A Comparative Analysis of Felid Conservation Strategies on four Continents:
Can one size fit all?

by

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Abstract

Large felid species are facing persistent population declines across the globe in the face of altered landscapes and behaviors due to human expansion. These species have many ecological roles that can be significant in ecosystem structure and functioning. Carnivores enforce ecological boundaries and control prey and mesopredator populations, as well as influence community structure and diversity. Large carnivores often function as keystone species, but can also act as effective umbrella species in which their conservation will benefit a plethora of other vertebrate species. Large carnivores need large areas of habitat, and have large ranging behavior and other ecological traits that cause conflict with humans and interferes with their conservation. Increasing human population and urbanization contributes to habitat loss and fragmentation, and a cascade of negative effects on carnivores including decreased genetic diversity and increased mortality. The conservation of large carnivores is paramount due to their persistent declines, and their significant impact on other species and ecosystems. I discuss the conflict and conservation of four large carnivore species on four different continents, the mountain lion Puma concolor in North America, the jaguar Panthera onca in South America, the lion Panthera leo in Africa, and the snow leopard Panthera uncia in Asia. I conduct an extensive literature review and comparative analysis of these four species on their ecological traits, ecosystem, geographical area and culture, and past conservation strategies. I underline the need for individual assessments of species and their surrounding landscape and culture to identify species-specific or global strategies when considering land management and conservation strategies. These strategies take a comprehensive approach that combines biological field research and models, socio-environmental programs, and policy changes. I propose the utilization of a landscape connectivity model for all large carnivore species in conjunction with the analysis of spatial-temporal movements to identify areas of most and least concern for future management practices and carnivore conservation. I also highlight a number of preventative workshops and social programs to mitigate conflict and develop positive relationships with carnivores, and propose a modification in policy to reduce genetic losses within species. Taken together these steps have the potential to stabilize large cat populations into the future, and reinforce the ecological boundaries they construct in ecosystems, benefitting ecosystems across the globe.

Introduction

Carnivores are an essential component of ecosystems, and their effects on other species and landscapes are far-reaching (Miller *et al*., 2001). The overlapping home ranges of carnivores with human activity and expansion creates human-carnivore conflict that is resulting in the decline of many carnivore species (Goodrich *et al*., 2015; Bauer *et al*., 2016). Increasing human population and urbanization contributes to habitat loss and fragmentation, conflicting with carnivores' large home ranges, and resulting in increased conflict between humans and carnivores. This human-carnivore conflict is prevalent throughout the globe in varying ecosystems, among a large range of species including felids, canids, ursids, and others (Kissui, 2008; Kellert *et al*., 1996). This conflict has existed for centuries, but increasing human populations compounds the conflict and its effects, and it is now escalating to points in which many large carnivore species are threatened, endangered, or have already fallen to extinction (Cardillo *et al*., 2004). Over three-fourths of large carnivore populations are declining across the globe, and these declines often produce a trophic cascade on ecosystems, and that can have detrimental effects on ecosystem structure and functioning (Ripple *et al*., 2014). These altered landscapes and increased contact and conflict between humans and carnivores results in livestock depredations and other conflicts and leads to animosity and retaliatory killings. Large carnivores are facing stressors from all angles as increasing human population and expansion negatively

impacts their ecosystems, populations, and behaviors, resulting in human-carnivore conflict that is disadvantageous to their survival.

Urbanization and human population growth is a catalyst to a cascade of negative effects on carnivores. With urbanization comes habitat loss and degradation, habitat fragmentation, edge effects, and decreased gene flow. All of these effects affect carnivore movements, reduce access to resources, and over time, reduce genetic diversity. Such stressors also affect carnivore behavior and increase intraspecific strife (Balme *et al*., 2010). The combination of these effects of human population growth greatly reduces carnivore populations. With humans and carnivores sharing the same habitat there is an increase in livestock depravation, retaliatory killings, poaching, trophy hunting, and poisonings (Kissui, 2008, Packer *et al*., 2009, Packer *et al*., 2010). Layered on top of these negative impacts on carnivore populations are social issues that perpetuate them. Limited education results in people not recognizing the ecological role of carnivores in ecosystem functioning, and negative attitudes towards carnivores (Zimmerman *et al*., 2005). In some cases, cultural norms perpetuated biases against carnivores and promoted the widespread killing of carnivores (Zimmerman *et al*., 2005). The impact of this anthropogenic litany has changed behavior, reduced reproductive success and genetic diversity, and caused significant declines in carnivore populations. Taken together, effective carnivore conservation must recognize and incorporate 1) the effects human populations have had on changing landscapes and the environment, 2) the direct impacts of human-carnivore conflicts, and 3) the contribution of social and cultural aspects.

The negative effects of human population growth on carnivore populations have implications on the ecosystem functioning due to the ecological roles carnivores hold in ecosystems. Ecosystems have many parts within the whole, with each species playing a role, however small or vital that may be. The role of a species in the functioning of an ecosystem differs depending on the strength of their input into the system. Large carnivores shape ecosystems through top-down regulation, acting as apex predators and keystone species (Wang *et al*., 2014; Anderson *et al*., 2006; Mills *et al*., 1993). The presence of carnivores indirectly influences the behavior of herbivores and other species, which can lead to a cascade of effects throughout trophic levels and the ecosystem as a whole (Miller *et al*., 2001). Large carnivore populations also have a regulatory effect on smaller carnivores and prey species by keeping their populations in check; and in the absence or decline of large carnivores, mesopredator release could suppress prey populations (Berger & Conner, 2008). Thus, carnivores are a vital component of the structure and functions of ecosystems. The visible decline in large carnivore populations throughout the globe emphasizes the immense need to mitigate human-carnivore conflict and implement successful carnivore conservation strategies.

The importance of identifying successful conservation strategies of carnivore species and their populations is substantial. Human-carnivore conflict continues to increase in response to complex environmental problems that are associated with human population growth and expansion. The behaviors and ecological traits of large carnivores make them extremely vulnerable to extinction. When this innate vulnerability is combined with the present altered landscapes and conflict with humans, it results in a cascade of implications for their conservation. In recent years, the majority of human-carnivore conflict arises when the livelihoods of individuals or communities are threatened by livestock depredations. (Balme *et al*., 2009; Kellert *et al*., 1996; Kissui, 2008; Mishra, 1997). The prevalence of human-carnivore conflict exists across species, geographical boundaries, and cultures across the globe. As a result, it is imperative to recognize and consider the interests of each group in order to successfully implement conservation strategies. Governments must consider the demands of both its citizens and its carnivores, and develop strategies that benefit both populations.

