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Connectivity of lions (*Panthera leo*) across a pastoralist landscape

Coexistence, conflict, and collective action for lion conservation in Ngorongoro, Tanzania

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Cover: Morning in the Ngorongoro Crater, Eugene and LK98 busy mating and consorting, briefly interrupted by a herder bringing his livestock to water. (photo: Ingela Jansson)

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Abstract

This thesis investigates human-lion coexistence and connectivity in the Ngorongoro Conservation Area (NCA). By combining ecological, genetic, and socio-ecological perspectives, it identifies key challenges and opportunities in managing shared landscapes between people and wildlife.

The findings show that lions avoid humans on the landscape, but when natural prey is scarce, they may prey on livestock, causing economic losses and prompting retaliatory killings. While lions disperse across the landscape, genetic analysis reveals limited exchange between populations, with the Crater lions showing low genetic diversity, inbreeding, and restricted gene flow, threatening long-term resilience. This isolation is exacerbated by the dominance of Crater-born males.

The NCA is at a critical crossroads where sustainable coexistence between humans and lions is still achievable. With pressures from climate change, population growth, and resource demands, this requires a balanced approach that fosters community-driven initiatives, effective conflict management, and recognizes that the futures of both lions and people are inherently connected.

Keywords: conservation incentive payments, dispersal, fragmentation, gene flow, genetic diversity, governance, habitat selection, human-wildlife conflict, pastoralism, socio-ecological perspective

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Abstrakt

Denna avhandling undersöker samexistens och konnektivitet mellan människor och lejon i Ngorongoro Conservation Area (NCA). Genom att kombinera ekologi och genetik med socioekologiska perspektiv identifieras viktiga utmaningar och möjligheter i förvaltningen av landskap som delas mellan människor och vilda djur.

Resultaten visar att lejon undviker människor i landskapet, men när det är ont om naturliga bytesdjur kan de ge sig på boskap, vilket orsakar ekonomiska förluster och leder till vedergällningsdödande. Även om lejonen sprider sig över landskapet visar de genetiska analyserna att utbytet mellan populationerna är begränsat. Kraterlejonen uppvisar tecken på genetisk utarmning, inavel och begränsat genflöde, vilket hotar deras långsiktiga motståndskraft. Denna isolering förvärras av dominansen hos hanar som är födda i Kratern.

NCA befinner sig vid ett kritiskt vägskäl där en hållbar samexistens mellan människor och lejon fortfarande är möjlig. Med påtryckningar från klimatförändringar, befolkningstillväxt och resurskrav kräver detta ett balanserat tillvägagångssätt som främjar samhällsdrivna initiativ, effektiv konflikthantering och med insikt om att både lejonens och människornas framtid hänger samman.

Keywords: rovdjursersättning, genetisk spridning, fragmentering, genflöde, genetisk mångfald, styrning och förvaltning, habitatval, viltkonflikt, pastoralism, socioekologiskt perspektiv

Dedication

To all people out there living and coexisting in ways we all ought to learn a little more from – thank you for all lessons and inspiration!

Contents

List of publications

This thesis is based on the work contained in the following papers, referred to by Roman numerals in the text:

I. Jansson, I., Parsons, A. W., Singh, N. J., Faust, L., Kissui, B. M., Mjingo, E., C., Sandström, C, Spong, G., (2024). Coexistence from a lion's perspective: movements and habitat selection by African lions (*Panthera leo*) across a multi-use landscape. *In revision, conditionally accepted*

II. Jansson, I., Capper, S., Jones, S., Lelya, R., Mjingo, E. E., Zeltsar, M., Kissui, B. M. Exploring predation patterns to guide conflict mitigation in pastoralist landscapes: a case from Ngorongoro Conservation Area, Tanzania. *Manuscript*

III. Jansson, I., Bertola, L., Kissui, B. M., Mjingo, E., Packer, C., Sandström, C., Spitzer, R., Spong, G. Genetic diversity, connectivity and dispersal patterns of a lion (*Panthera leo*) population across a pastoralist landscape – lions in Ngorongoro Conservation Area, Tanzania. *Manuscript*

IV. Parsons, A. W., Capper, S., Faust, L., Kissui, B. M., Packer, C., Sandström, C, Jansson, I., (2024?). The benefits of inclusive conservation for connectivity of lions across the Ngorongoro Conservation Area, Tanzania. *In review*

V. Pekor, A. Jansson, I. Seki, W O., Rentsch, D., Spong, G., Sandström, C. (2019). In search of new modes of governance: The potential of conservation incentive payment

policies to promote human–wildlife coexistence. In Nunan, F. (Ed). Governing renewable natural resources: Theories and frameworks. Abingdon, Routledge. pp.204-225.

The contribution of Ingela Jansson to the papers included in this thesis was as follows:

I. Main author. Led design and data collection. Collaborated with co-authors on data analyses, interpretation and writing of manuscript.

II. Main author. Led design, data collection and analyses. All co-authors collaborated on interpretation and writing of manuscript.

III. Main author. Led the field data collection. Collaborated with GS and LB on design and data analyses. All co-authors collaborated on interpretation and writing of manuscript.

IV. Co-author. Led data collection. Collaborated with AP on idea and design and analyses. All co-authors collaborated on interpretation and writing of manuscript.

V. Co-author. Collaborated on study design and analyses. Participated in the interviews together with AP and WOS. All co-authors collaborated on interpretation and writing of manuscript.

Abbreviations and definitions

Boma	A pastoralist homestead with a central livestock corral, surrounded by huts or small houses, and sometimes an outer fence.
COSTECH	Commission of Science and Technology
CBD	Convention on Biological Diversity
Dispersal	the movement from area of birth to area of breeding, leading to spatial geneflow
EVI	Enhanced Vegetation Index, a measure of vegetation "greenness", often used to correlate vegetation productivity
GBF	Global Biodiversity Framework
HWC	Human Wildlife Conflict
HWE	Hardy-Weinberg Equilibrium, HWE = $A^2 + 2Aa + a^2$, assumes closed and a randomly mating population, calculates expected heterozygosity (He) in diploid species
F_{is}	inbreeding coefficient, F_{is} = 1 - (Ho/He), comparing observed (Ho) versus expected (He) heterozygosity within subpopulations
F_{st}	fixation index, F_{st} = (Ht - Hs) / Ht, measuring genetic differentiation between subpopulations.
NCA	Ngorongoro Conservation Area
NCAA	Ngorongoro Conservation Area Authority

Polity	The formal structure and institutions that define a government or political entity.
Politics	The process of decision-making, negotiation, and power dynamics within groups or governments.
Policy	Actions or guidelines set by a government or organization to address specific issues.
RSF	Resource Selection Function, used to measure habitat selection at a larger scale, typically comparing home range to the wider landscape
SES	Social-Ecological Systems
SNP	Single Nucleotide Polymorphism
SSF	Step Selection Function, used to measure habitat selection at a finer scale, at habitat patch level
TAWIRI	Tanzania Wildlife Research Institute

1. Introduction

Our planet's biodiversity is undergoing unprecedented loss and degradation driven by pressures and demands of an expanding human population (Cardinale et al. 2012; Steffen et al. 2015; UNEP 2022). Preserving biodiversity and the ecosystems that rely on it has become a global priority (Cardinale et al. 2012; Steffen et al. 2015; UNEP 2022). Determining how to achieve this is both a theoretical and practical challenge, especially when it comes to conserving conflict-prone carnivores. As human encroachment reduces wild spaces, humans increasingly overlap with wide-ranging large carnivores, restricting their movements (Tucker et al. 2018; Creel et al. 2019) and leading to conflicts and persecution (Woodroffe & Ginsberg 1998; Carter & Linnell 2016; Lamb et al. 2020). Habitat loss and persecution are the main threats to large carnivores (Woodroffe & Ginsberg 1998; Ray et al. 2005; Ripple et al. 2014), resulting in local extinctions and fragmentation into small and increasingly isolated subpopulations (Saunders et al. 1991; Schmidt et al. 2020). The loss of connectivity and gene flow between fragmented small populations prevents recovery from stochastic events, reduces genetic variation, and lowers adaptive capacity to environmental changes, jeopardizing the long-term viability and persistence of these populations (Gibbs 2001; Frankham et al. 2019; Lamb et al. 2020; Schmidt et al. 2020).

The long-term preservation of carnivore populations in fragmented landscapes hinges on two primary strategies: safeguarding extensive areas (land-sparing) and promoting coexistence where human activities and carnivore presence are compatible (land-sharing). However, with rising human demands for space and resources, the feasibility of the land-sparing approach is decreasing, and even large protected areas face significant pressures (Veldhuis et al. 2019). Additionally, there is growing concerns

over the “fines and fences” strategy usually needed to enforce protection. Consequently, since the 1980’s the attention has shifted toward land-sharing approaches which are both politically supported and ethically justified (Wells et al. 1992; Dudley & Stolton 2020). There is also growing recognition of the need to preserve entire ecosystems and their processes, with humans as an integral part, as well as the importance of nature-based solutions (Estes et al. 2011; Cardinale et al. 2012; Cohen-Shacham et al. 2019; Dudley & Stolton 2020). This aligns with the globally endorsed Convention of Biological Diversity (CBD) and the recently adopted goals and targets of the Global Biodiversity Framework (GBF), which prioritize finding new and innovative ways to preserving biodiversity that are both sustainable and equitable (United Nations 1992; UNEP 2022).

Human-carnivore coexistence involves balancing the needs of carnivores with the interests of people as well as managing the conflicts that arise (Redpath et al. 2013; Pooley et al. 2017, 2021; IUCN 2023). The conservation efforts needed typically requires engaging rightsholders and stakeholders with different perspectives, including both pro- and anti-conservationist, as well as those who benefit and those who loose. Such situations can be defined as a traditional collective action challenge (collective action being the joint efforts of a group of stakeholders aimed at achieving a common goal), where inadequate collaboration leads to conflicts and stakeholders seem to lack either incentive or options to contribute to conflict resolution and consequently their overarching goals (Ostrom 1990). It is important to understand the underlying ecology and biological processes of the carnivore population under threat, but to effectively handle these situations and achieve long-term conservation gains, the underlying social context as well as the direct cost of the conflict must also be considered (Redpath et al. 2013).

With this background, I present my study on the ecology and status of a lion (*Panthera leo*) population and the human-lion conflict in a multiuse landscape. This research is conducted in the Ngorongoro Conservation Area (NCA) in northern Tanzania, where traditional pastoralism is practiced. In parallel with this research, I actively engaged in exploring and implementing conservation strategies. My aim is to contribute both theoretically and empirically to the fields of carnivore conservation, behavioural ecology, population genetics, and human-wildlife conflict management. This work hence addresses the global challenge of developing more sustainable,

equitable, and holistic approaches to biodiversity preservation and monitoring, focusing on the iconic African lion and the landscape that sustains it.

1.1 Connectivity across fragmented landscapes

Fragmented populations, existing within suitable habitat patches amidst an unsuitable landscape matrix, rely heavily on functional connectivity to sustain their meta-populations (Lande 1988; Clobert et al. 2012; Dolrenry et al. 2014). Increased fragmentation and isolation of small sub-populations heighten their susceptibility to environmental and demographic stochasticity, escalating risks of genetic diversity loss and inbreeding due to genetic drift and reduced gene flow (Schmidt et al., 2020). These factors collectively elevate the risk of extinction by rendering populations more vulnerable to environmental changes and diseases, and by compromising their long-term health and fecundity (Lande 1988; Frankham et al. 2019; Curry et al. 2021).

Dispersal

Dispersal is a life history trait and key component in the ecology of populations and evolution of species. In many mammal species, dispersal is sex-biased, strongly linked to the species parental care and sexual dimorphism (Greenwood 1980; Trochet et al. 2016). Defined as "movement leading to spatial geneflow" (Clobert et al. 2012), dispersal by individuals between subpopulations can mitigate the effects of genetic isolation (Peery et al. 2010; Bonte et al. 2012). Dispersal typically involves three phases: departure from the natal area, exploration and transition, and settling in a new area. Transitions between these phases are triggered by factors such as the individual's phenotype and life-stage, kin-competition, density-dependent factors within the source population, competition at the destination, habitat suitability and connectivity, landscape familiarity, and perceptions of risks and benefits (Clobert et al. 2012). Dispersal across fragmented landscapes is driven by a cost-benefit balance influenced by environmental conditions and population characteristics (Clobert et al. 2012; Dolrenry et al. 2014; Schmidt et al. 2020). The African lion is an example of species with sex-biased dispersal and where connectivity between metapopulations is male mediated (Pusey & Packer 1987; Spong & Creel 2001; Curry et al. 2019). This can be explained by lions mating system, sex-

dimorphism, territoriality and parental care (Trochet et al. 2016), the two latter roles held by females (Pusey & Packer 1987).

Source and sink dynamics

Fragmented landscapes within carnivore ranges provide both sink and source habitats. Studies on large carnivores indicate an increased mortality risk during dispersal through anthropogenically fragmented landscapes (Woodroffe & Ginsberg 1998; Loveridge et al. 2017; Nisi et al. 2023). By offering ample resources such as livestock and reduced intra-guild competition (Pereira et al. 2012), and posing new dangers to the naïve carnivore such as persecution and retaliatory killings, human-dominated habitats can become attractive sinks (Delibes et al. 2001). Additionally, scarcity of natural prey can drive carnivores into riskier behaviours, increasing overlap with human activities (Mills et al. 2023), thereby intensifying human-wildlife conflict. In species that exhibit sex-biased dispersal, transition and exploration across sink habitats often come with increased mortality risks for the dispersing sex – i.e., the individuals most crucial for population connectivity. The African lion is an example, where the mortality risk for dispersing males is further heightened by their tendency to be bolder and get into more conflicts (Patterson et al. 2004; Elliot et al. 2014b) and be more targeted in hunts (Kissui 2008; Hazzah et al. 2009; Packer et al. 2009; Becker et al. 2013).

Genetic challenges for fragmented populations

Genetic diversity is a cornerstone of biodiversity and plays a crucial role in enabling species and populations to adapt to changing environmental conditions. This is especially important in the face of rapid climate change and growing anthropogenic pressures on ecosystems. Small, fragmented populations are more susceptible to loss of genetic diversity through genetic drift and inbreeding (Allendorf et al. 2012a; Kyriazis et al. 2021; Pinto et al. 2024). In species with skewed mating systems, where few individuals contribute disproportionately to the gene pool, the effective population size (N_e) becomes even smaller, exacerbating these genetic challenges (Frankham 1995). Genetic drift, the random loss of alleles over time, can lead to the fixation of harmful alleles and the loss of beneficial ones (Allendorf et al. 2012a; Stevens et al. 2018). Inbreeding, or mating between related individuals, is almost inevitable in small populations and results in increased homozygosity. Although continuous inbreeding can lead to the purging of

deleterious alleles through natural selection, it is generally insufficient to offset the overall negative impacts on population health (Allendorf et al. 2012b; Kyriazis et al. 2021).

In the short term, loss of genetic variation can lead to inbreeding, ultimately resulting in negative fitness consequences. Inbreeding depression, the reduced fitness in inbred individuals, can manifest as lower survival rates, reduced fertility, and increased disease susceptibility (Crnokrak & Roff 1999; Allendorf et al. 2012b). It can vary between sexes, especially in sexually dimorphic species (Vega-Trejo et al. 2022). Assessing inbreeding depression in wild populations is challenged by environmental variability and the difficulty to obtain relevant fitness data, and the lack of evidence has led to doubts and debates of the impact from inbreeding (Lande 1988). However, numerous studies across various species, including carnivores, have shown heterosis in the wild, where outcrossed offspring exhibit improved fitness compared to their inbred counterparts (Spielman et al. 2004; Johnson et al. 2010; Frankham 2015; Åkesson et al. 2016; Miller et al. 2020; Penfold et al. 2022). Advances in genomics are now making assessments of impact from inbreeding depression more attainable (Kardos et al. 2016). Recent studies suggest that it can be masked by favourable environments but become pronounced under stress, such as those caused by climate change and habitat fragmentation (Crnokrak & Roff 1999; Fox & Reed 2011). This environment-dependent inbreeding depression is of particular concern for conservation, as environmental stress can push populations toward an extinction vortex in which reduced fitness of a small population results in an even smaller population with even stronger inbreeding effects (Frankham 2015).

