TR (2010) Emergence of diseases from wildlife reservoirs. *Veterinary Pathology* 47: 34-39.

Roelke ME, Martenson JS, O'Brien SJ (1993) The consequences of demographic reduction and genetic depletion in the endangered Florida panther. *Current Biology* 3: 340-350.

Sachedina H, Nelson F (2010) Protected areas and community incentives in savannah ecosystems: a case study of Tanzania's Maasai Steppe. *Oryx* 44: 390-398.

Saunders DA, Hobbs RJ, Margules CR (1991) Biological consequences of ecosystem fragmentation: a review. *Conservation Biology* 5: 18-32.

Scanlon LJ, Kull CA (2009) Untangling the links between wildlife benefits and community-based conservation at Torra Conservancy, Namibia. *Development Southern Africa* 26: 75-93.

Schiess-Meier M, Ramsauer S, Gabanapelo T, König B (2007) Livestock predation - insights from problem animal control registers in Botswana. *Journal of Wildlife Management* 71: 1267-1274.

Schwartz MK, Mills LS (2005) Gene flow after inbreeding leads to higher survival in deer mice. *Biological Conservation* 123: 413-420.

Scott ME (1988) The impact of infection and disease on animal populations: implications for conservation biology. *Conservation Biology* 2: 40-56.

Selebatso M, Moe SR, Swenson JE (2008) Do farmers support cheetah *Acinonyx jubatus* conservation in Botswana despite livestock depredation? *Oryx* 42: 430-436.

Seidensticker J, Christie S, Jackson P (1999) *Riding the Tiger. Tiger Conservation in Human-Dominated Landscapes*. Cambridge University Press, Cambridge, UK.

Shah U, Jaswal GS (1976) Victims of a rabid wolf in India: effect of severity and location of bites on development of rabies. *Journal of Infectious Diseases* 134: 25-29.

Sillero-Zubiri C, King AA, Macdonald DW (1996) Rabies and mortality in Ethiopian wolves (*Canis simensis*). *Journal of Wildlife Diseases* 32: 80-86.

Sillero-Zubiri C, Laurenson K (2001) Interactions between carnivores and local communities: conflict or co-existence? In: Gittleman JL, Funk SM, Macdonald DW, Wayne RK (eds) *Carnivore Conservation*, 11-34. Cambridge University Press, Cambridge, UK.

Slotow R (2012) Fencing for purpose: A case study of elephants in South Africa. In: Somers MJ, Hayward MW (eds) *Fencing for Conservation*, in press. Springer-US: New York.

Slotow R, Hunter LTB (2009) Reintroduction decisions taken at the incorrect social scale devalues their conservation contribution: the African lion in South Africa. In: Hayward MW, Somers MJ (eds) *Reintroduction of Top-Order Predators*, 43-71. Blackwell Publishing Ltd., Oxford, UK.

Stadler H (2006) Historical perspective on the development of problem animal management in the Cape Province. *Proceedings f a Workshop on Holistic Management of Human-Wildlife Conflict in the Agricultural Sector of South Africa. "Prevention is the Cure"!*,

11-17. The Conservation Breeding Specialist Group Southern Africa, Endangered Wildlife Trust, National Council of SPCAs, and Capenature, South Africa.

Stahl P, Vandel JM, Herrenschmidt V Migot P (2001) The effect of removing lynx in reducing attacks on sheep in the French Jura Mountains. *Biological Conservation* 101: 15-22.

Stander PE (1990) A suggested management strategy for stock-raiding lions in Namibia. *South African Journal of Wildlife Research* 20: 73-43.

Stander PE (1991) Demography of lions in Etosha National Park, Namibia. *Madoqua* 18: 1-9.

Stein AB, Fuller TK, Damery DT, Sievert L Marker LL (2010) Farm management and economic analyses of leopard conservation in north-central Namibia. *Animal Conservation* 13: 419-427.

Stuart CT (1986) The incidence of surplus killing by *Panthera pardus* and *Felis caracal* in Cape Province, South Africa. *Mammalia* 50: 556-558.

Sutherland WJ, Pullin AS, Dolman PM, Knight TM (2004) The need for evidence-based conservation. *Trends in Ecology and Evolution* 19(6): 305-308.

Swenson JE, Andrén H (2005) A tale of two countries: Large carnivore depredations and compensation schemes in Sweden and Norway. In: Woodroffe R, Thirgood S, Rabinowitz AR (eds) *People and Wildlife - Conflict or Coexistence?* 323-339. Cambridge University Press, Cambridge, UK.

Terborgh J (1999) *Requiem for Nature*. Island Press, Shearwater Books, Washington, DC, USA.

Thaker M, Vanak AT, Owen CR, Ogden MB, Niemann SM, Slotow R (2011) Minimizing predation risk in a landscape of multiple predators: effects on the spatial distribution of African ungulates. *Ecology* 92: 398-407.

Thirgood S, Woodroffe R, Rabinowitz A (2005) The impact of human-wildlife conflict on human lives and livelihoods. In: Woodroffe R, Thirgood S, Rabinowitz AR (eds)

People and Wildlife - Conflict or Coexistence? 13-26. Cambridge University Press, Cambridge, UK.

Traill LW, Brook BW, Frankham RR, Bradshaw CJA (2010) Pragmatic population viability targets in a rapidly changing world. *Biological Conservation* 143: 28-34.

Treves A, Karanth KU (2003) Human-carnivore conflict and perspectives on carnivore management worldwide. *Conservation Biology* 17: 1491-1499.

Treves A, Naughton-Treves L (1999) Risk and opportunity for humans coexisting with large carnivores. *Journal of Human Evolution* 36: 275-282.