Thus, a way forward could be to analyze conflicts between humans and large carnivore species across the globe and examine diverse conservation strategies already in place to identify which strategies are successful at increasing carnivore populations. To that end, I will review the large carnivore literature to determine what we know and where the hole in knowledge lays. Though there is considerable research and data on the conservation of large felids, the majority focuses on specific species and regions or other large carnivore species, leaving a gap in

knowledge and management applications. Second, I will synthesize literature on the conservation of similar large carnivore species to identify possible global management strategies. Lastly, I will incorporate the results from biological and social research conducted this past summer in the Maasai Steppe, Tanzania. This comparative analysis approach has the potential to identify key areas to focus on, and to utilize conservation strategies that have been successfully applied elsewhere to species and regions on a global scale. This analysis combines personal research in Africa with known literature to conduct a comparative analysis of large carnivore species across the globe, with a focus on cougars in North America, jaguars in South America, lions in Africa, and snow leopards in Asia, to explore the possibility of global conservation strategies.

Large carnivore populations are extremely vulnerable and have been declining across the globe as a result of complex ecosystem responses to increasing human population growth and urbanization. It is imperative to compare these large carnivore species to find commonalities in one species in one region that could apply to another species in another region. This comparison also identifies strategies that are not transferrable due to ecology, geography, or culture**.** Through this comparative analysis, emergent properties that could be effective for the conservation of all large felids will be identified, or those which are nontransferable, and management strategies could be modified accordingly. This information has the potential to decrease human-carnivore conflict, increase large carnivore populations, and positively impact threatened ecosystems on a global scale.

Human-Carnivore Conflict

Mountain Lions (Puma concolor)

In North America the distribution of mountain lions has been reduced by over two-thirds of its historical range (Pierce & Bleich, 2003). Before colonization and urbanization, mountain lions had the largest distribution of any carnivore in the Western Hemisphere (Clark *et al*., 2013). Mountain lions are not as infamous as other large felids and carnivores for their conflict and depredations; nor are they as sought after for trophies or Eastern medicine. Human-caused mortality is the leading cause of death for this species, with legal hunting accounting for the majority of the deaths (Clark *et al*., 2013).

Following colonization, mountain lions, like many of the carnivores native to the West, were persecuted relentlessly and viewed as a threat to human life and livelihoods (Clark *et al*., 2013). Hunting quotas for mountain lions were established in the 1970s when public concern for carnivores began to grow, and mountain lion populations have begun to rebound in many states, however, the overall population trend is still decreasing (Clark *et al*., 2013; Bauer *et al*., 2016). Like many other felids, they are elusive and hard to study in the field; which leads to concerns over the accuracy of population estimates and hunting quotas, creating implications for their population survival. Further, the Game and Fish Departments of states tend to determine wildlife management and the content of public discourse, which can lead to portions of the public left out of decision making, driving a wedge between communities and conservation (Clark *et al*., 2013).

Habitat fragmentation and loss of connectivity are of extreme concern as mountain lion populations become genetically isolated in the face of human expansion (Riley *et al*., 2014). Riley *et al*. (2014) studied a subpopulation of mountain lions that were genetically isolated due to a highway, and as a result, genetic diversity and dispersal were decreased, and inbreeding and intraspecific strife increased. In this case, intraspecific strife was the most common cause of mortality in the population; originally caused by habitat fragmentation, which impeded dispersal, decreasing genetic diversity and causing the associated intraspecific strife (Riley *et al*., 2014). Habitat fragmentation and the associated repercussions such as losses in connectivity, genetic diversity, and inbreeding has serious implications for the conservation of mountain lion populations.

Jaguars (Panthera onca)

In South America, jaguars have lost approximately half of their historical range in the last century, and their population has declined more than 25% in the last 21 years (Quigley *et al*., 2017). The jaguar is viewed as a symbol of wealth and power, as are many of the large felids, and consequently were hunted to extreme lengths before the establishment of CITES in 1973. Their current primary threat is habitat fragmentation and the resulting conflict that occurs. The loss of connectivity between populations reduces genetic exchange, increases genetic drift and inbreeding, which then reduces fitness and compromises the success of sub-populations and the species as a whole (Rabinowitz & Zeller, 2010).

Humans perceive jaguars as dangerous predators that hunt people and livestock. Conflict with jaguars has continued to rise in South America in conjunction with cattle production and the prevalent ranching industry (Weber & Rabinowitz, 1996; Woodroffe *et al*., 2005). Increasing habitat fragmentation and cattle production increases livestock depredations and conflict between jaguars and humans, resulting in further persecution of jaguars (Weber & Rabinowitz, 1996). However, livestock losses that blamed on jaguars are in actuality often due to disease, flooding, and theft (Weber & Rabinowitz, 1996). Further, in comparison to other large felids, there are few records of fatal jaguar attacks on people (Woodroffe *et al*., 2005). It is due to fear of human attacks and livestock depredations that many ranchers and communities directly oppose jaguar protection and conservation. The lack of communication and relationships between the native people, government, and NGOs leads to disagreements on the course of action towards jaguar conservation (Woodroffe *et al*., 2005).

Lions (Panthera leo)

In Africa, lions have lost approximately 83% of their historical distribution range in the last century, and their population has declined more than 43% in the last 27 years (Ray *et al*., 2005; Bauer *et al*., 2016). The ecology of carnivores affects the level of retaliation, due to traits that make them less or more vulnerable. Lions are extremely vulnerable to retaliatory killing due to their diurnal nature and their tendency to defend carcasses (Kissui, 2008). In contrast to leopards who are solitary and elusive, or hyenas who are nocturnal and do not protect their kills (Kissui, 2008). As a result, lions are consequently blamed for the majority of livestock depredations. In actuality, lions account for only roughly twenty-five percent livestock depredations, and hyenas are responsible for the majority at fifty-eight percent (Kissui, 2008). Additionally, livestock depredations occur more in the wet season than the dry season due to migrating prey species that overlap with villages and communities, leading to increased conflict (Kissui, 2008).