Maintaining genetic health and diversity in small and fragmented populations requires gene flow from migrants. According to (Mills & Allendorf 1996) the "one migrant per generation" rule-of-thumb is an acceptable minimum, but likely insufficient for many natural populations. Considering just the genetic effects, (Mills & Allendorf 1996) suggest a general rule of 1-10 migrants per generation. Ensuring regular and natural gene flow through migrants from nearby populations increases the likelihood that introduced genes are well-adapted to local conditions, thereby minimizing the risk of outbreeding depression and reducing the chance of the introduction of foreign pathogens. Conservation efforts should prioritize maintaining genetic diversity, managing inbreeding, and ensuring

connectivity between populations to enhance their adaptive potential and resilience to environmental changes.

Assessing population connectivity

Effective management strategies that promote coexistence are crucial for enhancing connectivity among anthropogenically fragmented carnivore populations (Oriol-Cotterill et al. 2015b; Gaynor et al. 2018; Wilkinson et al. 2020). The importance of considering the human dimension in setting these strategies has been discussed above. Equally important is a good understanding of the carnivore species biology and the population's demography and genetic status (Lande 1988), conflict patterns, adaptive capacity, and connectivity potential. The expanding field of conservation genomics provides valuable tools to assess genetic diversity and population status (Kardos et al. 2016; Chege et al. 2024). By analysing genetic material from individual animals, including non-invasively collected scat and hair, researchers can assess historical connectivity, population dynamics, evolutionary processes, and contemporary dispersal patterns (Spong & Creel 2001; Norman & Spong 2015; Walton et al. 2021; Chege et al. 2024). Additionally, telemetry and animal movement studies enable the evaluation of connectivity by analysing habitat use, identifying environmental features and contexts that provide refuge and resources, and assessing carnivores' ability to navigate human-occupied landscapes (Elliot et al. 2014b; Sargent et al. 2022). Gaining a better understanding of connectivity from the animals' perspective is essential for planning long-term conservation strategies.

1.1.1 The lion: status and context for coexistence

The lion (*Panthera leo*), iconic to the African savannah, has declined dramatically in both number and range in the last century, driven by anthropogenic activities (Riggio et al. 2013; Bauer et al. 2015). Categorized as Vulnerable on the IUCN Red List, the estimated 23,000 remaining lions (all aged two years or older) now inhabit only 7.4% of their historical range. (Nicholson et al. 2024). The once-connected lion range across much of Africa, excluding the dryest desert and deepest rainforest, is largely disrupted. Recent genetic studies of lions across Africa and in the remnant population in northern India reveals a phylogeographic split between a north (Central, North, and West Africa and Asia) and a south group (North East, East/Southern and South West Africa) (Bertola et al. 2016). Within Africa,

this north group consist of small, isolated populations and considered highly threatened, while there is much regional variation for the south group populations, with some positive trends in southern Africa (Nicholson et al. 2024). In the last 50 years, an estimated 50% of the connected lion range in east and southern Africa has been lost and there has been a 65% decline of East Africa's lion population (Loveridge et al. 2022). The fragmentation of populations are observed in recent genetic surveys in Kenya (Chege et al. 2024) and Tanzania (Smitz et al. 2018). Even the few remaining large populations of lions are impacted by humans by their range overlapping community land, and/or from edge-effect pressures (Woodroffe & Ginsberg 1998; Loveridge et al. 2017; Veldhuis et al. 2019). The main threats to lions are habitat loss, prey depletion, and human-lion conflict (Lindsey et al. 2017; Bauer et al. 2022). These threats are interconnected with underlying root causes such as resource competition, inadequate management, and civil unrest, which vary significantly across regions (Bauer et al., 2022).

The lion is adaptable to a variety of habitats, but soon ceases to persist in landscapes dominated by humans (Riggio et al. 2013; Sargent et al. 2022). Human land-uses compatible with naturally functioning landscapes, such as pastoralism, offer opportunities for coexistence with wildlife including lions (Homewood & Rodgers 1991; Nelson 2012; Schuette et al. 2013). However, in a pastoralist landscape, lions' attacks on livestock can be significant, triggering retaliatory killings that can have dramatic effects on the lion population (Ikanda & Packer 2008; Hazzah et al. 2009). Among the other large carnivores that commonly attack livestock, the spotted hyena (*Crocuta crocuta*) and leopard (*Panthera pardus*), lions are especially vulnerable to retaliatory killings due to their habits of primarily preying on cattle, the higher value livestock, and lingering by the kill to defend it (Patterson et al. 2004; Kissui 2008). In comparison, the spotted hyena and leopard tend to prey upon lower-value livestock, attack at night, and are more elusive to better escape persecution (Kissui 2008). In addition, traditional spearing of lions to demonstrate bravery is practiced among some pastoralist cultures, e.g. the Maasai (Ikanda & Packer 2008; Hazzah et al. 2009; Goldman et al. 2013), contributing to human-lion conflict and the lions' fear of people. The killings of lions by hunts and direct spearing, whether for retaliatory or ritual purpose, has undoubtably shaped a relationship that include fear and respect between lions and people, a necessary trait for their coexistence (Frank et al. 2008; Potratz et al. 2024).

However, lions have an established capacity for flexibility, exhibiting behavioural adaptations to avoid conflict with humans (e.g., becoming more nocturnal; Gaynor et al., 2018; Suraci et al., 2019), often resulting in improved survival. Whether these behaviours can improve success in connecting isolated subpopulations remains unclear, however understanding the behavioural choices of lions in shared landscapes will be critical for making the best decisions for lion conservation as anthropogenic landscapes expand across Africa.

1.2 Objective and outline of thesis

The overarching objective of this thesis is to explore human-lion conflict and co-existence in a rapidly evolving multi-use landscape, using Ngorongoro Conservation Area (NCA) in Tanzania as a case study. The research focuses on understanding how human-lion coexistence affects lion populations and exploring the potential for inclusive conservation strategies to enhance and sustain ecological connectivity for lions across a pastoralist landscape.

To achieve this objective, the thesis addresses the following research questions:

RQ 1: *How do environment and human factors influence lion movements and connectivity across the landscape?* (Paper **I**, II, III)

RQ 2: *What are the patterns and impacts of conflict between humans and predators, particularly lions, and how do these conflicts shape human-lion interactions?* (Paper I, **II, IV**)

RQ 3: *What is the impact of human-lion interactions on lion dispersal, gene flow, and genetic structure, and what are the implications for the long-term viability of the lion population?* (Paper I, II, **III**)

RQ 4: *What are the challenges and opportunities for improving human-lion coexistence strategies, and how might these affect population connectivity?* (Paper **IV, V**)

The thesis begins by providing a comprehensive background on the governance and status of the NCA, the landscape characteristics, the lion population, and the local communities, including their livelihoods and

interests. This background sets the stage for examining human-lion coexistence in the area. After summarizing the key findings from the five chapters, I discuss these results in relation to the four research questions, reflecting on the prospects for both lions and humans to coexist in shared landscapes. Drawing from the exploration of alternative approaches, I highlight the potential for more engaged and equitable strategies that foster coexistence, balancing the needs of both wildlife and local communities.

1.3 Background

To address human-lion conflict and promote coexistence, it is crucial to look beyond isolated incidents of lion attacks on livestock or retaliatory killings by humans. This section aims to provide context on the Ngorongoro Conservation Area (NCA) and its lion population within a broader socio-ecological context. Inspired by Ostrom's Social-Ecological Systems (SES) framework (Ostrom 2009) and the lion threat analysis by (Bauer et al. 2022), I focus on likely drivers of the complex human-lion conflict, as well as potential opportunities for collective action towards sustainable coexistence.

1.3.1 Protection status and governance

The NCA was established in 1959 as a protected multiple land-use area in 1959, where wildlife coexist with traditional pastoralists and their livestock (Århem 1985; Galvin et al. 2015). Recognized for its outstanding natural, geological, and anthropological values the NCA has been designated a World Heritage site (UNESCO 2024). Along with the Serengeti National Park, it is part of the Man and the Biosphere Program (UNESCO n.d.). The NCA is managed by the NCA Authority under the "Ngorongoro Conservation Area Ordinance", an area-specific law established in 1959 and amended in 1975 (URT 1959, 1975). Its mandate is to support and protect coexistence between humans and wildlife by balancing three main objectives: conserving natural resources, safeguarding the interests of resident pastoralists, and promoting tourism (Kipuri & Sørensen 2008; URT 2019).

Land-use in NCA is limited to traditional livestock grazing practiced by the resident pastoralist and photographic tourism. Since the 1975 Ordinance amendment, settlement in the Ngorongoro Crater and cultivation have been prohibited (URT 1975; Galvin et al. 2015).The cultivation ban was temporarily lifted in 1992 following protests due to food insecurities, but was

gradually reinstated from 2009 to 2013 amid concerns over land degradation and threat to conservation values (Galvin et al. 2015; URT 2019; UNESCO 2024). Construction of permanent infrastructure is strictly regulated, with most residents living in traditional bomas (Fig 1), which are multi-generation family homesteads with stick-and-mud huts surrounding livestock enclosures. Transport is limited to a few public and private vehicles, and motorcycle use (nowadays very common means of transport in similar pastoralist landscapes) is heavily restricted, so commuting is mainly on foot.

Figure 1. Bomas, typical pastoralist homesteads, in the landscape, Misigio village, NCA (Photo: Ingela Jansson)

The NCA Ordinance states that only "members of the Maasai tribe" have entry and residence rights (URT 1959). However, in practice both Maasai and Datooga pastoralist reside in the area. Aside from some immigration of agro-pastoralists during the temporary lifting of the cultivation ban, most resident families have long-standing ties to the area.

Since 2017, when restrictions were imposed on entering the Craters for pasture in (URT 2019), approximately 88% of the NCA's area remains open for livestock grazing and habitation. The remaining 12%, including the Craters, eastern highland forest, and part of Ndutu bordering Serengeti, is reserved exclusively for wildlife and habitat protection and photographic tourism. As in a national park, the wildlife in NCA is fully protected, while trophy hunting is permitted in adjacent Game Reserves to the south-west and north-west of the NCA (URT 2022b).

1.3.2 Ecological setting: landscape and seasons

The NCA, encompassing 8,300 km², lies just below the equator at approximately 3°S and 35°E, forming a vital part of the Greater Serengeti Ecosystem (Fig 2). The NCA's landscape is highly diverse, featuring forested highlands, rugged escarpments, volcanic calderas, *Vachellia*, *Senegalia* and *Commiphora* woodland savannahs, along with vast open grasslands. Altitudes range from 1,000 to 3,000 meter above sea level, with rainfall varying from 400 to 700 mm/year along a west-to-east gradient. To the east, the lush, forested highlands of the NCA abruptly transition to the farmlands and densely populated towns and villages of the Karatu region. To the west, the vast short-grass plains, covering about 40% of the NCA, seamlessly connect with the Serengeti National Park. These plains, although barren for much of the year, provide nutrient-rich pasture during the rainy season (Metzger et al. 2015), a critical driver of the great Serengeti ungulate migration (Holdo et al. 2009; Hopcraft et al. 2010). In the Ndutu area, these homogeneous plains are interspersed with woodlands surrounding soda lakes, water drainages, and natural springs.

Wildebeest migration, Hidden valley, Ndutu, NCA. (Photo: Ingela Jansson)

The NCA's diverse topography, climate, vegetation, and seasonal dynamics create a heterogeneous landscape that supports abundant wildlife and provides valuable pasture for livestock. Most of the NCA is accessible for grazing and settlement by resident pastoralists and their livestock, with certain areas, including the Ngorongoro Crater, a section of Ndutu, and the eastern highland forest, reserved exclusively for wildlife (Fig 2).

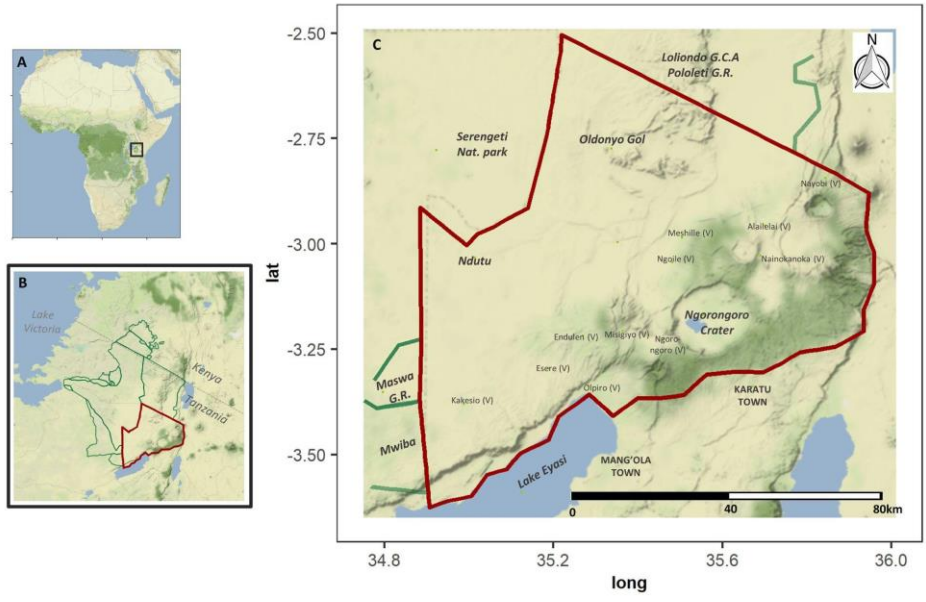

Figure 2. Map of the NCA, a multiple land-use protected area in northern Tanzania, East Africa (A). It forms a large component of the Greater Serengeti Ecosystem, with vast dry shortgrass plains in the west and wetter forested highlands in the east.

The NCA experiences distinct wet and dry seasonal patterns, shaping conditions essential for both wildlife and pastoralists. During the dry season, migratory ungulates depart, resulting in a significant reduction in wild herbivores. Pastoralists must expand their efforts and movements to secure sufficient pasture for their livestock yet confined to areas with available water. This results in increased temporary settlements near water sources and high local concentrations of livestock, intensifying competition for resources.

When the rains return, vast herds of migratory ungulates, including approximately 1.5 million wildebeest (*Connochaetes taurinus*) (Pennycuick 1975; Hopcraft et al. 2010; Sinclair et al. 2015), migrate back to the shortgrass plains. Between January and April, pastoralists remove their cattle from the shortgrass plains during the wildebeest calving period (Estes 1976) to avoid the risk of Malignant Catarrhal Fever, which can be transmitted from wildebeest placentas and newborn calves (Plowright 1965; Cleaveland et al. 2023). The abundance of pasture and water during the rains also allows pastoralists to return to their more permanent homesteads. This creates a

natural separation of livestock from wildlife on the shortgrass plains during the wet season, which then hosts a super-abundance of wildlife. Consequently, lions on the NCA's short-grass plains experience a wet season with abundant natural prey and minimal human-lion conflict, followed by a dry season characterized by scarce natural prey, local high concentrations of livestock, and elevated risk of conflict with humans.

1.3.3 Ecological setting: the lion

Lions are a group-living species with a complex social structure, with some regional variation (Bauer et al. 2003; Funston et al. 2003; Palmer et al. 2023). The social patterns documented from the long-term research in Serengeti and Ngorongoro Crater (Packer 2023) apply directly to this study. Lions are sexually dimorphic, with males being nearly twice the size of females and distinguished by their conspicuous manes (West & Packer 2002). In terms of their mating system, females exhibit egalitarian behaviour (Packer et al. 2001), while males gain mating opportunities by establishing themselves as the resident males of a pride, either as solitary individuals or, more commonly, in coalitions. Most lions are members of matrilineal and territorial prides, typically composed of 2-10 related adult females, their dependent offspring, and their current resident males. Lion prides function as fission-fusion societies, where members often split into sub-groups. Resident males spend more time with the pride during mating periods and when females have young cubs. Lions have a prolonged developmental period, with cubs remaining dependent on their mothers for up to two years, during which they learn essential survival and social skills. In the wild, female lions can live up to 16 years, while males rarely exceed 13 years.