Treves A, Naughton-Treves L (2005) Evaluating lethal control in the management of human-wildlife conflict. In: Woodroffe R, Thirgood S, Rabinowitz AR (eds) *People and Wildlife - Conflict or Coexistence?* 86-106. Cambridge University Press, Cambridge, UK.

Trinkel M, Fleischmann PH, Kastberger G (2006) Comparison of land-use strategies of spotted hyenas (*Crocuta crocuta*) in different ecosystems. *African Journal of Ecology* 44: 537-539.

Trinkel M, Funston PJ, Hofmeyr MD, Hofmeyr D, Dell S, Packer C, Slotow R (2010) Inbreeding and density-dependent population growth in a small, isolated lion population. *Animal Conservation* 13: 374-382.

Valeix M, Loveridge AJ, Davidson Z, Madzikanda H, Fritz H, Macdonald DW (2010) How key habitat features influence large terrestrial carnivore movements: waterholes and African lions in a semi-arid savanna of north-western Zimbabwe. *Landscape Ecology* 25: 337-351.

Van Bommel L, Bij de Vaate MD, De Boer WF, De Iongh HH (2007) Factors affecting livestock predation by lions in Cameroon. *African Journal of Ecology* 45: 490-498.

Van Dyk G, Slotow R (2003) The effects of fences and lions on the ecology of African wild dogs reintroduced to Pilanesberg National Park, South Africa. *African Zoology* 38: 79-94.

Van Orsdol KG, Hanby JP, Bygott JD (1985) Ecological correlates of lion social organisation (*Panthera leo*). *Journal of Zoology* 206: 97-112.

Watts HE, Holekamp KE (2009) Ecological determinants of survival and reproduction in the spotted hyena. *Journal of Mammalogy* 90: 461-471.

Waylen KA, Fischer A, McGowan PJK, Thirgood SJ, Milner-Gulland EJ (2010) Effect of local cultural context on the success of community-based conservation interventions. *Conservation Biology* 24(4): 1119-1129.

Weaver LC, Skyer P (2003) Conservancies: integrating wildlife land-use options into the livelihood, development, and conservation strategies of Namibian communities. *Animal Health and Development Forum. Fifth World Parks Congress*. Durban, South Africa.

Weber W, Rabinowitz A (1996) A global perspective on large carnivore conservation. *Conservation Biology* 10: 1046-1054.

Weiss JA (1989) The powers of problem definition: the case of government paperwork. *Policy Sciences* 22: 97-121.

Whitman K, Starfield AM, Quadling HS, Packer C (2004) Sustainable trophy hunting of African lions. *Nature* 428: 175-178.

Whitman KL, Starfield AM, Quadling H, Packer C (2007) Modeling the effects of trophy selection and environmental disturbance on a simulated population of African lions. *Conservation Biology* 21(3): 591-601.

Wilshusen PR, Brechin SR, Fortwangler CL, West PC (2002) Reinventing a square wheel: critique of a resurgent "protection paradigm" in international biodiversity conservation. *Society and Natural Resources* 15: 17-40.

Woodroffe R (2000) Predators and people: using human densities to interpret declines of large carnivores. *Animal Conservation* 3: 165-173.

Woodroffe R (2001) Strategies for carnivore conservation: lessons from contemporary extinctions. In: Gittleman JL, Funk SM, Macdonald DW, Wayne RK (eds) *Carnivore Conservation*, 61-92. Cambridge University Press, Cambridge, UK.

Woodroffe R (2010) Ranging Behaviour of African Wild Dog Packs in a Human-Dominated Landscape. *Journal of Zoology* 283(2): 88-97.

Woodroffe R, Cleaveland S, Courtenay O, Laurenson MK, Artois M (2004) Infectious disease in the management and conservation of wild canids. In: Macdonald DW, Sillero-Zubiri C (eds) *The Biology and Conservation of Wild Canids*, 123-142. Oxford University Press, Oxford, UK.

Woodroffe R, Frank LG (2005) Lethal control of African lions (*Panthera leo*): local and regional population impacts. *Animal Conservation* 8: 91-98.

Woodroffe R, Ginsberg JR (2005) King of the beasts? Evidence for guild redundancy among large mammalian carnivores. In: Ray JC, Redford KH, Steneck RS, Berger J (eds) *Large Carnivores and the Conservation of Biodiversity*, 154-158. Island Press, Washington, USA.

Woodroffe R, Lindsey P, Romañach S, Stein A, ole Ranah SMK (2005a) Livestock predation by endangered African wild dogs (*Lycaon pictus*) in northern Kenya. *Biological Conservation* 124: 225-234.

Woodroffe R, Thirgood S, Rabinowitz A (2005b) The impact of human-wildlife conflict on natural systems. In: Woodroffe R, Thirgood S, Rabinowitz AR (eds) *People and Wildlife - Conflict or Coexistence?* 1-12. Cambridge University Press, Cambridge, UK.

Woodroffe R, Frank LG, Lindsey PA, ole Ranah MK, Romañach S (2007a) Livestock husbandry as a tool for carnivore conservation in Africa's community rangelands: a case-control study. *Biodiversity Conservation* 16: 1245-1260.

Woodroffe R, Lindsey P, Romañach S, ole Ranah SMK (2007b) African wild dogs (*Lycaon pictus*) can subsist on small prey: implications for conservation. *Journal of Mammalogy* 88: 181-193.

Worm B, Duffy JE (2003) Biodiversity, productivity and stability in real food webs. *Trends in Ecology and Evolution* 18: 628-632.