Pastoralism is prevalent in Africa, and overlap between livestock and lion populations exists even in protected areas. Lions tend to predate more upon cattle than other livestock and predators. Unfortunately, cattle have the highest value among the livestock and therefore the economic loss is higher (Kissui, 2008). Further, cattle are a symbol of wealth and identity in the local Maasai culture, therefore cattle depredations can incite retaliation more than any other livestock as they are viewed as an attack on their identity and status (Kissui, 2008). Kissui (2008) found that one-hundred percent of predations by lions led to retaliatory lion hunts, signifying the necessity in conflict mitigation strategies to reduce depredations and retaliatory killings. Further, lion hunting is a traditional act of coming to manhood for the Maasai, and though it has been banned, some communities still practice it. Built upon that tradition, retaliatory lion hunts are an opportunity to showcase bravery, giving a higher incentive to participate (Kissui, 2008). The ecology of lions as well as the cultural and social practices of the local people make lions extremely vulnerable to retaliatory killings and threatens their conservation.

Trophy hunting poses an exceptional risk to lion populations due to their ecology, with the extensive paternal investment and cub mortality during male replacement (Packer *et al*., 2009). Mortality from state-sanctioned trophy hunting as well as illegal poaching has greatly contributed to the population decline of lions (Packer *et al*., 2009). Trophy hunting accounts for the majority of lion mortality (Packer *et al*., 2009). A ten percent harvest can result in a future fifty percent population decline in lions depending on age, and lion harvests have reached thirty percent some years (Packer *et al*., 2010). This practice has significant repercussions on pride populations and dynamics as replacement males kill all cubs and the breeding clock is set back.

Compounding the effects of the removal of male lions and their genes from the population, habitat fragmentation decreases connectivity and gene flow between populations. Fragmentation reduces the capability of male lions to disperse and successfully transfer their genes into other populations. The decreased genetic diversity then leads to inbreeding depression and increases their susceptibility to disease (Cushman *et al*., 2015; Packer *et al*., 2009). The Ngorongoro Crater in Tanzania is an example of a population bottleneck, with decreased genetic diversity and increased inbreeding from a lack of successful male immigration into the Crater since the 1960s (Packer *et al*., 1991; Kissui & Packer, 2004). Continuous disease outbreaks in Crater lion populations including canine distemper virus and *Stomoxys* further exemplifies the lack of genetic diversity leading to increased vulnerability to disease (Kissui & Packer, 2004).

Lions are exceptionally vulnerable to human-carnivore conflict due to their ecological traits, social and cultural relationships, as well as the migratory nature of their prey that leads to more overlap with human populations and increased potential for conflict. Trophy hunting poses an exceptional risk to this species due to the paternal investment and cub mortality following male replacement. Increasing human population and urbanization is further fragmenting habitat and decreasing connectivity, leading to decreased genetic diversity and increased vulnerability to disease and inbreeding depression.

Snow Leopards (Panthera uncia)

In Asia, snow leopards have lost over two-thirds of their historical range and a 20% population decline in the last two decades, and an additional 10% is expected in the coming decade (McCarthy *et al*., 2017; Lyngdoh *et al*., 2014). The decline in native-prey abundance and the resulting shift in prey preference towards livestock has negative implications for snow leopard conservation (Mishra, 1997). Conflict mitigation strategies will be difficult to implement due to the snow leopard's reliance on livestock in its diet, however, local perceptions towards carnivore conservation will likely prove to be a valuable resource.

Pastoralism is dominant in India, with a large number of pastoralists living within national parks and protected areas. Livestock grazing occurs in over seventy percent of wildlife sanctuaries and forty percent of national parks, increasing the likelihood of depredations (Mishra, 1997). Livestock populations greatly outnumber native ungulates, and these disproportionate populations increase the likelihood of depredations and therefore human-carnivore conflict. Mishra (1997) found that livestock were preyed upon at a frequency proportional to their relative abundance. Conflict between carnivores and the agro-pastoralists present in the Trans-Himalayas is high due to the high densities of livestock populations and consequent depredations; however, the snow leopard is not the carnivore that is primarily persecuted (Mishra, 1997). Wolves have been driven to extirpation, locals simply drive snow leopards away from livestock kills, with only one accidental death of a snow leopard reported (Mishra, 1997).

In some regions of the Trans-Himalayas, the human population is remaining constant, but the conflict with snow leopards is increasing (Mishra, 1997). This increase in conflict can be explained by the increase in pastoralism and livestock populations, and a decrease in prey populations, which causes a shift in the carnivore diet that contributes to conflict (Mishra, 1997). Snow leopards are dependent upon livestock for over half of their diet; emphasizing a dependence on a practice that is detrimental to their conservation (Bagchi & Mishra, 2006). With livestock depredations accounting for more than a quarter of household income in some regions, relationships with snow leopards are negative (Olie *et al*., 1994). Snow leopards are also immediately blamed for livestock losses, similar to lions and jaguars, though the actual cause can be unknown or unfounded (Mishra, 1997; Kissui, 2008; Weber & Rabinowitz, 1996). However, unlike other large felids, snow leopards are increasingly dependent on livestock in their diet and are responsible for a large proportion of depredations and conflict in the Trans-Himilayas (Bagchi & Mishra, 2006).

Unlike other large felids, snow leopards are not actively persecuted or retaliated against, but they are responsible for the majority of livestock depredations (Bagchi & Mishra, 2006; Mishra, 1997). Local attitudes towards snow leopards are distinctly different than previously seen with lions but somewhat similar to jaguars. There was an overall positive attitude towards the conservation of snow leopards and protected areas, though thirty percent of respondents had a negative attitude (Bagchi & Mishra, 2006). Unlike many other regions and carnivore species, snow leopards are not actively persecuted in the Trans-Himilayas (Bagchi & Mishra, 2006; Mishra, 1997). However, local attitudes still do not entirely support the conservation of snow leopards (Bagchi & Mishra, 2006). Increasing animal husbandry has negatively affected native ungulate populations, leading to a disproportionate ratio of livestock to native ungulates in the Trans-Himalayas that has altered snow leopard hunting and diet. The shift in the snow leopard's diet has strong implications for its conservation, with the reliance on livestock depredations making reducing conflict exceedingly difficult.