The primary driver of lion social behaviour is cooperation for competition and defence. Females collaborate to rear cubs and defend the pride's territory, while males form lifelong coalitions to compete for pride tenure and protect females and their offspring (Mosser & Packer 2009). Social interactions with other lions have a profound impact on a lion's life, and often the greatest immediate threat to a lion is another lion.

Lions exhibit different behaviours depending on their sex and life stage, making unique decisions based on their familiarity with the landscape and responses to threats (Pusey & Packer 1987; Elliot et al. 2014a). While females are generally philopatric and territorial, males depart from their natal prides at maturity, becoming nomadic until they are able to gain resident

status with a pride. A male's tenure in a pride is temporary, typically lasting 2-3 years, after which he is either ousted by rival males or leaves voluntarily, resuming a nomadic phase (Pusey & Packer 1987). Nomadic males do not hold territories and are subordinate to resident males, wandering widely in search of food and females, often relegated to suboptimal habitats to avoid conflicts with other lions (Pusey & Packer 1987; Elliot et al. 2014b).

The NCA's multiuse area connects the small, high-density lion subpopulation of the Ngorongoro Crater with the larger Serengeti population. It is widely believed that increasing human activity and human-lion conflicts have been major factors contributing to the decline and disappearance of lion populations across the NCA, impeding dispersal and isolating the Ngorongoro Crater subpopulation (Packer et al. 1991; Ikanda & Packer 2008).

The long-term demography study of the Ngorongoro Crater lion population, where each lion is identified and pedigrees traced to their putative parents or potential parent groups, reveal a population with many generations of close inbreeding. Although there are no obvious visual morphological defects among the Crater lions, a study conducted in the 1980s found higher levels of sperm abnormalities in Crater males compared to their counterparts in the nearby Serengeti (Wildt et al. 1987).

1.3.4 Socio-economic setting: people and interests

The great majority of the residents in NCA are traditional pastoralist of the Maasai or Datooga ethnic groups, of which most rely entirely or largely on livestock as their livelihood. The education and health services within NCA are limited and opportunities for alternative livelihoods are rare (Melita & Mendlinger 2013; Galvin et al. 2015). Poverty, limitations from low or no formal education (including language) or vocational training, lack of awareness about how to access opportunities elsewhere, history and family ties, strong traditions and love for the land and pastoralist livelihood are commonly mentioned when discussing with people about their reason to stay on here in NCA, despite the limited alternatives.

Since NCA's gazettement as multiuse protected area in 1959, there has been a 10-fold increase in the resident population, mainly through natural growth. The last country-wide census in August 2022, counted 100,793 people residing in the NCA (URT 2022a), a population density of roughly 12 persons per km^2. Meanwhile the number of livestock units have remained

rather stable, with a recent shift towards more sheep and goats than cattle, which require higher quality pastures (Fig 3). Droughts frequently cause large livestock losses (Manzano & Yamat 2017) as this system relies entirely on the local natural resources and mobility to other areas is restricted. The trend of decreasing livestock per capita and growing poverty among pastoralist families from and limited alternative opportunities, increase the residents vulnerability (Kipuri & Sørensen 2008; Galvin et al. 2015). The historical pattern of seasonal mobility has decreased, and NCA's pastoralist families have become increasingly sedentary, a trend attributed to increasing land-use restrictions and population density, and a shift towards a more modern lifestyle with increasing aspirations for livelihood diversification, social services and cash income (Homewood et al. 2009).

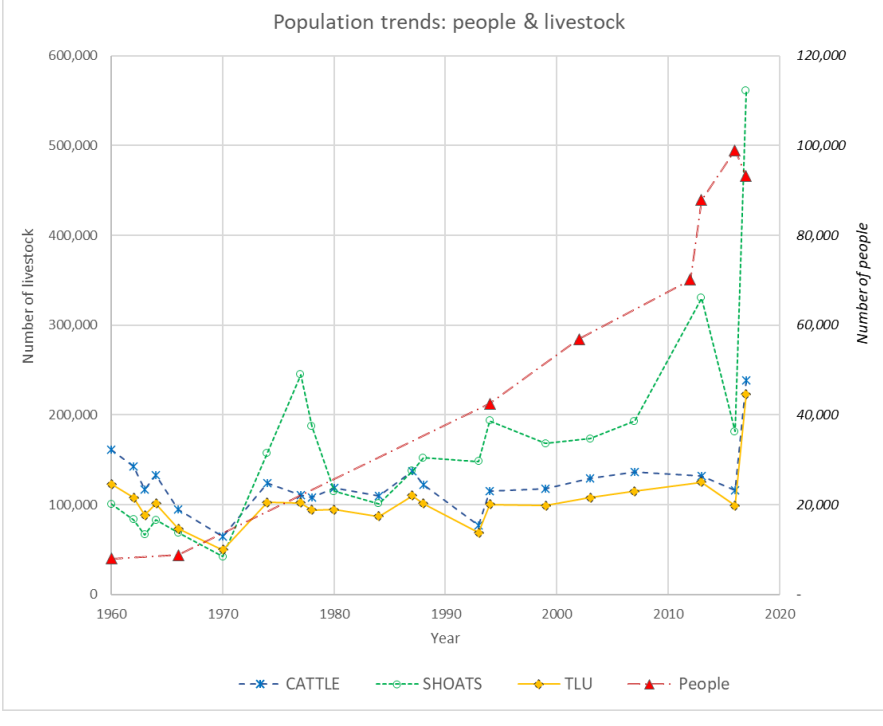

Figure 3. Livestock and human population trends in NCA since 1960, based on official census data. While the human population has increased significantly, the livestock numbers, when calculated as Tropical Livestock Units (TLU), have been relatively unchanged over time. SHOATS = sheep and goats.

Human-lion coexistence in NCA

The human-lion coexistence functions similarly among the traditional Maasai and the Datooga pastoralists. For both groups, livestock is their everything (Fig 4), and cultural taboos prohibit them from consuming meat that is not from their livestock. They invest considerable effort in caring for and protecting their livestock through constant herding, returning animals to secure nighttime enclosures. This protection also includes retaliatory killings of predators, typically by spearing.

Figure 4. Livestock is everything to NCA's pastoralist. Here at the Orng'esher ceremony as the warrior responsibility is passed on to the younger age-group. (Photo: Ingela Jansson)

Historically and to small degree still occurring today, Maasai and Datooga warriors— a stage that all men undergo, during which they are responsible for protecting their communities—have practiced the ritual spearing of lions. For the Maasai, this act confers bravery status (Hazzah et al. 2009). Among the Datooga, spearing a dangerous animal, such as a lion, or shooting it with a bow and arrow serves as a rite of passage, though it does not necessarily involve killing the animal (Silo Gisun'guda and Olpiro community members, pers. comm.). We now observe this tradition fading away, as it is replaced by other values in today's youth, as community leaders commit to

conservation agreements, and by the threat of legal punishments. Both the Maasai and Datooga traditionally practice respect for living things, with taboos against unnecessary killings and a strong disapproval of poisoning. While lions are seen as a significant danger to livestock, they are also respected and admired (Dheer et al. 2021).

From a lion's perspective, the lifestyles and taboos of the Maasai and Datooga offer the presence of alternative prey, unlike many other sub-Saharan landscapes where human activity has significantly reduced wild prey through bushmeat poaching, with notable impacts on lion populations (Lindsey et al. 2017). In the NCA, lions face the risk of being speared in retaliation for livestock attacks and during ritual hunts, but the threat of mass killings is limited. This blend of conflict and respect between pastoralist and lions has undoubtably shaped a relationship that is crucial for coexistence. If lions were to lose their fear of people in this landscape, it could swiftly lead to their demise (Frank et al. 2008; Packer 2023).

Tourism in NCA

While the NCA communities and landscape have faced increasing challenges over time, the tourism sector within NCA has flourished. Over the past 20 years, visitor numbers to this renowned wildlife safari destination have risen significantly (URT 2019; BOT et al. 2024), with lions being a top attraction for many tourists (Willemen et al. 2015; BOT et al. 2024), Fig 5. The substantial tourism revenue generated by the NCA is a vital source of income for Tanzania (URT 2019; BOT et al. 2024), where there are many pressing needs given its status as a developing country.

Figure 5. Ngorongoro Crater is a world-famous tourism destination. Lions are among the top attractions. (Photo: Ingela Jansson)

Tourism also contributes significantly to employment opportunities. However, in the NCA, most jobs are filled by individuals from outside the area, partly due to the lack of qualifications among local residents (Melita & Mendlinger 2013). The primary way NCA communities directly benefit from tourism is through "cultural bomas," traditional Maasai homesteads that tourists can visit to learn about Maasai culture and purchase handicrafts (Melita & Mendlinger 2013; URT 2019). Additionally, NCA communities have also benefited from tourism revenue through the provision of community services, scholarships, and food subsidies by the NCA Authority via budgets provided to the Ngorongoro Pastoralist Council. However, as the population and its needs have grown, this per-capita support has become increasingly limited. Moreover, the link between wildlife conservation and the benefits received by local communities is poorly recognized. Fig 6 pictures a scenic landscape in the wider NCA.

Figure 6. Photo of a scenic hillside in the wider NCA, a few women returning home from a celebration. (Photo: Ingela Jansson)

2. Methods

2.1 Philosophical and ethical considerations

Before and during the studies I lived and worked in the study area, which undoubtably influenced my understanding and interpretation of the situation. I collaborated closely with various key stakeholder groups, including the local authorities, tourism operators and particularly with the local pastoralist communities. My research and data collection were conducted alongside efforts to develop and implement community conservation activities in the area. Together with local collaborators a non-profit organization was established to operate formally and employ people, with a mission to promote human-lion coexistence. Consequently, I became a stakeholder in the area I was studying.

Conducting un-biased research is crucial to objectively reveal and describe any situation. While this is often more straightforward in purely ecological research, even here we make choices by investing time and resources differently (Padovani et al. 2015). I strove to gather data and information from all perspectives and to maintain outward neutrality. In engagement with other stakeholders, I strove to take the role of an "Honest Broker of Policy Alternatives [that] seeks explicitly to integrate scientific knowledge with stakeholder concerns in the form of alternative possible courses of action." (Pielke 2007). Aware of my own interest and views, I made conscious efforts to prevent these from influencing my assessments.

My background is in wildlife biology, and when I first began working directly with local communities, I was unprepared for the nuances of community engagement. For example, my initial lack of understanding of leadership hierarchies led me to overstep boundaries, resulting in serious

distrust within one village. It took considerable time to rebuild trust after the initial damage was done. While this unpreparedness certainly had its limitations (Sheppard et al. 2024), it allowed me, as well described in (Musante & DeWalt 2010), to remain open to learning and adapting as I went along, guided by the context of this landscape, the people living here, and their traditional ecological knowledge. My initial interest in, and concern for, the lion population quickly led me to encounter the layered complexity of the human-lion coexistence, highlighting the need for a transdisciplinary approach. This research was further motivated by the need expressed by various stakeholder groups for relevant and up-to-date knowledge on human-wildlife conflict and coexistence, and for more tools and strategies on how to manage these challenges effectively.

The introduction and discussion sections of this thesis reflect my independent analysis and synthesis. The results, including the methodology, are the product of a collaborative effort involving multiple contributors. This collaboration has been instrumental in gathering data, designing research approach, and ensuring robustness of the analysis. While my individual input was critical in applying the methods, interpreting and integrating the findings, the collective work of my colleagues and collaborators was essential to the set up the studies and to provide education in the PhD program. My individual contributions in the articles/manuscripts are specified on page 12.

2.1.1 Field research and data collection ethics

All research, fieldwork and data collection, including animal-handling to deploy collars on lions, complied with the Tanzania Wildlife Research Institute (Conduct of Wildlife Research) Regulations (Tanzania Wildlife Research Institute 2020). It was carried out under the yearly renewed research permits granted to our research project titled "Balancing Pastoralist Livelihoods and Wildlife Management in Ngorongoro", and to each individual researcher, by the Tanzania Commission for Science and Technology (COSTECH; Dar es Salaam, Tanzania; rclearance@costech.or.tz) and Tanzania Wildlife Research Institute (TAWIRI; Arusha, Tanzania; researchclearance@tawiri.or.tz). IJ was granted research permits No's 2012-73-ER-90-15, 2013-147-NA-90-15, 2014-159-ER-2007-15, 2015-125-NA-2014-1165, 2016-229-NA-2014-165, 2017-243-NA-2007-15, 2018-362-NA-2014-165, 2019-341-NA-2006-79,

2020-256-NA-2019-065, 2021-548-NA-2019-065, 2022-771-NA-2019-068, and 2023-793-ER-2019-068. A further permission to deploy collars was granted by NCA Authority, in letters No. NCAA/D/240/VOL.XXI/78, date 30/10/2012, to collar up to six lions simultaneously, and No. BD/158/711/01'E'/54, date 14/12/2021, permission renewed to collar up to eight lions simultaneously (NCAA; Ngorongoro Crater, Arusha, Tanzania; cc@ncaa.go.tz). Initially, I conducted most of the lion research activities. However, after extensive training of local field staff, many of whom lacked formal education but possessed valuable ecological skills, these activities were increasingly done by them as they gained experience.

Animal handling and collaring

In compliance with Tanzanian law, all immobilizations and captures for deploying or replacing collars were performed by an NCA Authority or TAWIRI veterinarian, who held the outmost responsibility for the welfare of the immobilized animals. All collars featured a remote drop-off function, which could be activated via a timer or radio-command using a release transmitter (VECTRONIC Aerospace 2024). Therefore, re-capture of the lions was not necessary for collar removals. Collars were removed if they malfunctioned, their batteries ran low (typically after 770 or 1,400 days, depending on the model), or if the purpose of collaring the animal had been fulfilled.

Lions in NCA community lands are few and elusive, hence finding and capturing them to deploy collars is challenging and done opportunistically, mainly at night, following observations of lions in the area. To attract lions closer to the vehicle for immobilization, we used a speaker (model Krakatoa, by FoxPro, USA) to broadcast a high-volume recording of feeding hyenas, a bleating buffalo calf, or the roars of a lion. To capture the lions, they were chemically immobilized with a drug mixture providing sedative, tranquilizing, and anaesthetic effects (e.g., Zoletil and medetomidine), administered via a dart shot from a CO_2-powered dart-gun (Dan-Inject or Pneu-Dart) from a vehicle at a 10-20 meter distance, following protocols described in (Kock & Burroughs 2012). The sedation time was typically less than one hour, during which time the veterinarian and the researcher monitored body conditions closely (breathing, temperature, circulation). The collars were fitted by an experienced field researcher supervised by the veterinarian. Afterwards we remained with the lion to closely monitor it until alert and deemed safe and well recovered after the immobilization.

We only targeted fully grown lions for collaring, and with collars weighing approximately 1.2 kg, this represented 1% or less of an adult lion's bodyweight and well within recommended limits (Wilson et al. 2021). On two occasions, we collared sub-adult males who were expected to continue gaining muscle and neck girth. In these cases, we monitored the collar fit with extra care and removed the collars before there was any risk of them becoming too tight. We closely monitored all collared individuals through visual observations and field signs, and via daily checks of their movements as transmitted by the collars. We were observant of any signs of distress or negative short- or long-term impacts from the collars, including effects on reproduction, hunting and feeding behaviours, and social interactions. No apparent side effects from the collars were detected. In addition to the research on lions fine-scale movements, these collars have become a very important tool for preventing human-lion conflict, leading to improved safety for the collared lion and its group.

Genetic sampling

For the genetic study, we collected samples containing DNA from lions, including hair, faeces and tissue. All samples were taken from wild lions in their natural environment, both from living lions and a few carcasses of lions found dead. Most collections were opportunistic and non-invasive, such as faeces and hair. We collected tissue samples from lions immobilized for other purposes. Between December 2014 and October 2015, our research permission included biopsy darting, a mildly invasive sampling technique. This was conducted by a veterinarian, who free-darted lions from a vehicle at 10–20-meters with a biopsy dart (essentially a 3 mm wide cylinder with a sharp end to nip a small piece of tissue) with a Dan-Inject CO2 rifle (Dan-Inject, Denmark). The biopsy darting tends to momentarily startle the lion, that reacts with a short growl, standing up and sometimes moving a few meters – as if puzzled by what suddenly nipped it, then returning to rest.

As there were no facilities to perform the intended genetic analyses of the lion samples in Tanzania, we secured all required permission for exporting samples from lions (hair, faecal, tissue) to the molecular laboratory at SLU, Umeå, Sweden (Year 2015: Export of 264 samples of hair, faeces, saliva, tissue; CITES export permit (Tanzania) No. 29091; CITES import permit (Sweden) No. 4.10.18-9878/15. Year 2021: Export of 140 samples of hair faeces, tissue; CITES export permit (Tanzania) No. 33084; CITES import permit (Sweden) No. 4.10.18.17147/2020).

Interviews

For all interviews, we obtained informed consent, and our data handling procedures ensured full anonymity. Data storage was on personal computers, not uploaded to any cloud services, and with access strictly limited to collaborators.

2.2 NCA as a critical case study

The NCA can be defined a critical case of a protected multiple use landscape for purposes of identifying problems and opportunities relating to the collective-action challenges embedded in human-wildlife conflict and coexistence. Based on the critical case study method, we assume that a single case can be valid for all (or many) cases, as long as it includes similar characteristics and is representative of the general problem addressed (Yin 2003; Flyvbjerg 2011).

NCA can be considered an appropriate case study area for several reasons. First, the NCA is governed to achieve a triple objective: (i) to conserve its natural resources; (ii) to safeguard the interest of the resident population; and (iii) to promote tourism. This is similar to many other multiple- use areas, such as for example the World Heritage Site; Laponia in the Northern part of Sweden (Reimerson 2013), or the Cairngorm National Park in Scotland (Dinnie et al. 2012) which seek to balance various social, ecological, and economic interests and goals. As in many other areas, this has led to collective action problems for which long-term solutions are critically needed.

Second, the NCA is a key area for large carnivore species, which require large and connected landscapes to maintain viable populations (Tucker et al. 2018; Creel et al. 2019) and often play important roles as umbrella and/or flagship species and indicators of ecosystem health (Simberloff 1998; Ray et al. 2005; Sergio et al. 2008). While large carnivores can provide many indirect and non-monetary benefits (Stolton & Dudley 2019) and are often important for generating tourism revenue, they also pose risks and cause harm to humans and livestock, which results in costs to both resident human and carnivore populations. In addition, with the detailed monitoring of the population demography of the lion population in the Ngorongoro Crater since the 1960's (Packer 2023), and Ndutu since 2010 (Parsons et al. in

review), using NCA as a case study offers an opportunity to measure the impact from coexistence on the lion population itself.

Third, the NCA is a classic example of an area with increasing demands for natural resources by a growing human population, making it increasingly challenging to maintain biodiversity, including wildlife populations. As a result, there is an urgency to develop sustainable solutions to balance the growing and often opposing needs of people and wildlife (Garnett et al. 2007; Rands et al. 2010; Tucker et al. 2018; UNEP 2022).

As mentioned above, collective action may be hampered by opposing objectives and strong economic interests, as well as power imbalances and a lack of interdependence (ref. Ostrom 2007) (Ostrom 2009). In the case of the NCA, all of these factors are present, creating a great challenge in generating the cooperation among involved actors needed to reach a match of social-ecological scales and achieve the NCA's triple objectives. It is therefore reasonable to assume that the problems we identify here are also valid for many other similar multiple use landscapes.

2.3 Data collection

A combination of quantitative and some qualitative methods was used to map the human-lion interaction and coexistence situation in the NCA. Analyses of habitat selection, patterns of direct conflicts, and population genetics was applied to understand how lions use the coexistence landscape – how lions disperse and connect between subpopulations, how they cause and avoid conflicts, and how these conflicts in turn impacts their population structure. Further, focal group interviews, literature reviews and document analyses and were conducted to understand the social and governance structure of NCA, people's views, and the wider socio-ecological situation.

Lion demography data

To track the lion population demography, the population range was visited for regular search and visual observations of lions, aiming to see all residents regularly throughout their lifespan and to find all or most of any transient lions. Once found, the lions were approached in a vehicle to record data on location and life history traits, with each lion uniquely identified using natural markings, e.g., whisker spot pattern, scars (Pennycuick & Rudnai 1970) and a well-maintained photo-ID database (Fig 7). My study benefit

greatly from the long-term demographic study of the Crater lions by the Serengeti Lion Project, dating back to 1962 (Packer 2023). Together with the field team I maintain the Crater lion monitoring. Since 2010 the Ndutu resident lions were included in the demography monitoring, with addition of photographic data since 2007. The multiuse area between the Crater and Ndutu have some lion presence, but at far lower density and the lions tend to be very elusive, and much of the area is difficult or impossible terrain for vehicle access. Regular lion observation and identification is an aim, but it is opportunistic and infrequent. Here the observation normally happens at night, broadcasting recordings attractive to lions (feeding hyenas, bleating buffalo calf, and/or lion roar) to lure the lions to the vehicle.

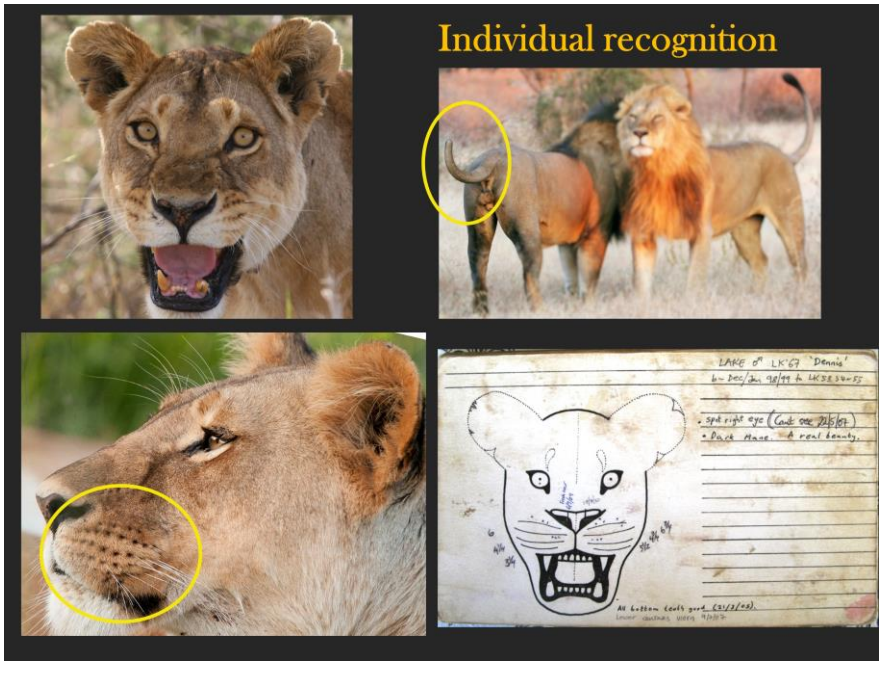

Figure 7. We identify each lion by natural markings, primarily their whisker spot pattern, a lion's "fingerprint", and by naturally accumulating ear notches, broken teeth, body scars etc. Each lion gets a unique ID, using ID cards and a continuously updated ID-photo catalogue. (Photos and arrangement by Ingela Jansson)

Lion movement data

To capture lion movements and use of habitat, we deployed satellite GPS collars on lions of both sexes. We used the collar models GPS Plus and Vertex Lite (VECTRONIC Aerospace 2024). Between October 2012 and March 2023, we had 22 different individuals collared: eight females (190 months total) and 14 males (252 months total). On average, individual lions were collared 19.9 months (range: 1.7 to 56.4 months). The collars had Iridium satellite data transmission (for regular data transfer), VHF-beacon (for real-time manual tracking), remote drop-off function, and were scheduled to take positions every 1-2 hours continuously, day or night. The collar batteries lasted for 2-3.5 years, after which the collar was either removed (using remote drop-off) or replaced. We targeted lions for collaring from adult or fully grown subadult individuals of either sex in NCA's multiuse area, from different groups and regions (Fig 8). We prioritized lions in areas that experienced higher conflicts from lions. The purpose of collaring lions was two-fold; to study lions' habitat use through fine-scale movements and to provide early-warning to livestock herders in the area.

Lions in NCA community lands are few and elusive, hence immobilization to deploy collars is challenging and done opportunistically, mainly at night, following observations of lions in the area. To attract lions closer to the vehicle for immobilization, we broadcasted a high-volume recording of feeding hyenas, a bleating buffalo calf, or the roars of a lion. The lions were immobilized and collared under permission from TAWIRI and the NCAA, whose veterinarians immobilized and supervised the collaring of all animals. Lions were free-darted from a vehicle at 10–20-meter distance using a CO2 powered rifle, and collars were fitted by myself or by our other most experienced field researcher. We closely monitored all lions until alert and deemed safe and well recovered after waking up from the immobilization.

Lion genetic data

We used Single Nucleotide Polymorphism (SNP) to genotype samples from lions to assess the genetic diversity and contemporary dispersal patterns of the Ngorongoro lion population. This was preceded by collection and export of samples, and the development of a lion-specific SNP panel. GS and other collaborators led the development of the SNP panel, using the samples from

Ngorongoro and a range of lion populations across Africa (in prep.). The resulting SNP panel used to assess our samples have 100 markers, including eight mitochondrial alleles and three sex-determining alleles.

Between 2011 and 2021 we collected samples of hair, faeces and tissue from lions for genetic analysis. Samples were carefully collected and stored to avoid DNA-denaturing and contamination. Most collections were opportunistic and non-invasive, e.g. faeces and hair. We collected tissue samples from lions immobilized for other purposes, and from any encountered. Between December 2014 and October 2015, we also collected tissue from 21 lions using mildly invasive biopsy-darting, conducted by their veterinarian. With the biopsy darting we were able to target the sampling for genetic study purposes, and thus targeted lions from different prides and those least related to each other, their putative relatedness based on our demography study.

Of 404 exported, 284 had sufficient DNA material for further processing and SNP-genotyping.

Figure 8. Collaring and team-work weighing of Puyol , a previously unknown male, established as resident male in Twin Hill pride. (Photo: Ingela Jansson)

2.3.1 Human-Lion conflicts and coexistence

Lion-livestock conflict events

To explore the type and level of human-carnivore interactions in the NCA and their impact on pastoralist livelihoods, we employed enumerators locally to collect quantitative data on carnivore-livestock depredations within their home-communities. Our ambition was to record all wildlife-livestock attacks that occurred during the study period during a 1-year period between 2012 and 2014. The enumerators went to each attack event directly to verify and collect temporal, spatial and contextual data of the attacks (if at "boma" or at pasture, livestock species attacked, carnivore species blamed) and its relative impact on the affected household.

Landscape and human activity variables

We modelled lion habitat selection using landscape variables representing habitat characteristics and conflict risk (i.e., humans on the landscape). We limited the habitat selection study to our main field study area, encompassing 4,800 km^2 of the central expanse of the NCA, from and including the Ngorongoro Crater westward to the border of SNP. Habitat covariates included vegetation cover, to capture lion preference for sheltering and/or stalking under cover (Hopcraft et al. 2005; Loarie et al. 2013); a terrain ruggedness (Riley et al. 1999) to capture lions' use of rugged, less accessible areas for shelter and/or stalking; an Enhanced Vegetation Index, hereafter EVI, by MODIS (Didan 2015) to capture greenness to capture vegetation greenness, a proxy for forage quality and quantity(Villamuelas et al. 2016), which tends to influence both wild and domestic herbivore (lion prey) distribution (Zengeya et al. 2015); and the distance to the nearest riverbed which lions commonly use for stalking prey or resting in thick riverine vegetation (Hopcraft et al. 2005; Mosser et al. 2009). We got the landscape variables from open source and other available spatial data resources from the region. Our field team collected all the water points and a large portion of the boma locations during field surveys, and others were located from a Google Earth satellite map by a staff familiar with the area, with knowledge of the boma distribution, its owners and what seasons the bomas were inhabited. The AI generated buildings layer by Song et al., (2023) helped in the Google Earth mapping process.

To capture human activity across the landscape, we recorded GPS locations of bomas, buildings, and water-points (i.e., rivers, springs, wells,

and dams with drinkable water for people and animals) within our study area between 2013-2020. Bomas are a pastoralist family homestead, with a large corral for livestock in the centre surrounded by huts and occasionally small houses. Bomas are the centre of livestock herding activity, where livestock depart every day for pasture and water, typically ranging up to 10 km per day from bomas. Bomas are either inhabited year-around or seasonally (used only in the dry or wet season) with exact locations varying over time even as the general settlement areas have remained the same. The area used by the collared lions occasionally exceeded our main study area. Our field team expanded the field mapping of water-points to cover this area, while team members well familiar with the area viewed Google Earth satellite map to remotely map all the bomas and assigning them as permanent or seasonal bomas. To aid this process, we overlaid the artificially generated building locations by (Song et al. 2023), which pinpointed each building structure, regardless of size, anything from a small hut to a large school building. Our aim was to map each boma, not each individual hut, hence our field and manual boma mapping, as well as assignment of permanent or seasonal use remained important.

Of the 5,058 habitations inside NCA, 67% were bomas (of which 33% were mapped in the field), 21% single buildings in village centres, 6% buildings at tourism lodges and permanent camps, 5% other buildings like schools, hospital, museum, ranger posts, and 1% were single buildings among the boma settlements. Of the bomas mapped in field, 1,073 included a count of huts with an average 4.6 huts per boma (SD=3.44, range 0-30). This included both large and small, permanent and seasonal bomas, thus a good representation for boma structures across the NCA. In comparison to the widespread bomas, buildings and concentrated settlements are clustered. To geo-locate individual buildings in a built-up area we drew polygons around all clusters of buildings on the Google Earth map from which we extracted individual buildings from (Song et al. 2023) building layer. This resulted in 42 polygons around village centres, schools, the NCA's hospital, ranger posts, tourism lodges and camps, sized between 0.2 to 56.4 ha of a total 284 ha, being a 0.05% coverage of the study area. We combined the location data of bomas and buildings into a "boma" spatial layer, that we used in the model as a proxy for human activity. The resulting variables for the habitat selection analysed were distance to the nearest boma, distance to the nearest water point, and density of bomas.

Unlike most other studies of wide-ranging animal habitat selection, we did not include roads as we assumed them to have little or no impact on lion movements. The roads in the NCA consist of a limited network of dirt and gravel roads, night-time driving and motorbikes are restricted, and vehicles are few. The main road crossing the NCA from east to west into the Serengeti can have hundreds of vehicles in a day, in pulses of tourism and local transport traffic. On other roads, the traffic is very limited, often with an unclear continuum between road and a path used by livestock and wildlife.

Interviews

For the qualitative data on human-wildlife conflict (article V), we conducted interviews and focus group discussions from June to September 2017 with members of four key stakeholder groups: the NCA Authority, the Ngorongoro Pastoral Council (NPC), the NCA communities, and tourism operators. During the same period, we also held follow-up meetings with community members in three wards within the study area, all of which experience some level of human-lion conflict. In each ward, we engaged five different stakeholder groups: (1) village council members; (2) traditional Maasai leaders; (3) village elders; (4) current and recently retired warriors; and (5) general community members. Through these engagements, we obtained views on conservation and human-lion conflict in the NCA, opinions on current governance and management systems, and preferences regarding alternative policies and policy instruments to handle human-wildlife conflict. In total, we conducted 14 focus groups and 15 interviews.