Large Felids

Though this literature review focuses on just four species of large felids, they exhibit the continuous decline of large carnivores and the urgent necessity for the improvement of conservation strategies based upon the ecological traits of species, and the needs and cultures of

the communities in conflict with them. Increasing human population, urbanization, and pastoralism increases the opportunity for conflict, as well as interfering with carnivore dispersal methods, gene flow, and prey availability. Carnivores are exceptionally vulnerable to habitat fragmentation and its effects on genetic diversity. The survival of wildlife populations strongly depends not only on the surrounding environmental conditions, but also the social, political, and economic conditions of surrounding human communities.

Ecological Role of Large Carnivores

Members of the order Carnivora fulfill important ecological roles through density-mediated and trait-mediated direct and indirect effects that control species populations, influence prey behavior, biodiversity, and landscape (Ordiz *et al*., 2013). They do this through top-down regulation and trophic cascades in ecosystems and the promotion of prey species diversity (Wang *et al*., 2014). This top-down regulation can show how carnivores have some of the smallest populations, but exert the strongest influence on ecosystem functions and biodiversity (Mills *et al*., 1993). With top-down regulation, carnivores control herbivore populations, which in turn control plant biomass (Miller *et al*., 2001). Additionally, carnivores suppress mesopredator populations directly through lethal encounters, and indirectly through instilling fear and changing mesopredator behaviors (Ritchie & Johnson, 2009). This paradigm exhibits the strong interactions between trophic levels, and the strength that carnivores have at the top of the system to erect and enforce ecological boundaries, and generate trophic cascades.

Impacts of carnivores on prey and landscape/Top-down regulation

Top-down regulation results in trophic cascades through both direct and indirect behaviors and relationships between prey and carnivores. Trophic cascades can occur through the direct predation of prey by predators, influencing the population dynamics of herbivores, which in turn influences the plant trophic level (Anderson *et al*., 2006; Miller *et al*., 2001). Trophic cascades can also occur indirectly through predator presence limiting the foraging behaviors of herbivores, influencing other species behaviors and affecting plant biomass (Anderson *et al*., 2006).

Herbivores play a key role in creating the landscape of ecosystems through migratory patterns as well as their foraging behavior. As a result, if their populations move past carrying capacity, they will deplete the landscape until their population crashes, creating devastating effects on the ecosystem. The presence of carnivores impact prey indirectly through influencing their foraging behavior and movements, and directly by regulating prey populations (Miller *et al*., 2001; Noss *et al*., 1996). The absence of jaguars and cougars on an island resulted in the population densities of rodents, monkeys, iguanas, and leaf-cutter ants to increase dramatically. This negatively affected seedling and saplings of canopy trees – altering the landscape and exhibiting a trophic cascade that occurred due to the absence of large carnivores (Terbough *et al*., 2001). Further, Pierce *et al*. (2012) found that top-down regulation of mule deer by mountain lions was visible from deer selecting habitat that reduced predation and increased forage benefits. Strengthening the assessment of top-down regulation, food was not found to be a limiting factor for mule deer populations during population growth, and mountain lion predation was the most significant contributor to deer mortality during the increase (Pierce *et al*., 2012). Large carnivores have density-mediated lethal effects through their predation on prey populations, and have trait-mediated behavioral effects that influence prey behavior and habitat use.

Top-down control is crucial in ecosystem functioning, and predator removal significantly increases herbivore populations and plant damage and decreases plant biomass and reproductive output (Schmitz *et al*., 2000). The trophic cascade that occurred in Yellowstone National Park after the reintroduction of wolves exhibited the influence of carnivores and the strength of herbivore behavior on landscapes and ecosystems. The lack of predators influenced the foraging

behavior of herbivores in the national park, allowing for heavy browsing behavior, and resulted in the decreased biomass of quaking aspen (Ripple *et al*., 2001). In contrast, the reintroduction of wolves into Yellowstone National Park affected the behavioral responses of herbivores through increased vigilance and caused a shift in foraging behavior that increased quaking aspen abundance (Laundre *et al*., 2001). The reintroduction of a large carnivore into its ecosystem re-established a "landscape of fear", and the resulting behavioral responses were likely much more powerful than direct predation (Laundre *et al*., 2001). Carnivores play a crucial role in influencing the behavior of abundant prey species that have the ability to fundamentally change the structure and function of landscapes and ecosystems.

Further, carnivores construct ecological boundaries through their predation on dominant prey species, reducing competition between prey species and allowing less abundant species to persevere (Miller *et al*., 2001). Therefore, carnivores increase diversity among prey species and reduce the likelihood of competitive exclusion (Miller *et al*., 2001). In contrast, when the number of available prey species are reduced, the links between predator and prey are fewer and stronger (Miller *et al*., 2001). The stronger dependence on fewer prey species leads to destabilization and a system that is weaker than one with more prey species and therefore more links (Miller *et al*., 2001). Carnivores facilitate biodiversity and natural selection through density-mediated consumptive effects of their predation, enforcing natural selection. The decline or extinction of large carnivores will remove these ecological boundaries that are fundamental in the construct of predator-prey and prey-prey relationships that determine the diversity of species present in an ecosystem, as well as the structure and function through the landscape and ecosystem (Miller *et al*., 2001).

The benefit of top-down regulation by lions can be seen with increased biodiversity leading to increased adaptive potential in zebras. Prey species that are most influenced by top-down regulation are more resistant to environmental stressors than those that are limited by food availability (Grange & Duncan, 2006). This effect was visible in zebra populations by African lions during a drought, in comparison to other ungulates that were less influenced by top-down control (Grange & Duncan, 2006). Ecosystems that have conserved populations of large carnivores tend to support native vegetation, diverse native species, and historical ecological processes, supporting biodiversity and the integrity of ecosystems (Noss *et al*., 1996). These ecosystems exemplify the benefits and importance of carnivore conservation.