Literature review and policy analyses

The literature review includes peer reviewed publications on the region's history and ecology and reports containing socio-economic data for the region (URT 2019, 2022a) Ngorongoro Community (2022), NCAA (2006). Relevant laws and regulations documents were analysed, including the Ngorongoro Conservation Area Act, Ord. No. 14 of 1959, as amended (URT 1959, 1975), the NCA Authority by-laws, 1992 (URT 1992), the NCA (Establishment of Pastoral Council) Rules, 2000, the NCA General Management Plan (2006 - 2016), the Wildlife Conservation Act, 2009 (URT 1975, 2022b), and the Wildlife Conservation (Dangerous Animals Damage Consolation) Regulations, 2011 (URT 2011), to identify relevant policy and governance aspects for the human-lion coexistence situation in NCA.

2.4 Data analyses

The primary focus of this work is ecology, specifically evaluating lions' habitat use, depredation patterns, and the genetic status and connectivity of the well-studied lion population in the NCA. This evaluation is framed within a socio-ecological perspective, guided by Ostrom's Socio-Ecological Systems (SES) framework (Ostrom 2009). This approach considers the interconnectedness of supporting resources (such as rangelands for pastoralists and wildlife for tourism), the needs of lions and their impacts on human livelihoods, the context of key stakeholders with their diverging interests, and the laws, regulations, and cultural taboos that govern the area (Ostrom 2005, 2009; Vogt et al. 2015). These elements were mapped and analysed to determine the drivers of conflict and explore potential solutions. The findings were then used to discuss new, feasible, and more sustainable models for collaborative coexistence.

2.4.1 Quantitative analyses

Habitat selection analyses

To understand how lions use the landscape, where they settle, how they move around as they cause and avoid conflict, we analysed their habitat selection (article II). We used locations from GPS collared lions to compare used versus available habitat from a selection of spatial data layers that we deemed important for a lion's habitat choice. The habitat selection patterns often depends on scale (McGarigal et al. 2016). Therefore we analysed how lions select habitats at the landscape scale, using resource selection functions, hereafter "RSF", and how they then navigate those chosen habitats at the finer local scale, using step-selection functions, hereafter "SSF", (Avgar et al. 2016). As a lion, depending on its sex and social context, have different requirements, we ran a separate set of models for three different lion categories: resident males (i.e., those settled with a pride and not making long-distance movements), nomadic males (i.e., males not associated with a pride, making frequent long-range movements) and females (settled, requiring shelter and more resources when raising young). Our definitions of the social status of a male were based on our long-term detailed lion monitoring with direct observations and individual recognition (Packer 2023). A male was defined as nomadic when he departed from his natal pride (usually by 2-3 years of age), and/or when he ceased to be the resident male

of a pride. A male was defined as a resident when he was seen consecutive times with a pride and actively engaging with the females, a status that typically lasts for 2-3 years (Pusey & Packer 1987).

As lions are likely to use habitat differently depending on conditions for resources and risk (Suraci et al. 2019; Mills et al. 2023), we modelled habitat selection (RSF and SSF) separately for wet and dry seasons and for nocturnal and diurnal movements. We separated into day- and night-time positions using the R package suncalc (Thieurmel & Elmarhraoui 2022).

Lion genetic connectivity

For the genetic analyses we extracted DNA from tissue, faeces, and hair samples and genotyped them on our lion-specific SNP panel, containing 100 markers, including 89 autosomal, eight mitochondrial, and three Y-chromosome markers. After low-quality samples were filtered out, we used the R package allelematch (Galpern et al. 2012) which identified unique individuals, and following also manual verification against field data, we retained 197 high-quality genotypes. These included 116 from known individuals, 17 from known groups, and 64 without individual information. We also included 32 high-quality genotypes from southern Tanzania as an outgroup anchor genetic structure assessments.

We assessed population structure using and Discriminant Analysis of Principal Components (DAPC), which looks for differences within as well as between clusters, and spatial PCA (sPCA) using R package adegenet (Jombart 2008). We also used STRUCTURE 2.3.3 for Bayesian clustering (Pritchard et al. 2000; Earl & vonHoldt 2012). We used DAPC to identifying optimal subpopulation clusters (Jombart et al. 2010), and STRUCTURE to determine the most likely number of clusters based on allele frequencies. The clustering results were visualized using the package mapmixture (Jenkins 2024), and we conducted downstream analyses to compare, including heterozygosity (using the Kruskal-Wallis test and Dunn's post-hoc Bonferroni test), Hardy-Weinberg Equilibrium (HWE) (Guo & Thompson 1992), and the F-statistics F_{st} (genetic variation between populations) and F_{is} (inbreeding coefficient), estimated using the R package hierfstat (Goudet 2005).

To assess contemporary dispersal, we calculated pairwise relatedness (r-values) (Lynch & Ritland 1999) using the R package SNPRelate (Zheng et al. 2012) to identify first-order relationships (parent-offspring or full siblings). We focused on r-values between 0.4 and 0.8 and excluded all

individuals under 2.5 years of age as considered dependent and still with their mothers. We then plotted the remaining putative PO or FS pairs on a map to detect signs of dispersal and gene-flow between subpopulations, a primary objective of this study. Additional demographic data, such as age, natal area, and last known location, were incorporated to infer dispersal patterns

Human-wildlife interaction

We analysed presence-only data on livestock attacks, identifying the most frequently involved predators and comparing their predation patterns. Using R (R Core Team 2024), a Pearson's Chi-square test was conducted to examine attacks by key predators against five factors: attack context (boma, pasture herded, pasture lost), season (wet/dry), livestock type (cattle, donkey, shoat, dog), month, and time of day. The wet season was defined from December to May, and the dry season from June to November.

To further analyse predator behaviour, we applied stepwise model selection based on the Akaike Information Criterion (AIC) using the nnet and MASS packages in R, with lions as the reference category. Multinomial log-linear models (Venables & Ripley 2002) were used to compare against hyenas and leopards, with predictors based on typical lion behaviour.

We assessed the distances from attack locations to owners' homesteads using the Kruskal-Wallis test and Dunn's post-hoc comparisons, focusing on pasture attacks. For economic impact, we calculated livestock and monetary losses relative to ownership, standardizing losses using Tropical Livestock Units (TLU) based on species and category values.

Kernel Density Heat Maps were generated in QGIS (Version 3.28) with a 2.5 km radius, visualizing attack locations by predator and overlaid on NCA boundaries and relevant geographic features.

2.4.2 Qualitative analyses

The system perspective requires some qualitative analyses to put the situation into context, and to be able to answer the research questions 2 and 4. Consequently, ethnographic methods and thematic analysis were used.

Participant observation

The ethnographic methods included participant observation (Musante & DeWalt 2010; Bernard 2018) where I in prolonged field work, participated

in the daily lives of key right- and stakeholders in this case study and is therefore able to place specific events (e.g., human-lion conflicts) in a broader context of the NCA's conflict situation. The observation data on people's relations to lions, actions, relations between stakeholder groups, the varied and context dependent views on coexistence were analysed on the basis of Ostrom's SES framework.

Literature review, interviews and policy analyses

The collected data was analysed from the outset of both social and ecological aspects inspired by Ostrom's SES framework. For the analysis of policy documents and interviews (article V), we employed thematic analysis (Thomas 2006) to identify and interpret important themes related to the conservation and management of the area, as well as potential solutions to handle conflicts. We followed a four-step approach inspired by (Clarke & Braun 2017; Herzog et al. 2017): (1) transcription and familiarization with the documents to select representative quotations; (2) identification of key terms and patterns; (3) coding to capture core messages; and (4) theme development to organize codes into patterns. This structured approach enhances consistency and replicability in data interpretation, ensuring thoroughness and minimizing bias while systematically progressing from initial data engagement to the identification of themes related to the research questions.

2.5 Limitations in methodology and data availability

As with any real-time study requiring opportunistic data collection, there are inevitably data we hoped to obtain but did not. With genetic samples from a larger proportion of the population, our analyses of relatedness and assessments of current gene flow within the population would be more comprehensive and less patchy.

The presence-only-data in our depredation study, i.e., records solely of predator-livestock attacks, limited the assessment of risk due to the lack of data on locations and contexts where attacks did not occur. Furthermore, with attack-only data, I was unable to evaluate the relative impact of lions and other carnivores on livestock and livelihoods or compare carnivore conflict rates to losses from other causes such as drought and disease. However, such assessments have been conducted in similar landscapes, and based on the

observations, it is reasonable to assume that the proportion of impacts is similar in the NCA.

My lack of understanding of formalised tracking of social data, such as coding for appropriate qualitative assessments, led to many missed opportunities of data gathering from the many informal meetings and discussions that have taken place over the years.

The abundance and distribution of natural prey are identified as important factors influencing lion movements and habitat use. However concrete measures of natural prey abundance across the landscape were unavailable, so season and EVI were used as proxies instead. Future studies that measure prey relative abundance across the NCA will be important to improving our understanding of the dynamics between lions, natural prey and humans as lions move through the landscape. Second, bomas was used as a proxy for human and livestock presence, however exact boma locations shift regularly and most livestock depredations happen at pasture which may not be well captured by boma locations and/or EVI. Since livestock represent both an attracting force (as food) and a repelling force (as a source of conflict), more data on livestock relative abundance over space and time would provide a better understanding of direct interactions between lions and livestock, and thus context for human-lion conflict in the NCA.

For assessment of genetic diversity and relatedness, our study would have benefitted from a greater coverage of the population, especially given that there are very few dispersals into the Crater, and with a higher proportion of the population sampled, we would have a greater chance to document those rare events. The genetic study might also have benefitted from greater number of SNPs for higher and more reliable resolution to the patterns of relatedness (Nazareno et al. 2017) and heterozygosity (Kardos et al. 2016). The SNP panel we used was especially developed for optimizing results from low quality genetic samples like faeces, and with this come the trade-offs between quality and quantity. While tissue samples are the optimal sample for genotyping, the most likely sample to catch from an elusive lion in the wider landscape is finding its faeces or hairs.

3. Results

Connectivity between subpopulations is vital for the persistence of large carnivores in fragmented landscapes, enabling genetic exchange and recovery from stochastic events. As wild spaces diminish, and populations become increasingly fragmented, large carnivore declines are driven by reduced individual opportunity to move between isolated groups. Where anthropogenic landscapes separate these subpopulations, connectivity depends on the socio-ecological conditions that support coexistence and the behavioural choices of dispersing individuals. With that in mind, the key results from the five chapters are presented.

3.1 Movements and habitat selection by lions across a multi-use landscape (paper I)

To better understand how lions navigate the wider NCA landscape, avoiding or causing conflict, we used data from GPS collared lions to assess habitat selection. This study revealed that lions strongly select for cover to avoid humans, with avoidance patterns varying by scale, time of day, season, and individual characteristics. At both local and landscape scales, lions, particularly females and resident males, avoid areas of high human density, utilizing cover to navigate safely and adjust their movements temporally. Human presence impacts habitat use, with significant seasonal differences in avoidance patterns.

Female lions showed consistent avoidance of humans, while male lions exhibited greater variation, suggesting different risk tolerances. The study highlighted that understanding individual and sex-based differences in lion behaviour is critical for assessing their response to human presence and promoting coexistence.

The resistance map (Fig 9) show that around the Crater highlands and escarpment, a mosaic of high and low resistance areas was observed, with small village centres presenting high resistance but interspersed with low-resistance patches. The western short-grass plains exhibited intermediate resistance due to sparse cover and human settlements, with some areas southwest of Ndutu showing low resistance due to the absence of human presence.

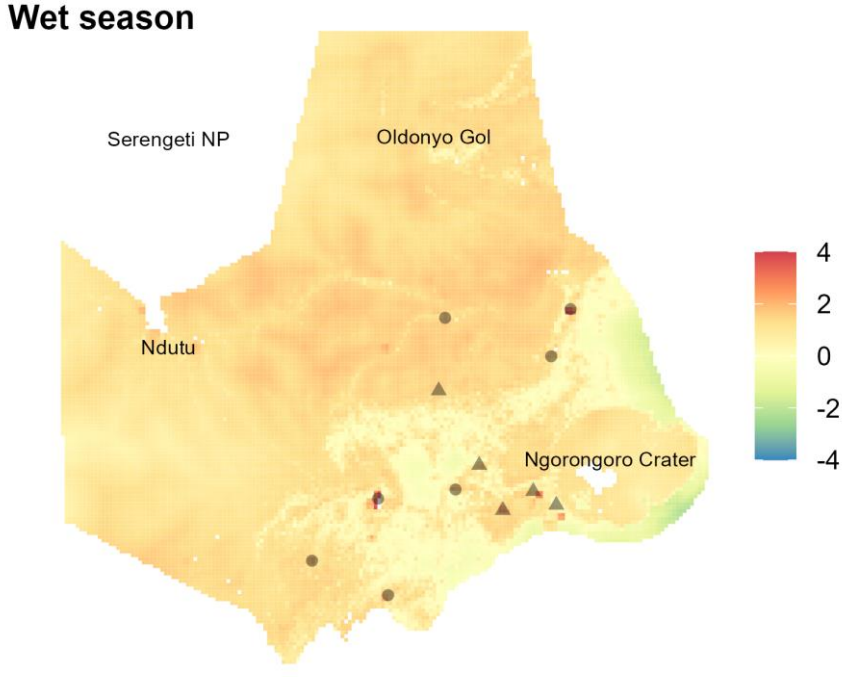

Figure 9. Resistance map of the NCA for nomadic male lions during the wet season, likely reflecting dispersal behaviour. The map shows relative resistance values (red = high resistance, yellow = neutral, blue = low resistance) based on local-scale habitat selection (SSF). Resistance is highest in densely settled areas west and north of the Ngorongoro Crater and in steep terrain, while forested areas nearby show the least resistance. Major regions, ward centres (circles), and villages (triangles) are included for reference.

This resistance map indicated no major barriers to lion movement between the Ngorongoro Crater and the Serengeti National Park, suggesting that current human presence does not significantly impede connectivity between lion subpopulations. However, resistance was highest in densely populated human areas and steep terrain, while least resistance was found in forested habitats near these human-occupied regions. The analysis highlights the ability of lions to navigate the multi-use landscape, although the findings are based on a small sample size, which may not fully represent the entire lion population.

3.2 Human-lion interactions – direct conflict patterns in NCA by large carnivores' livestock attacks (Paper II)

This study investigates the patterns and drivers of livestock predation by large carnivores in the NCA where traditional pastoralism and wildlife conservation overlap. Human-wildlife conflict, particularly due to livestock predation by lions, leopards (*Panthera pardus*), and spotted hyenas (*Crocuta crocuta*), poses significant challenges to local livelihoods and conservation efforts. The aim of this study is to understand predation patterns to inform targeted and effective mitigation strategies.

Two juveniles of the Masek pride just caught a lost cow. (Photo: Ingela Jansson)

Over a one-year period, we documented 755 livestock depredation events, with spotted hyenas responsible for the highest proportion of attacks (34%), followed by leopards (29%) and lions (18%). Key findings (Fig 10) indicate

that spotted hyenas predominantly attacked cattle, at night, mostly livestock lost at pasture, with no strong seasonal preference. Leopards mainly targeted the smaller sheep and goats, especially by attacking bomas at night, with no seasonal difference. Lions most often attacked cattle, particularly in the late afternoon, and or at night, on livestock at pasture, and more attacks during the dry season. Lion and leopard attacks were more concentrated to the Ngorongoro highlands and the escarpment towards Lake Eyasi, seemingly avoiding the wider open regions.

Multinomial logistic regression confirmed that the risk of attack by each predator species was significantly influenced by a combination of factors, including livestock type, time of day, season, and attack context.