Predation beginning at large carnivores produces trophic cascades from the top-down that have extensive impacts on a variety of levels within an ecosystem, ranging from individual behaviors to system dynamics (Estes *et al*., 2011). Large carnivores have a multitude of density-mediated and trait-mediated effects that can create trophic cascades, and influence fundamental structures and processes of ecosystems (Ordiz *et al*., 2013). It is critical to consider the impact that carnivores have on the landscape and habitats as well as species diversity within an ecosystem, otherwise, the structure and function of ecosystems will be irreparably altered (Miller *et al*., 2001). Landscapes with large carnivores and an intact food web have a high potential for ecological integrity, making carnivores essential tools when considering conservation of individual species, as well as entire systems (Noss *et al*., 1996).

Impacts of carnivores on mesopredators

Similar to the trophic cascade seen with top-down regulation, a behaviorally mediated trophic cascade can be seen with mesopredator control and release by carnivores (Ritchie & Johnson, 2009). Large carnivores control and regulate smaller carnivores or "mesopredator" populations both directly and indirectly. Large carnivores have two motivations to kill mesopredators: predation for food, or interspecific predation to reduce competition (Ritchie & Johnson, 2009). Mesopredator behavior changes in the presence of large carnivores through avoidance, impacting the distribution and abundance of both mesopredator and prey species (Miller *et al*., 2001; Noss *et al*., 1996).

The effect of predation by large carnivores on mesopredators influences the population dynamics and demographics of mesopredator populations (Ritchie & Johnson, 2009). The avoidance of large carnivores by mesopredators creates habitat and prey restrictions. These restrictions affect the reproduction and reduce mesopredator populations, even without active predation by carnivores (Sergio & Hiraldo, 2008) Direct predation as well as altered behavior due to the presence of large carnivores has kept African wild dog population densities low in Africa (Gorman *et al*., 1998). Hyenas and lions actively steal prey from African wild dogs, forcing them to increase their hunting efforts and energy output (Gorman *et al*., 1998). The combination of direct predation by large carnivores and indirectly altered behaviors, has caused the distribution and abundance of African wild dogs to be suppressed (Gorman *et al*., 1998). A similar effect has been observed with cheetahs (Durant, 2000). Further, mountain lions have accounted for roughly twenty percent of coyote mortality (Berger & Geese, 2007). Large carnivores effectively control mesopredator populations through the density-mediated lethal and consumptive effects, and through trait-mediated behavioral effects that enforce habitat and prey restrictions.

Large carnivores are more successful at regulating and suppressing prey populations than smaller carnivores. Mesopredators are more opportunistic predators than large carnivores, which have more specialized prey preferences (Noss *et al*., 1996). Mesopredators are less effective predators of large ungulates and more effective predators of smaller prey populations, and mesopredator release has implications on the populations of prey species and the resulting effects on the ecosystem. (Wilmers *et al*., 2007; Noss *et al*., 1996). Wilmers *et al*. (2007) found that mountain lions were more effective at the regulation and suppression of deer populations than mesopredators such as coyotes. Though mesopredators are less successful at regulating larger prey populations, they are exceedingly successful in decimating smaller prey populations, such as songbirds (Soulé *et al*., 1988). The absence of large carnivores can allow mesopredator populations to greatly increase predation pressure on smaller prey species, leading to a decrease in diversity (Ritchie & Johnson 2009; Terbough & Estes, 2010). The increased predation pressure leads to prey population declines, which negatively affect community structures (Brashares *et al*., 2010; Miller *et al*., 2001). Further, large carnivores are exceptionally effective at controlling mesopredator populations in landscapes with habitat fragmentation, which has and will continue to increase in the coming years (Noss *et al*., 1996). Mesopredators are ineffective at regulating larger prey populations, and therefore cannot perform top-down control on an ecosystem as successfully as large carnivores; which has implications on the structure and function of ecosystems (Wilmers *et al*., 2007).

Mesopredators are opportune and generalist predators, and have a strong capacity to reach high population densities, exert high predation pressure on a wide range of prey species, and decrease biodiversity in the decline or absence of large carnivores (Ritchie & Johnson, 2009). Large carnivores regulate mesopredator populations and behaviors, restore historical ecological processes, and support biodiversity (Ritchie & Johnson, 2009). The decline of large carnivores can allow for mesopredator populations to increase, which can result in a decline of prey populations, and affect community structures (Brashares *et al*., 2010; Miller *et al*., 2001). Mesopredator suppression by large carnivores has extensive impacts on biodiversity within an ecosystem, as well as the capability to shape the landscape through influencing mesopredator behavior and populations both indirectly and directly (Ritchie & Johnson, 2009; Noss *et al*., 1996; Miller *et al*., 2001).