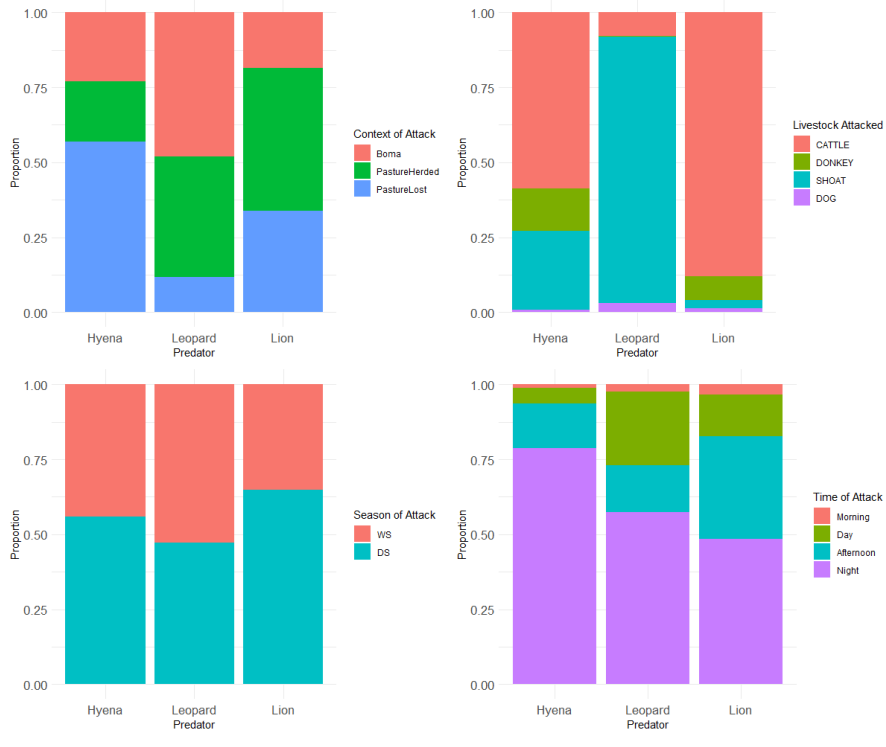

Figure 10. Predation patterns by hyena, leopard, and lion, the predators responsible for most livestock attacks in the NCA. The figure shows the relationships for each predator in relation to Context of attack, Livestock attacked, Season of attack, and Time of attack. All patterns were significantly different, except for leopard attacks in relation to season.

The study reveals that predator-specific patterns of attack are shaped by a complex interplay of environmental factors, prey availability, and husbandry practices. This understanding is crucial for developing targeted mitigation measures. For example, reinforcing bomas, improving night-time livestock protection, extra vigilance when bringing livestock back in the evening, and implementing seasonal grazing adjustments could significantly reduce the frequency and severity of attacks.

Our findings also highlight the economic impact of livestock losses, which impact local livelihoods and contribute to negative attitudes toward wildlife conservation. In the NCA, where pastoral communities depend heavily on livestock for their income and food security, the cumulative economic losses from predation can be substantial.

3.3 Ngorongoro lions' population structure, genetic status and connectivity (Paper III)

Human encroachment and habitat fragmentation are major threats to large carnivores, causing population isolation, reduced genetic diversity, and limited connectivity. This study focuses on assessing the genetic diversity, population structure, and dispersal patterns of lions in the NCA based on SNP-genotyped lion samples to understand the impact of isolation and to contribute towards population conservation strategies the consideration of genetic diversity and long-term viability.

The analysis revealed significant genetic differentiation between the lions in the Ngorongoro Crater and those in the nearby Ndutu and the adjacent Serengeti National Park (Fig 11). The Crater population showing markedly lower genetic diversity and higher levels of inbreeding, likely due to repeated bottlenecks in the past and limited gene flow. The presence of monomorphic SNPs and lower heterozygosity further indicate inbreeding and genetic drift in the Crater population. Evidence of restricted dispersal into the Crater was observed, with few putative parent-offspring or full-sibling links, suggesting limited gene flow that could threaten the population's long-term viability and resilience to environmental changes.

To mitigate further genetic isolation and inbreeding, the study recommends enhancing gene flow through natural migration and reducing human-lion conflict via community-engaged conservation strategies. The

"corridor of tolerance" approach, which involves community involvement and conflict mitigation, shows potential for improving connectivity and supporting coexistence between lions and local communities. However, significant challenges remain, including overcoming the resilience of established male coalitions within the Crater, which seemingly impedes the successful integration of incoming migrants.

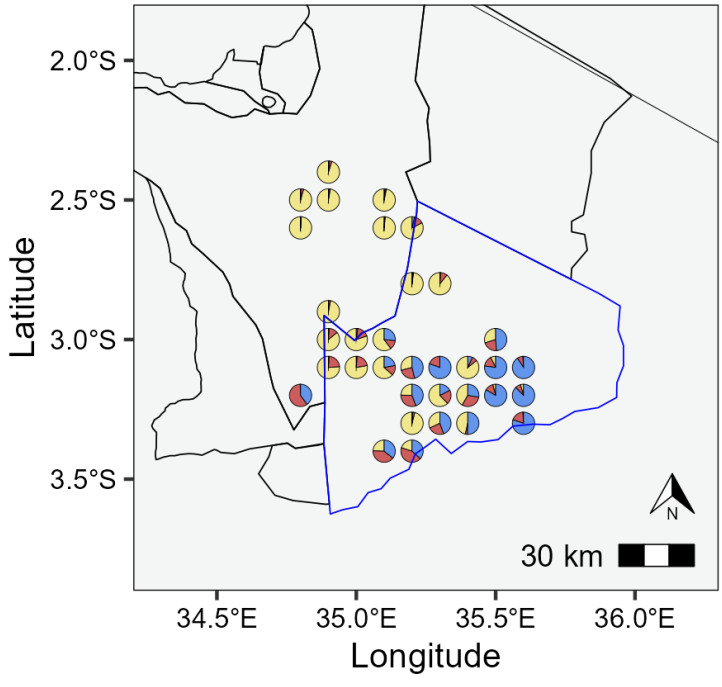

Figure 11. Map of the NCA (blue outline) and Greater Serengeti Ecosystem (black outline) showing admixture proportions (K=3) based on STRUCTURE results for 89 autosomal SNPs from 197 lions. Pie plots represent sampling locations, highlighting a gradient shift in admixture from the Serengeti to Ndutu and toward the Crater.

3.4 Improving connectivity by collective conservation action (Paper IV)

For large carnivores, which are often prone to conflict with humans, connecting populations separated by human-dominated habitats is particularly challenging. It requires dedicated efforts to increase tolerance, mitigate conflicts, prevent carnivore killings, and foster human-wildlife coexistence. This study evaluated the impact of inclusive conservation actions in the NCA on lion connectivity across these landscapes. The conservation measures implemented included preventing both traditional and retaliatory lion hunts, engaging communities in lion conservation, issuing early warnings of lion presence, reinforcing bomas, and treating livestock wounds after attacks. Using lion observation data (1962-2023) and GPS collar movement data (2012-2023), we found that conflict mitigation efforts were positively associated with increased lion movements across human-occupied areas, suggesting enhanced connectivity. After conservation activities began in 2011, we documented previously unknown male coalitions entering into the Crater in 2013 and 2015, contributing to population growth (Fig 12). In 2018, a coalition of two young males from the Ndutu area near Serengeti National Park entered the Crater, though they were unable to establish residency. Our results show that the number of new lions moving into the Crater each year was positively associated with conflict mitigation efforts, indicating that conservation activities are effectively enhancing connectivity for lions in the region. Additionally, precipitation appeared to enhance the ability of lions to occupy and move through the greater NCA, while the presence of large male coalitions in the Crater seemed to discourage new immigrants, likely due to larger resident coalitions being better able to chase off solitary immigrants or smaller coalitions (Packer 2023).

We also documented, even more frequent and successful, the dispersal out from the Crater and to nearby Serengeti. Since monitoring began in the Ndutu area in 2010, no Crater-born lions were observed there until 2019, when the first dispersal events (n=4 males) from the Crater to Ndutu were recorded. This was followed by further dispersals in 2020 (n=3 males) and 2021 (n=3 males), with all these male coalitions successfully establishing residency with lion prides in Ndutu. GPS tracking indicated limited overall movement between the Crater and the greater NCA but showed a significant increase in the likelihood of Crater-born lions dispersing over time.

While the primary goal of conservation efforts was to enhance the ability of lions to safely cross multi-use areas and maintain connectivity between the NCA and the greater Serengeti ecosystem, another key indicator of success was the ability of lions to settle in and utilize multi-use habitats. After 2011, as conservation efforts increased, we observed longer forays by collared male lions into the greater NCA and the first documented cases of Crater lions settling in these areas, some of whom were later joined by nomadic males from outside the Crater.

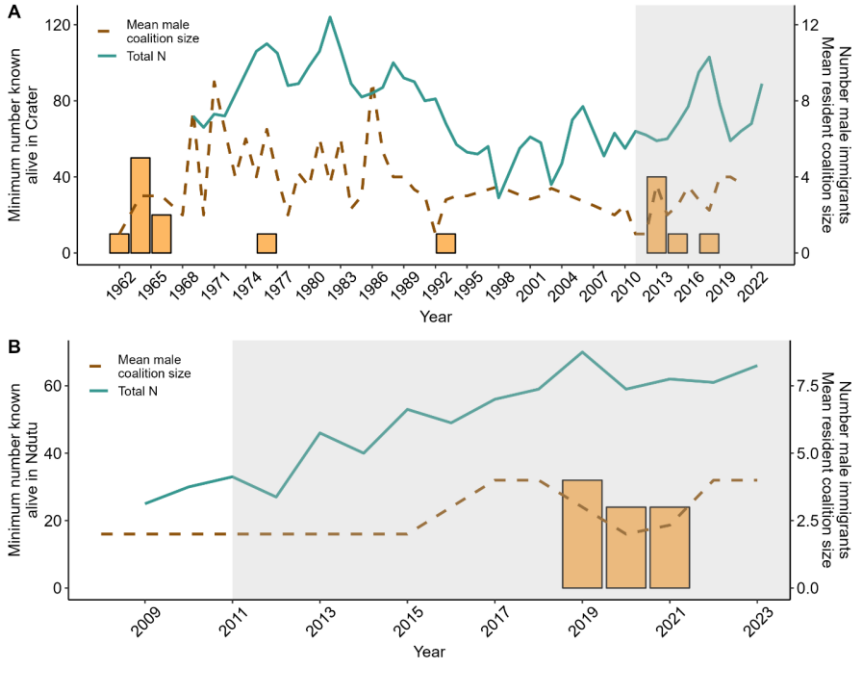

Figure 12: Indices of lion abundance ("Total N"), resident male coalition size and male immigrants over time for the Ngorongoro Crater from 1969-2023 (A) and Ndutu from 2009-2023 (B). An index of lion abundance (minimum number of unique individuals known alive) in each area (Crater and Ndutu, respectively) is shown in the blue line, the average resident male coalition size is shown in the red dashed line and the number of known male immigrants into the population is shown in the orange bars. The grey shading represents the era of KopeLion conflict mitigation (2011-present). The lion population in the Crater increased after an initial influx of males in the early 1960s, dropping to 29 in 1998 from a peak of 124 in 1982. The population subsequently increased again following an influx of males in 2013, 2015 and 2018, the largest since the 1960s. The lion population of Ndutu also steadily increased from 2009 to 2023, with the first Crater-born males successfully dispersing to Ndutu in 2019, with further dispersers detected and establishing as resident males in 2020 and 2021.

Although human-lion conflict declined from 2016 to 2021, an extreme drought and an influx of people from a neighbouring protected area in 2022 caused a sharp escalation in conflict, resulting in increased retaliatory lion killings and livestock attacks. Conflict levels decreased again in 2023, but these events highlight the ongoing challenges and the need for adaptable, long-term strategies to maintain balance amid changing socio-ecological conditions. Overall, while our results demonstrate the benefits of inclusive conservation for enhancing connectivity among large carnivore populations, they also point to persistent challenges and the need for flexible, long-term approaches to sustain coexistence between humans and large carnivores.

3.5 The potential of conservation incentive payment policies to promote human–wildlife coexistence (Paper V)

Over the past two decades, Conservation Incentive Payments (CIPs) have emerged as tools to promote human-wildlife coexistence by aligning local economic interests with conservation goals. The success of CIPs depends on the interplay of three governance elements: polity (governance structures), politics (negotiation processes), and policy (rules and instruments). This chapter analyses how policy changes can drive shifts in governance and power dynamics, enhancing CIP effectiveness.

We examine the potential of CIPs in Tanzania's Ngorongoro Conservation Area (NCA), where human-lion conflict persists due to retaliatory killings and exclusion from governance decisions. To explore piloting a CIP program in the NCA, we reviewed legal documents and engaged stakeholders through interviews, focus groups, and a joint-stakeholder workshop. This process identified key issues, developed program options, and led to the conditional approval of a pilot CIP program. In 2019, a CIP Design Committee was formed with representatives from all stakeholder groups to finalize the program's terms. Some of the many views of lions from the discussions in Fig 13.

Our findings show that CIP effectiveness depends on understanding local socio-economic and cultural contexts. The NCA's historical top-down governance model has caused resentment and distrust, but involving local stakeholders in the CIP design can foster more participatory governance. Stakeholders recognized benefits such as community partnership in

conservation and fair benefit distribution but also noted challenges, including verifying lion presence and fair fund management. Our collaborative approach was essential in addressing these concerns.

While CIPs can align local and conservation interests, success requires integrating them with broader governance reforms to safeguard local rights and livelihoods. The NCA case underscores the need for a comprehensive approach that includes political, social, and policy considerations for sustainable governance in human-wildlife conflict areas.

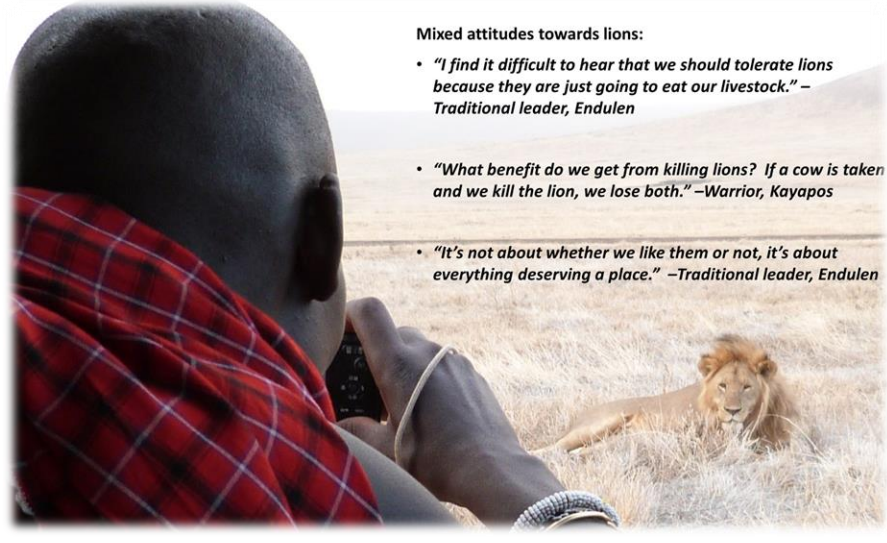

Figure 13: Some of the many views on lions and on the coexistence context in NCA.

4. Discussion

The overarching objective of this thesis is to explore human-lion conflict and coexistence in a rapidly evolving multi use landscape, focusing on its impact on the lion population and the potential of inclusive conservation to maintain and strengthen the ecological connectivity of lions across a pastoralist landscape.

*RQ 1: How do environmental and human factors influence lion movements and connectivity across the landscape? (Paper **I**, II, III)*

The findings revealed that lions adjust their movements both spatially and temporally to avoid humans, that lions strongly select for cover to avoid humans, with avoidance patterns varying by scale, time of day, season, and individual characteristics. At both local and landscape scales, lions, particularly females and resident males, avoid areas of high human density, utilizing cover to navigate safely and adjust their movements temporally. Human presence impacts habitat use, with significant seasonal differences in avoidance patterns.

Female lions showed consistent avoidance of humans, while male lions exhibited greater variation, suggesting different risk tolerances. The study highlighted that understanding individual and sex-based differences in lion behaviour is critical for assessing their response to human presence and promoting coexistence. These behaviours align with recent studies on other carnivores, showing how behavioural plasticity can promote coexistence with humans (Oriol-Cotterill et al. 2015a; Suraci et al. 2019; Mills et al. 2023), including preferentially seeking cover habitats and approaching humans only at night. These types of behavioural adaptations have been noted for other carnivores living near humans (Ordiz et al. 2011; Leighton et al. 2022) and exemplify the ways in which carnivore behavioural plasticity can promote coexistence with humans.

Resistance mapping indicates that the current level of sparse pastoralist settlements in the NCA does not significantly block lion subpopulation connectivity, which is primarily facilitated by nomadic males. Compared to resident lions, nomadic males display a stronger tendency to avoid human presence, suggesting an adaptive strategy to minimize conflict while exploiting available resources (Mills et al. 2023).

In the NCA, humans represent both a risk and a potential resource for lions, leading to a delicate balance in their movement patterns. While very long-distance movements of lions have been documented in other regions, such as Kenya, Uganda and Zimbabwe, including traverse rivers and densely populated areas, such movements have not been observed here. This is likely because nomadic lions in the NCA find suitable habitats within closer proximity, reducing the need for extensive travel. However, it is also possible that these rare, exploratory movements could easily be missed.

*RQ 2: What are the patterns and impacts of conflict between humans and predators, particularly lions, and how do these conflicts shape human-lion interactions? (Paper I, **II**, IV)*

Finding avoidance but no blockage in the environment, including the pastoralist settlements, corroborates the prediction that human-lion conflicts are a main driver for the apparent lack of connectivity across NCA's landscape. Conflicts are common-place, and as in similar areas, lions are targeting the most valuable livestock. The killing of lions has been a common retaliatory reaction. It can also help to shape the important relationship between man and lion, so they continue to have respectful fear for each other.

However, humans remain dangerous to carnivores, with retaliatory killings still a major cause of lion mortality in NCA's multiuse landscape (Jansson 2023). With the human population increasing in the NCA (URT 2022a) and across the lion's range (Riggio et al. 2013; Sargent et al. 2022), increased levels of conflict can be expected. Strategies to promote human-lion coexistence in the NCA are being implemented, including carnivore conflict mitigation, community engagement, and incentivization programs. Early signs are encouraging that human tolerance for lions in the NCA can be increased, however the extent to which human behavioural plasticity can match lion behavioural choices to mitigate conflict remains to be seen. Results suggest that external factors such as vegetation productivity and abundance of natural prey on the landscape can affect the potential for

conflict through changes in lion habitat use. Environmental changes that negatively affect pasture productivity and/or wild prey abundance (e.g., climate change, drought, degradation of rangelands, invasive species) could be expected to increase levels of human-lion conflict. As human and lion ranges increasingly overlap across fragmented landscapes under changing environmental conditions, a better understanding of factors affecting lion habitat use and behavioural adaptations will be critical for the continued conservation of this iconic species in the NCA and throughout Africa.

RQ 3: What is the impact of human-lion interactions on lion dispersal, gene flow, and genetic structure and its implications on the long-term lion population viability? (Paper I, II, ***III****)*

The genetic study largely supports findings from long-term demographic research, revealing very limited connectivity between the Crater subpopulation and the nearby Serengeti lions. A distinct subpopulation structure exists, with Crater lions showing significantly lower genetic variation and higher relatedness compared to those in Ndutu and the Serengeti, indicating a source-sink dynamic. The presence of strong male coalitions born in the Crater deters immigration from other males, further limiting gene flow into the Crater. While human interactions are likely a contributing factor, as seen in other lion studies, the dominant local male coalitions also play a critical role in restricting genetic diversity.

Effective connectivity for conservation is best achieved when migrants come from nearby populations, as this reduces the risk of introducing new pathogens and ensures that new genes are well-adapted to local conditions, minimizing the risk of outbreeding depression. Introducing individuals from distant populations to enhance genetic diversity should only be considered as a last resort. Therefore, conservation efforts should focus on maintaining genetic diversity, managing inbreeding, and ensuring connectivity between populations to enhance their adaptive potential and resilience to environmental changes.

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genetic diversity, managing inbreeding, and ensuring connectivity between populations to enhance their adaptive potential and resilience to environmental changes.

*RQ 4: What are the challenges and opportunities for improving human-lion coexistence strategies, and how might these affect population connectivity? (Paper III, **IV**, **V**)*

The evaluation focused on whether activities aimed at mitigating human-wildlife conflict in multi-use habitats are enhancing lions' ability to exploit human-use areas and promoting movement between lion sub-populations. Like other studies of lions in Africa (Blackburn et al. 2016; Western et al. 2019) encouraging signs that increased tolerance for lions is possible with concerted conservation efforts was found. Pastoralists on the landscape indicated support and engagement with lion conservation activities. Consistent with conservation activities improving connectivity for Crater lions with lions in the greater NCA, evidence was found of increased lion immigration into the Crater, dispersals of Crater-born lions into adjacent areas, and lion presence and settling in the multiuse area following initiation of conservation actions. During the same period, a drop in retaliatory and ritual killings was identified, which have likely been major factors for lions' disappearance from the landscape. Specifically, a positive relationship between an index of conflict mitigation representing KopeLion activities and the number of lions moving into the Crater each year could be detected. This is good news for the Crater lion population given its history of isolation and inbreeding (Packer et al. 1991; Packer 2023; Jansson et al. n.d.) and provides evidence that conservation efforts can successfully provide connectivity between the Crater population with the larger Serengeti lion population. However, increases in lion and human populations on the landscape, coupled with severe drought in 2022, have recently arrested the improvement of human-lion coexistence in the NCA, highlighting the need for continued work to mitigate conflicts and ensure the future of the Ngorongoro lions.

Living among wildlife, especially large carnivores, can impose a significant financial burden and often the local people shouldering that burden do not receive the financial benefits of wildlife conservation (i.e., tourism dollars). Conservation Incentive Payments (CIP) have been proposed to decrease that financial burden and increase the ceiling of social carrying capacity for carnivores (Pekor et al. 2019). KopeLion is currently

piloting a 3-year CIP program in six villages of the NCA to further mitigate human-lion conflict. Under this program, communities can earn monetary incentives for allowing lions to occupy and safely pass through community lands. CIP payments are based on a verified minimal count of lions on village land each month, estimated by KopeLion monitoring activities, with penalties incurred for any lion killings. Thus, communities are empowered to provide conservation services in return for receiving incentive-based payments related to a lion's estimated potential cost in terms of the number of livestock it may attack (Pekor et al. 2019). While further evaluation of the success of this program and others like it is warranted, early indications are encouraging, with community members reporting greater appreciation of having lions on the landscape (Pekor et al. 2024). Thus, the prospects for the future of lions, lion connectivity and human-lion coexistence in the NCA look hopeful, but success will require continued flexible, creative, and determined conservation efforts that engage and earn the support of local communities. As countries around the world re-commit to a future where people live more in balance with nature (UNEP, 2022), the successes and lessons learned from the NCA provide encouraging signs for inclusive conservation, and avenues for further work, in coexistence landscapes where the persistence of large carnivores lies in the balance.

4.1 Summary

This brings me back to the introduction where interdisciplinary, community-led model of multifunctional landscape management, as suggested in this thesis and outlined in the Global Biodiversity Framework (GBF), has the potential to offer a more equitable approach to conservation by involving indigenous peoples and local communities. This model, while maintaining pastoralism—a practice deeply co-adapted with the landscape—may support the global goal of protecting 30% of the Earth's land and oceans by 2030. This also aligns with nature-based solutions by offering environmental, as well as social and economic benefits.

The case of the human-lion situation in NCA show some promise for sustainable coexistence but faces challenges due to conflicting conservation paradigms. While the current government favours a land-sparing approach,

in contrast to global trends emphasizing coexistence, this thesis points out opportunities within the land-sharing model, albeit not yet systematically tested. Empowering local communities to engage meaningfully in governance and collective action is key to resolving the social dilemma identified in this thesis. Successful initiatives like Lion Guardians and KopeLion demonstrate how collaboration can foster lasting human-lion coexistence, while incentive-based programs offer additional tools for conflict mitigation and cost-value sharing.

4.1.1 Reflections on Theory and Methods

This study of lion connectivity and coexistence embraced an interdisciplinary approach, combining multiple fields to capture both detailed ecological data and broader socio-ecological insights.

By integrating spatial ecology, genetics, population demography, and social sciences—such as policy analysis and social-ecological system mapping—the research provided a comprehensive view of human-lion coexistence. The inclusion of interviews and thematic analyses added important socio-cultural dimensions that are often absent in purely ecological studies.

While there is a potential risk of being perceived as a "Jack of all trades, master of none" with this approach, the interdisciplinary framework enhances the overall depth of understanding. Rather than compromising rigor, this blending of disciplines enables a more holistic perspective that is vital for tackling complex conservation challenges.

The long-term observational study provided valuable insights into lion population dynamics and individual behaviours, crucial for understanding long-lived species with low population numbers. Although this depth made broad generalizations difficult, it ensured that the findings were grounded in meaningful, long-term data

Similarly, the genetic analysis uncovered patterns of diversity, population structure, and gene flow that would not have been apparent through observation alone, revealing the functional connectivity between lion populations. While this method is resource-intensive and requires specialized expertise, it is invaluable for identifying genetic trends critical to conservation planning.

Building trust through long-term community engagement was key to fostering local support for conservation. Although time-consuming and

dependent on community readiness, this approach lays a strong foundation for sustained conservation success. While it may not be feasible for shorter research projects, its importance in aligning conservation goals with local interests cannot be overstated.

Focusing on lions, a flagship species, helped gain broad support from local communities, tourism operators, and the public due to their iconic status. However, this focus could overshadow less charismatic but equally important species, like hyenas, and create reliance on the lions' appeal for funding and interest. Fig 14 photo of lionesses with cubs headed out onto the open grass-plains of the Serengeti.

Overall, this study underscores the value of a balanced interdisciplinary approach. Integrating detailed biological research with broader socio-ecological perspectives ensures a more comprehensive understanding of human-wildlife coexistence while acknowledging and navigating the challenges inherent in such a multifaceted approach.

4.1.2 Recommendations for Future Research

This study has identified several knowledge gaps, suggesting the following areas for future research:

- Investigate ex-pride mating pattern, whether Crater females mate with short-term visiting males to understand genetic exchange and connectivity between lion subpopulations.
- Increase sampling efforts to improve population coverage of genetic data representativeness and accuracy. Biopsy sampling, which minimally disturbs Crater lions, can increase broaden population coverage by targeting which individuals to sample.
- Study prey-preferences by lions, comparing where and when they take livestock versus natural prey.
- Explorations for improved rangeland productivity: if low natural prey depletion drives lions’ attacks on livestock, how can that be improved?
- Assess demographic trends: Conduct a comprehensive analysis of demographic data to identify trends in survival and reproduction, aiding in understanding population dynamics and potential threats to the Crater lions' long-term viability. Much data is available but requires dedicated time and skill investment for thorough analysis.
- Evaluate new policy trials: Systematically assess new conservation policy trials, such as community-based initiatives and conflict mitigation

strategies, to refine management approaches and evaluate its feasibility to promote sustainable human-wildlife coexistence. This will provide important lessons to guide future models aimed at improving connectivity across human-fragmented landscapes.

Figure 14. Lions heading into the open unknown. (Photo: Ingela Jansson)

5. Conclusion

This thesis explored the complexities in the human-lion coexistence and connectivity in the NCA, revealing both challenges and opportunities of managing shared landscapes. The key conclusions are:

Lions adapt their movements and behaviours to avoid direct conflict with humans, yet the risk-reward trade-off in a pastoralist landscape can make lions a significant predator on livestock, especially when natural prey is limited. This cause unpredictable losses for local communities, and can trigger retaliatory hunts and killings, underscoring the need for more effective conflict mitigation strategies.

The analysis of lion movements and their increasing use of the area indicates that, although dispersing lions face higher risks, connectivity persists. This connectivity is not reflected in the genetic data, which reveals a fragmented population with limited gene flow into the Crater population, in the long term a threat to genetic diversity and resilience. This isolation is further reinforced by the dominance of Crater-born males.

The growing pressures on land use, disrupted connectivity, and escalating human-wildlife conflict suggest that the NCA is nearing its social and ecological limits. Without significant changes and efforts, this delicate balance may not be sustainable in the future. Signs of resilience and untapped potential are there. The deep cultural ties between local communities and the land reflect a longstanding interconnectedness. Community-based conservation efforts, such as Lion Guardians and KopeLion, show promise for sustainable coexistence by involving local communities in collaborative conflict mitigation and protection efforts.

Nevertheless, future uncertainties, including climate change, population growth, and resource demands, could overwhelm both the ecosystem and local communities if not managed carefully.

These findings align with the Global Biodiversity Framework (GBF), advocating for equitable, community-led conservation to promote human-wildlife coexistence. But such goals often clash with political priorities and economic needs, creating tension between global and national conservation objectives and local strategies.

In conclusion, while fostering sustainable human-lion coexistence appears possible, the NCA stands at a crossroads - how to balance biodiversity conservation with the pressures of human development, economic demands, and political priorities (URT 2019; Ngorongoro Community 2022). A viable long-term solution requires stronger support for community-led initiatives, effective policies to mitigate conflict, and a recognition that the futures of both lions and people are intricately and precariously connected.

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Popular science summary

This thesis explores the complexities of human-lion coexistence and connectivity in the Ngorongoro Conservation Area (NCA) by analysing the ecology and genetics of a well-studied lion population, alongside the dynamics of human-lion conflicts. By combining ecological and genetic insights with a broader socio-ecological perspective, the study addresses the challenges and opportunities of managing shared landscapes between people and wildlife.

The key findings are:

- Lions in the NCA prefer habitats with dense vegetation cover and adjust their behaviour to avoid humans. However, during periods or in areas where natural prey is limited, they may prey on livestock, causing unpredictable losses for local communities and occasionally leading to retaliatory killings. This ongoing conflict impacts both people and lions, highlighting an urgent need for more effective conflict mitigation strategies.
- While there is some connectivity among lion populations due to dispersal, genetic analysis reveals clear differentiation between the Crater population and those in Ndutu and Serengeti. Crater lions show a lack of genetic diversity and signs of inbreeding, with limited gene flow threatening the population's long-term resilience. The isolation of this population is further strengthened by the dominance of males born within the Crater.
- Rising land use pressures, disrupted wildlife corridors, and increasing human-lion conflicts indicate that the NCA is approaching its social and ecological limits. Without significant interventions, maintaining the current balance may be unsustainable. However, community-based

conservation programs, such as Lion Guardians and KopeLion, and strong cultural ties of local communities to the landscape offer hope for sustainable coexistence through collaborative conflict resolution and wildlife protection.

- Climate change, population growth, and increased resource demands could heighten challenges for ecosystems and communities. These findings align with the Global Biodiversity Framework's call for equitable, community-led conservation, but balancing global conservation goals with local political and economic priorities remains a challenge.

In conclusion, the NCA is at a critical crossroad where sustainable human-lion coexistence is still possible but requires a careful balance between biodiversity conservation and human development. Achieving this balance will require greater support for community-driven initiatives, effective conflict management, and recognizing that the futures of both lions and people are inherently connected.

Populärvetenskaplig sammanfattning

Denna avhandling "Undersökning av lejonens (*Panthera leo*) sammanlänkning i ett pastoralt landskap: Samexistens, konflikter och gemensamma bevarandeåtgärder i Ngorongoro Conservation Area (NCA), Tanzania" utforskar komplexiteten i samexistens och konnektivitet mellan människor och lejon i NCA genom att analysera ekologin och genetiken hos en välstuderad lejonpopulation, tillsammans med dynamiken i konflikter mellan människor och lejon. Genom att kombinera ekologiska och genetiska insikter med ett bredare socioekologiskt perspektiv tar studien upp utmaningarna och möjligheterna med att förvalta landskap som där människor och rovdjur samexisterar. De viktigaste resultaten är följande:

- Lejonen i NCA föredrar livsmiljöer med tät vegetation och anpassar sitt beteende för att undvika människor. Under perioder eller i områden där de naturliga bytesdjuren är begränsade kan de dock ge sig på boskap, vilket orsakar oförutsägbara förluster för lokalsamhällena och ibland leder till hämndaktioner. Denna pågående konflikt påverkar både människor och lejon, vilket understryker det akuta behovet av effektivare strategier för att mildra konflikten.