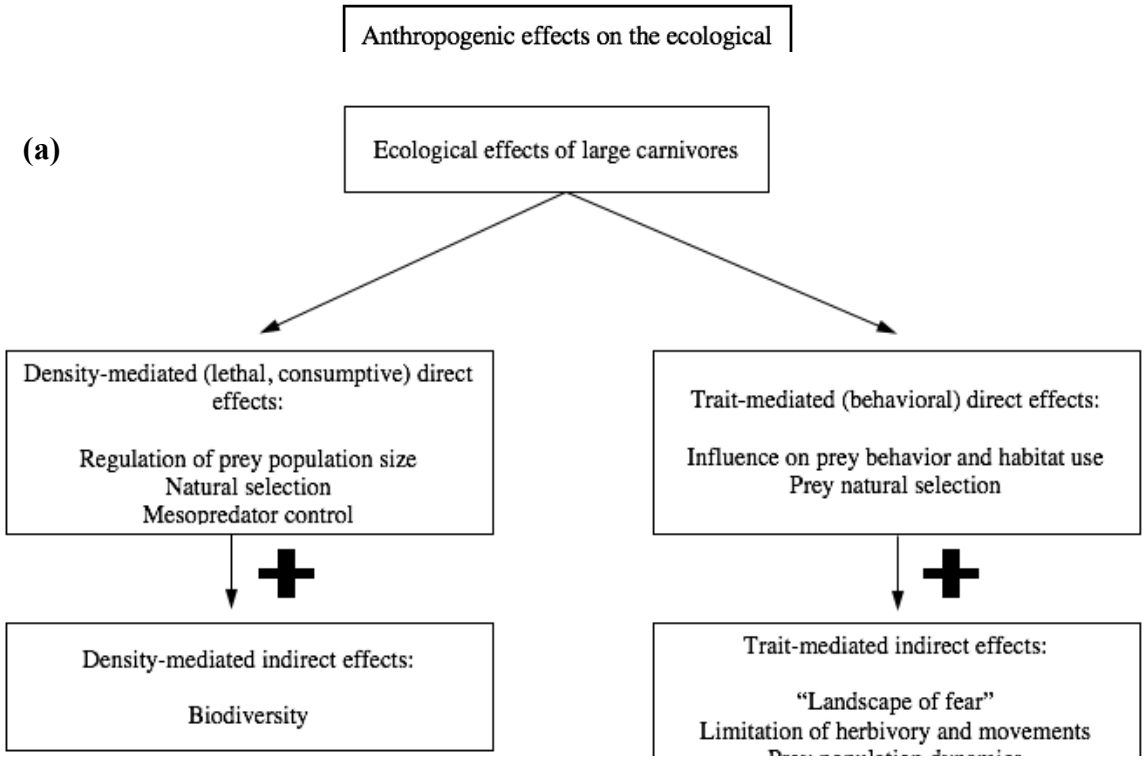

Figure 1. (a) Large carnivores' direct and indirect ecological effects on ecosystems. (b) Reduced ecological effects of carnivores from anthropogenic influences.

Large carnivores fill a variety of roles and ecological niches that make them imperative to the structure and function of ecosystems. Their presence and predatory behavior enforce top-down regulation and influence the landscapes of ecosystems to a degree that supports ecosystem function and biodiversity. Further, the decline or removal of large carnivores and their associated density-mediated and trait-mediated direct and indirect effects on mesopredators can have detrimental effects on population dynamics and diversity in prey species. Large carnivores are essential for the structure and function of ecosystems, with their presence, ecological traits, and behaviors shaping the landscape and food webs. The decline and loss of large carnivores will have major implications on biodiversity and the integrity of ecosystems.

Conservation Strategies

Conservation strategies take many forms and cover many topics. Here I will limit my discussion to strategies that have been applied to the species in this review. First, I will review the ecology of carnivores and wildlife corridors as a strategy to decrease human-carnivore conflict and improve dispersal patterns. Second, I will focus on socio-environmental strategies to decrease conflict and improve tolerance of carnivores. Third, I will discuss changes in wildlife management and policy that could conserve carnivores. Lastly, I will define carnivores as umbrella species, that could effectively conserve other species and ecosystems.

Increasing human populations and urbanization that further fragments landscapes creates a cascade of negative implications for carnivore populations. Conservation strategies that focus on increasing connectivity is key to restoring and conserving populations. Due to the extensive home ranges of carnivores, isolated and large protected areas and reserves protect a minimal amount of individuals, and cannot support a viable population without dispersing individuals (Noss *et al*., 1996). Dispersal methods are a fundamental aspect of carnivore ecology and are vital to their genetic diversity, reproduction, population, and species survival. Dispersing males can perform demographic and genetic rescue for a variety of carnivores including lions, grizzlies, wolves, and panthers (Noss *et al*., 1996; Pimm *et al*., 2005; Riley *et al*., 2004). Establishing wildlife corridors and creating a viable network to promote movement is, therefore, crucial for the dispersal and conservation of large carnivores. Wildlife corridors both increase animal movements and links populations through decreasing barriers, while also decreasing human-carnivore conflict (Noss *et al*., 1996). Rabinowitz & Zeller (2010) created a model of landscape connectivity and identified areas of most and least concern for promoting movement of jaguars.

Preventative management strategies are often the most effective strategy for reducing human-carnivore conflict. These strategies include informational workshops that promote alternative husbandry practices such as predator-proof boma constructions, guard placement, and the rapid disposal of livestock carcasses (Balme *et al*., 2009). Further, educational programs can foster tolerance and build relationships with the environment and carnivores. In South America involving jaguar conservation, workshops have been introduced to foster relationships and give each stakeholder a voice; and in response, ranchers began to express their ideas on management strategies and how to mitigate conflict (Woodroffe *et al*., 2005). It was through this engagement with the local community that positive relationships were formed between different stakeholders involving jaguar conservation (Woodroffe *et al*., 2005).

Many pastoralists in Africa construct enclosures in an attempt to protect their livestock from depredations. The majority of barriers that are built-in bomas to protect livestock are made of thorns and brush and are ineffective at keeping predators out (Kissui, 2008). However, chain-link "predator-proof" bomas can be purchased for a low cost and be implemented in high-conflict areas. The extensive home ranges of carnivores and movement causes the majority of conflict with humans as the overlap increases the chance of contact and coinciding conflict. The majority of lion prey are migratory species, and therefore lions will migrate with them, and establish patterns of movement in the wet and dry seasons (Ikanda & Packer, 2008). As lions follow their migrating prey in and out of protected areas, the potential for conflict increases. Depredations increase in the wet season, as do retaliatory killings of lions (Ikanda & Packer, 2008). Mountain lions also display migratory behavior as they follow mule deer to their summer and winter ranges (Pierce *et al*., 1999). Migratory movement increases the potential for conflict with humans, through depredations and road casualties. Information on the spatial-temporal movements of carnivores could be essential in decreasing conflict and increasing efforts in areas that are more prone to depredations (Kissui, 2008).

Preventative workshops in South Africa have fostered tolerance to leopards, and decreased conflict; leading to positive demographic changes in leopard populations including increased populations and reproduction, and decreased mortality (Balme *et al*., 2009). Positive perceptions and the ecological, economic, and social importance of large carnivores should be promoted to shift perspectives on wildlife. This could be constructed through educational

programs that begin at a young age and foster positive relationships with the environment and towards wildlife.

In addition to preventative workshops, compensation programs have been implemented to offset the economic costs that carnivores often create (Morehouse *et al*., 2018). Mishra (1997) recorded that self-financed compensation programs may be a feasible solution, in regards to snow leopard conflict, and could be supplemented with grant money. Financial compensation is not a permanent solution to the conflict with carnivores, but is often used when other strategies are not applicable; as seen with the snow leopards due to their shift in diet towards livestock, in response to decreasing abundances of native prey (Mishra, 1997). Though snow leopards are responsible for more depredations than other large carnivores, local pastoralist perceptions towards snow leopards in the Trans-Himalayas are less hostile when compared to other species and geographic regions (Mishra, 1997).

The removal or killing of problem individuals can act as a short-term solution to mitigate conflict, however, territorial vacancies will likely be filled and the same conflict arises (Balme *et al*., 2009). Permitting the killing of problem individuals is a potential solution to the removal of problem individuals while also satisfying trophy hunting quotas. However, there would need to be strict policies in place to confirm problem individuals and prevent misuse. Balme *et al*. (2009) implemented policies to prevent the misuse of leopard destruction permits through a set of guidelines where three confirmed depredations events must occur within a two month period. Presently, only landowners or officials may use destruction permits, but perhaps a shift towards stricter policy could reduce human-carnivore conflict through filling trophy hunting quotas with problem individuals (Balme *et al*., 2009).

Large carnivores are effective umbrella species due to their ecological traits and land and habitat requirements, and conservation efforts towards one will likely benefit many others (Balme *et al*., 2009; Noss *et al*., 1996). Paquet (unpublished report) found that protecting the habitat of carnivores in the Rocky Mountains would also protect 403 of the 407 terrestrial vertebrate species, therefore acting as successful umbrella species for not only other carnivores but vertebrate species (Noss *et al*. 1996). Efforts focused on the conservation of large carnivores have the potential to be widely beneficial for ecosystems through simultaneously conserving a multitude of other species.

Table 1. Comparison of ecological traits and variables for four large felid species on four continents.
AFR – Age of first reproduction (females)

	Mountain Lions	**Jaguars**	**Lions**	**Snow Leopards**
Scientific Name	*Puma concolor*	*Panthera onca*	*Panthera leo*	*Panthera uncia*
IUCN Status	Least Concern[1]	Near Threatened[2]	Vulnerable[3]	Vulnerable[4]
Population Trend	Decreasing[1]	Decreasing[2]	Decreasing[3]	Decreasing[4]
Number of Mature Individuals	Lack of good data	Lack of good data	23,000-39,000[3]	4,080 – 6,590[4]
Geographic Realm	North, Central, and South America[1]	Central and South America; concentrated in Amazon Rainforest[2]	Sub-Saharan Africa[3]	Himalayas, Central Asia, Southern Siberia[4]
Habitat	Forest, Desert, Grassland, Savanna, Shrubland[1]	Forest, Shrubland, Wetlands, Savanna, Grassland[2]	Forest, Grassland, Shrubland, Savanna[3]	Shrubland, Rocky areas (inland cliffs, mountain peaks), Forest, Grassland[4]
Area of Occupied Range	Lack of good data	8.6 million km^2[2,2]	3.4 million km^2[2,3]	2.8 million km^2[2,4]
Home Range Size	32 – 1,031 km^2,[2,1]	25 – 386 km^2[2,2]	266 – 4,532 km^2[2,3]	100 – 1,000 km^2[2,4]
Density	0.3 – 8 per 100 km^2[2,1]	0.74 – 11.7 per 100 km^2[2,2]	1.5-55 per 100 km^2[2,3]	Low[4]
Activity Pattern	Crepuscular, nocturnal[12]	Crepuscular, nocturnal; diurnal in dense forest habitat[13]	Diurnal, crepuscular, nocturnal[14]	Crepuscular, diurnal, nocturnal[7]
Social Behavior	Solitary except when raising young, dispersing with siblings, or mating[12]	Solitary except when raising young, dispersing with siblings, or mating[12]	Formation of prides with males forming coalitions[3]; varying in size from 2-18 females and 1-7 males[10]	Solitary except when raising young, dispersing with siblings, or mating[12,7]
Reproductive Behavior	AFR – 2.5 + 0.15 years[9] Average litter size – 2 cubs[9] Age of independence –13.7 + 1.6 months[8]	AFR – 3.5 years[2] Average litter size – 2 cubs[2] Age of independence – 24 months[2]	AFR – 3.5 years[5] Age of independence – 18 months[11]	AFR – 3.9 years[6] Average litter size – 1-3 cubs[6]

[1] Bauer *et al*., 2016
[2] Nielsen *et al*., 2015
[3] Quigley *et al*., 2017
[4] McCarthy *et al*., 2017
[5] Packer *et al*., 1998
[6] Bloomqvist & Sten, 1982
[7] Jackson & Ahlborn, 1989
[8] Sweanor *et al*., 2000
[9] Ross & Jalkotzy, 1992
[10] Packer & Pusey, 1987
[11] Packer & Pusey, 1983
[12] Pierce & Bleich, 2003
[13] Astete *et al*., 2008
[14] Hayward & Hayward, 2006

Carnivore Management & Conservation as a Wicked Problem

The conservation of carnivores ranks as a wicked problem. It involves a multitude of different stakeholders, and the roots of the issue are complex. Some problems are "tame", in which a defined solution identifies and acknowledge every aspect of the problem. Wicked problems on the other hand, contain social problems with deeply rooted social, political, and cultural dynamics that make solutions exceedingly complex (Duit & Löf, 2015). When wicked problems arise, there are multiple stakeholders involved, creating disagreements on the issue and solutions and leading to conflicting proposed solutions. A collaborative strategy is necessary to involve as many stakeholders as possible, and for fields to work together to create the most effective solutions. In the following paragraphs, I outline a combination of biological science, social science, and political science approaches to confront carnivore conservation and management as a wicked problem.

I propose that the complexity of carnivore conservation be met with a multi-pronged approach in order to address as much of the problem as possible. My solution incorporates three components: science, socio-environmental, and political. First, scientists need to employ a combination of a landscape connectivity model with the analysis of spatial-temporal movements of carnivores to identify areas of high and low concern, and guide mitigation strategies. Second, we need to concentrate on socio-environmental strategies in these identified areas, establishing preventative workshops, educational programs, and financial compensation. Third, leaders must prioritize conservation efforts and enact policies that refocus trophy hunting and destruction permits on removing problem individuals to reduce conflict and improve genetic diversity. Employing strategies that combine environmental, social, and political aspects will address and involve a multitude of stakeholders to have the largest impact on the wicked problem that is carnivore conservation.

First wildlife biologists and managers need to work together and use the science and research to identify areas of high concern. Next, NGOs and government agencies need to develop and implement preventative and educational community programs in the areas of high concern. Further, wildlife managers should focus efforts on the high concern areas, monitor populations, relocate problem individuals, and utilize other management strategies. Lastly, legislators need to fund enforcement, land protection, compensation plans, and modify policy for the shift from trophy hunting to destruction permits in these areas of high concern. Once established, all stakeholders will regularly reassess progress and evaluate if areas of high concern shift and modify the plan accordingly.

Conservation strategies must consider the ecological traits of the species in question, as well as the region in regards to landscape, culture, livelihoods, and local perceptions. Habitat fragmentation decreases connectivity between populations of large carnivores and subsequently has negative implications on diversity, reproduction, and the survival of species. It is crucial to increase connectivity between landscapes and carnivore populations to increase their population viability and genetic diversity. Creating a network of reserves and protected areas, as well as establishing wildlife corridors has the potential to be more viable than disconnected larger reserves (Noss *et al*., 1996). The landscape connectivity model that Rabinowitz & Zeller (2010) created identified areas of most and least concern for promoting movement of jaguars. This model should be used to guide conservation efforts with other species, with the establishment of wildlife corridors and protected areas accordingly. This conservation model and analyses should be applied in other regions and carnivore species of concern including mountain lions in North America, snow leopards in Asia, and lions in Africa.

Analyzing the spatial-temporal movements of carnivores to identify areas higher in human-carnivore conflict could shift mitigation strategies towards areas of high-concern (Kissui, 2008). Wildlife management utilizing information on the spatial-temporal movement of lions in Africa with the construction of predator-proof bomas could drastically reduce depredations and therefore human-carnivore conflict in areas. Additionally, in areas with an increased

susceptibility of attacks due to migratory movements or landscape features, funds could be allocated from the government or organizations to implement predator-proof bomas. Further, spatial-temporal analysis of other carnivores such as cougars, jaguars, snow leopards, or even wolves could be utilized on a global scale to identify areas with higher conflict and shift mitigation strategies towards areas of high concern. Spatial-temporal analysis in combination with the landscape connectivity model would identify areas of high-concern and areas that could benefit the most from socio-environmental mitigation strategies.

The spatial-temporal movement and landscape connectivity models are similar in that they do not actively conserve carnivores, but provide crucial information on areas of most concern for carnivore conservation. These models and methods can be employed for carnivores across the globe to identify areas of high concern and guide conservation efforts. Additionally, these models can be utilized for other species that are negatively affected by human population growth, urbanization, and habitat fragmentation and resulting negative effects.

Human population growth increases the probability of human-carnivore conflict and retaliatory killings that can extirpate individuals in solitary species, such as jaguars or mountain lions, as well as prides and packs in social species, such as lions and wolves. It is crucial to mitigate conflict between humans and carnivores through employing a plethora of socio-environmental strategies including preventative workshops, educational programs, and financial compensation (Kissui, 2008; Balme *et al*., 2009). Different species will require different social strategies. For example, local perceptions of snow leopard are less hostile and more sympathetic than other carnivore species and geographic regions (Mishra, 1997). Due to the significant change in prey abundance, husbandry practices, and the snow leopard's dependence upon livestock, financial compensation is likely the best way to decrease conflict with snow leopards. In contrast, local perceptions towards lions are exceedingly negative, and conflict often results in retaliatory killings (Kissui, 2008). Depredations also commonly occur due to the migratory behavior of prey species, and improving animal husbandry practices could decrease conflict (Ikanda & Packer, 2008, Kissui, 2008). Educational programs have the potential to foster tolerance towards carnivores and shift perspectives towards conservation by educating local communities on the importance of carnivores on the landscape and their environment. Preventative workshops can provide alternate husbandry practices that can decrease depredations and human-carnivore conflict, and strengthen positive relationships with carnivores, furthering their conservation. Analyzing both the natural environment, as well as the social and cultural environment is necessary to determine which socio-environmental strategies will be most effective at decreasing human-carnivore conflict, in order to employ them accordingly.

Predator control has implications on the long-term conservation of large carnivores. However, if predator control is only utilized with strict policy and requirements to simultaneously satisfy trophy hunting quotas, it has the potential to benefit carnivore populations. Trophy hunting remains a strong force on carnivore populations and has the potential to disrupt social hierarchy, and greatly reduce populations and genetic diversity. Instead of removing viable and non-problem males from the gene pool, I propose permitting the killing of problem individuals to satisfy trophy hunting quotas while decreasing human-carnivore conflict. Further, strict policies would need to be implemented to prevent the misuse of destruction permits, and I recommend the policies set in place by Balme *et al*.. (2009). Under this policy, officials must 1) inspect depredation sites within 24 hours of the event, and 2) once an event is verified, the problem individual must be identified by deploying camera traps. Destruction permits can only be obtained if 3) an individual is responsible for at least three depredations within a two month period and 4) if the landowner has utilized multiple preventative management and animal husbandry practices. Once a destruction permit is obtained, it can be sold similarly to a trophy hunting permit. The proper identification of the problem individual is paramount in this circumstance, and trophy hunters and their guides must utilize camera trap pictures for identification, and face considerable fines if the incorrect individual is killed. These strategies would be especially effective on popular trophy hunting species such as lions, leopards, and wolves, but would also have potential with jaguars and mountain lions.

The conservation of large carnivores will require environmental, social, and political approaches to be successful in both the short and long term. Many carnivore conservation strategies have the potential to be applicable on a global scale, while others must have a more narrowed and specific focus to be successful. The major issue in almost all carnivore-conflict conservation is the gap that exists between conservation groups and local communities. It is essential to involve native people and communities, who are the primary stakeholders, to bridge the rift that causes so many conservation efforts to fail. Successful conservation strategies for large carnivores will have to employ a plethora of both landscape and species management strategies, as well as social and political strategies that work to protect, improve relationships with, and shift perspectives on carnivores and the environment. Once applied, these conservation strategies have the potential to benefit ecosystems by strengthening the ecological processes and boundaries carnivores enforce that have been weakened by urban expansion. The nature of carnivores to act as umbrella species also positively implicates a plethora of other species for their conservation, benefitting ecosystems further.

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