- Även om det finns en viss sammanlänkning mellan lejonstammarna, vad gäller lejons rörelser över området, så visar den genetiska analysen att det finns en tydlig genetisk skillnad mellan lejonen i Ngorongoro Kratern och de i närliggande Ndutu och Serengeti. Lejonen i Ngorongoro Kratern uppvisar en tecken på genetisk utarmning och inavel, med begränsat genflöde som hotar stammens långsiktiga livskraft och motståndskraft. Isoleringen av denna lejonstam förstärks ytterligare av dominansen av hanar som är födda i Kratern.

- Ökande markanvändningstryck, störda viltkorridorer, och ökande konflikter mellan människor och lejon tyder på att NCA närmar sig både sina

sociala och ekologiska gränser. Utan betydande ingripanden kan det vara ohållbart att upprätthålla den nuvarande balansen. Bevarandeprogram som är baserade i lokalsamhället, som t.ex. Lion Guardians och KopeLion, och befolkningens starka kulturella band till landskapet ger dock hopp om hållbar samexistens genom gemensam konfliktlösning och viltbevarande.

- Klimatförändringar, befolkningstillväxt och ökade krav på resurser kan öka utmaningarna för ekosystem och samhällen. Dessa resultat ligger i linje med det globala ramverket för biologisk mångfald, som efterlyser ett rättvist och lokalt ledd bevarande, men det är fortfarande en utmaning att balansera globala bevarandemål med lokala politiska och ekonomiska prioriteringar.

NCA befinner sig vid en kritisk vägskäl där hållbar samexistens mellan människor och lejon fortfarande är möjlig, men kräver en noggrann balans mellan bevarande av biologisk mångfald och människors rätt till utveckling. För att uppnå denna balans krävs ökat stöd för samhällsdrivna initiativ, effektiv konflikthantering och insikt om att både lejonens och människornas framtid hänger samman.

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V

11

IN SEARCH OF NEW MODES OF GOVERNANCE

The potential of conservation incentive payment policies to promote human–wildlife coexistence

Adam Pekor, Ingela Jansson, William Ole Seki, Dennis Rentsch, Göran Spong and Camilla Sandström

Introduction

The search for new paths to sustainable development is closely related to the search for new modes of governance. Most research in this area has focused on how to configure and improve governance processes through the inclusion of actors (Ansell and Gash, 2007) or how to design the 'rules of the game' that shape the interactions between actors (Decker et al., 2016; Mayntz, 2004; Ostrom, 2009; Rosenau, 1992). Although studies based on these two dimensions of governance—often denoted as the 'polity' and 'politics' dimensions—provide useful insights, they do not by themselves explain the full complexity of governance phenomena (Lange et al., 2013). What is often missing is the role of the policy dimension, that is, the specific content of governance, including both policy objectives and policy instruments (Orach and Schlüter, 2016; Treib et al., 2007).

Over the past two decades, a suite of innovative policy instruments known as conservation incentive payments (CIPs) have gained appeal as a way to promote human–wildlife coexistence by bridging the sharp disconnect that often exists between conservation policy and the sociocultural and economic interests of local people (Dickman et al., 2011; Kaczan et al., 2013; Marino and Pellegrino, 2018). For many communities, wildlife impose a significant financial burden, both directly, in the form of crop damage and livestock depredation, and indirectly, in the form of land-use restrictions designed to maintain suitable wildlife habitat (Langpap, 2006; Redpath et al., 2015). Yet the vast majority of the economic benefits derived from wildlife (e.g., through tourism and hunting concessions) are often captured by central governments or other outside actors (Nelson et al., 2010). As a result, it is often too costly for people to tolerate wildlife. CIPs help mitigate this problem by aligning the economic interests of local communities with conservation goals (Kaczan et al., 2013). (We use 'CIPs' as an umbrella term to include all policy instruments that promote conservation through the

use of economic incentives, including payments for ecosystem services, performance payments, etc.) Under a CIP program, local stakeholders are paid directly for conserving species or their habitat, thereby minimizing (or eliminating) the financial burden imposed by wildlife (Dinerstein et al., 2013; Lapeyre, 2015). By transforming the economic impact of wildlife, CIPs can make conservation a financially viable option for local communities and improve outcomes for both people and wildlife.

Historically, the literature on governance, on the one hand, and on the characteristics of policy instruments like CIPs, on the other, have developed more or less independently. The two literatures should, however, be connected, since governance is best understood in the context of achieving policy goals and hence in relationship to policy instruments (Héritier, 2002). Moreover, governance systems are rarely capable of achieving policy goals without adequate policy instruments and actors to promote them. Accordingly, this chapter focuses on the nexus between governance and policy and demonstrates that each approach can help illuminate the other (Le Coq et al., 2015). In particular, we show that the introduction of a CIP program, a new kind of policy instrument, if successful, can facilitate a change from a top-down and hierarchical mode of governance to what could be described as a public–social partnership (Bjärstig and Sandström, 2017) or an interactive mode of governance (Lange et al., 2013).

To illustrate our argument, we use Tanzania's Ngorongoro Conservation Area (NCA) as a case study. In the NCA, intense human–lion conflict over the past several decades has threatened the government's stated objectives of conserving the NCA's natural resources, safeguarding the interests of its indigenous residents (all traditional pastoralists), and promoting tourism in the area (Jansson et al., forthcoming). In this regard, the NCA is not unique but rather representative of the problems faced by multiple-use commons around the world. We show how the introduction of a new policy instrument in the NCA has the potential to promote human–wildlife coexistence, while at the same time opening up the system for social inclusion and participation through interactive modes of governance.

Multidimensional approach to the analysis of governance

The implementation of 'new' environmental policy instruments like eco-taxes and payments for ecosystem services (PES) has led to both a 'fundamental transition' in environmental policy (Golub, 1998: xiii) and changes in modes of governance (e.g., from top-down to more interactive modes like public–private or public–social partnerships) (Lange et al., 2013). The main reasons for these changes have been a dissatisfaction with the effectiveness of traditional top-down regulatory instruments and the desire for greater local-level involvement through subsidiarity. These instruments are often 'proposed, designed and implemented by non-state actors, sometimes working alongside state actors, but sometimes also independently' (Jordan et al., 2005: 481).

As mentioned above, one such policy instrument is a CIP scheme, which takes the form of a voluntary transaction between at least one 'purchaser' (e.g., a government or nongovernmental organization) and one 'provider' (e.g., an individual or a community) in which the purchaser pays the provider if and only if the provider takes an agreed-on conservation action (e.g., refrains from hunting a target species) or achieves an agreed-on conservation goal (e.g., maintains a certain amount of the species' habitat) (Khalumba et al., 2014). The defining feature of a CIP scheme is that payment is conditioned on the performance of the conservation action and/or achievement of the conservation goal (Nelson et al., 2010). If the action is not taken and/or the goal is not achieved, no payment is made. Thus, a CIP scheme requires the establishment of a governing process whereby public and private actors, as interdependent partners, may benefit by combining their knowhow and expertise, but also financial and other resources, to deliver collective goods in a more efficient way, compared to top-down governance and privatization (Hodge and Greve, 2007).

A central theme in the discourse on CIPs has been economic efficiency (Ferraro and Kiss, 2002; Wunder, 2007). In particular, much attention has been focused on evaluating the costs of CIP schemes compared to other conservation approaches (Ferraro, 2001) and assessing how to achieve CIP efficiencies through the use of bidding processes and other market mechanisms (Groth, 2011). However, as a number of conservation practitioners have observed, determining the most efficient level of payment that will incentivize pro-conservation actions is just one issue to consider in implementing a CIP program, and perhaps not even the most important (Muradian et al., 2010). The successful design and implementation of a CIP scheme also requires coherence between policy aims and acceptance among involved actors, which are likely to be determined by factors relating to the three dimensions of governance: the local socio-economic, political and cultural conditions (politics); the level of collaboration, engagement, and fairness achieved in designing and implementing the scheme (polity); and, finally, the degree to which the implementing instrument is tailored to formal and informal institutions, laws, and norms (policy).

Politics: socioeconomic, cultural, and political context

As CIP schemes are, at bottom, interventions intended to conserve species or ecosystems, focusing on ecological considerations like the setting and monitoring of meaningful conservation targets is critical (Clifton, 2013; Jack et al., 2008; Prager et al., 2016; Sommerville et al., 2011). However, at the outset, equally important factors to consider are the socioeconomic, cultural, and political conditions in the target area, including current and previous modes of governance (Mishra et al., 2003). Indeed, without a basic understanding of the local people and the issues they face, program administrators are unlikely to be able to design a CIP scheme that the community will support. Despite the importance of understanding local stakeholders' needs and values, however, the vast majority of CIP programs pay little attention to them (Sorice and Donlan, 2015).

To gain a true understanding of local conditions, historical context is essential. For example, having dealt with inefficient, corrupt, or authoritarian governance systems may cause local stakeholders to be skeptical of participating in a CIP program or other conservation initiative (Bowden, 2004; Gonzalez and Jentoft, 2011; Petheram and Campbell, 2010). This was the case in Nicaragua's Pearl Cays, where local stakeholders were leery of establishing a marine protected area after years of having their fishing rights trampled on by what they viewed as a corrupt national government (Gonzalez and Jentoft, 2011). Likewise, in the South African province of KwaZulu-Natal, a history of top-down governance and fortress conservation made local stakeholders uneasy about establishing a community-based natural resource management (CBNRM) scheme (Bowden, 2004). Understanding and adapting the policy instrument to this type of historical political context can allow CIP programs to gain local support. For example, in southern Vietnam, Petheram and Campbell (2010) found that due to historical mistrust of government officials, local stakeholders were more comfortable entering into a CIP agreement, similar to a private–social partnership, administered by an outside conservation organization.

While investigating and understanding local political conditions and culture takes time and resources, these efforts can yield lasting benefits for a conservation project. As Manjengwa and Murphree (2011) noted with respect to a CBNRM project in Zimbabwe, the time taken at the beginning of the project to understand the community with which it was being established was invaluable in building consensus and achieving successful outcomes later on. By contrast, a failure to account for context can not only doom a conservation project but even harm the local communities involved. For example, an attempt to establish a community-based conservancy (CBC) in northern Kenya without fully understanding the social, cultural, and political dynamics of the area exacerbated tensions between local ethnic groups over the distribution of CBC benefits and actually led to a 'full-scale guerrilla-type war' (Greiner, 2012).

Finally, independent of any CIP scheme, many local people undoubtedly have important relationships with and noneconomic reasons for valuing the environment. While setting up a CIP program, it is important to explore these motivations for conservation and ensure that the values are complemented, not supplanted, by incentive payments. Structuring a CIP program to align with, rather than 'crowd out,' noneconomic reasons for protecting wildlife may not only bolster the CIP program but also help ensure that the local conservation ethic persists even if the program ends (Baker et al., 2013; Muradian et al., 2010; Sorice and Donlan, 2015).

Polity: engagement, collaboration, and fairness

Recognizing local stakeholders as collaborators is also critical to the success of a community conservation endeavor like a CIP program (Ansell and Gash, 2007; Emerson et al., 2011; Engel et al., 2008; Mbaiwa and Stronza, 2011). Not only

does working with local institutions and community members allow the program to benefit from their wealth of local knowledge and experience, but it is also essential to building trust, forging important relationships and establishing the legitimacy of the program (Gross-Camp et al., 2012).

In establishing a CIP program, local stakeholders should be engaged as early as possible in co-designing the various components of the program. 'If the process gets off on the wrong foot, it can be irreconcilable, preventing any meaningful engagement going forward' (Gerner et al., 2011). Thus, demonstrating to local people at the earliest phases that their views are valued and their concerns understood can help engender vital community support (Baker et al., 2013; Manjengwa and Murphree, 2011). Indeed, the incorporation of local stakeholders' preferences and recommendations is likely to be among the most important factors in determining the program's success (Gross-Camp et al., 2012). And, even if particular recommendations are not accepted, the process of engagement can itself generate goodwill with the community. Early engagement is also key to developing the specific components of the policy instrument, in terms of both governance and technical details. Here, it important not only to agree-on basic ecological targets but also develop what Emerson and Nabatchi (2015) define as a shared theory of change—the common objectives of the program and how they can be achieved.

Even if stakeholders are effectively engaged, incentive payments are likely to work only if they are fair and equitable to local people. Fairness relates both to the process of establishing a CIP program and to the outcome—the actual amount, form, timing and method of the payments made (Ansell and Gash, 2007; Gross-Camp et al., 2012). With regard to process, fairness means including local stakeholders in all aspects of decision making (García et al., 2014). Researchers on one PES project in Rwanda learned that involving local institutions and community members in designing the features of the program was essential to obtaining their buy-in. Just as important as the payments made under the program was the perception on the part of community members that they were being treated fairly throughout the process (Gross-Camp et al., 2012). Accordingly, taking steps to make sure that the poor, elderly, uneducated, and other marginalized groups are not excluded from the process by language and other socioeconomic barriers is critical (Clifton, 2013).

Fairness is also inherently tied to the equitability of how payments are distributed (Gross-Camp et al., 2012). In a number of PES and other community-conservation programs, the inequitable distribution of benefits in favor of local elites (and non-locals) was among the chief complaints of local stakeholders (Clifton, 2013; Kangalawe and Noe, 2012). Many CIP programs establish a method for distributing payments without explicitly considering the criteria used to assess equity (Pascual et al., 2010). However, because the interests and influence of program participants can vary widely, thinking critically about how equity will be determined is essential, both from an ethical perspective and in order to generate the greatest level of program support.

Policy: institutional fit and property rights

Finally, a CIP program is unlikely to be effective unless the policy is tailored to the local institutional and legal framework. This means, among other things, accounting for the strengths and weaknesses of local governance institutions—formal and informal—to determine the most effective means of establishing a CIP program. Functioning institutions are necessary to negotiate CIP terms, enter into an agreement, consolidate community support for the program, and distribute payments (Milne and Niesten, 2009). However, in many places where CIP programs have been established or are being considered, local governments and other civil institutions may not be functioning properly. In Cambodia, for example, one local committee that was responsible for administering a CIP agreement was nonfunctional for two years due to political infighting, which effectively suspended the program during that period (Milne and Niesten, 2009). In such cases, it may be appropriate for nongovernmental organizations (NGOs) and other nonstate actors to help administer the CIP and assure local stakeholders that they will receive payments for providing the agreed-on services (Jack et al., 2008).

Similarly, because CIPs often condition payments on land use, understanding local property rights is also important. Conflicting claims to land may exacerbate conflict and lead to contested claims for payment (Greiner, 2012; Milne and Niesten, 2009). Thus, CIPs are more likely to be successful in places with well-defined and enforceable property rights. For example, in Tanzania, rural villages have a discrete corporate form, legal status, and geographic boundary (Nelson et al., 2010). Among other things, Tanzanian village councils are responsible for managing village lands and can own property, enter into contracts and take legal action to enforce their rights (Nelson et al., 2010). In northern Tanzania, these features of village governance have allowed for the successful implementation of a CIP program that pays villages for conserving a key wildlife dispersal area adjacent to Tarangire National Park (Nelson et al., 2010).

Case study: human–lion conflict in Tanzania's NCA

Overview of the NCA

The case we use to analyze the nexus between governance and policy is the NCA, an 8,300 km^2 multiuse protected area in northern Tanzania established in 1959 (Figure 11.1). Together with Serengeti National Park and surrounding areas, the NCA forms one of the largest savanna ecosystems in the world and has been designated as a UNESCO World Heritage Site and as part of the Serengeti-Ngorongoro Man and the Biosphere Reserve for its outstanding natural and cultural values. In addition to its high biodiversity, varied habitats, and abundant wildlife, the NCA is a particularly important site for lion conservation; among other things, the lions of the Ngorongoro Crater form one of the densest populations in Africa and have been studied extensively for over 50 years. The NCA's lions, along with its renowned natural features and archaeological sites,

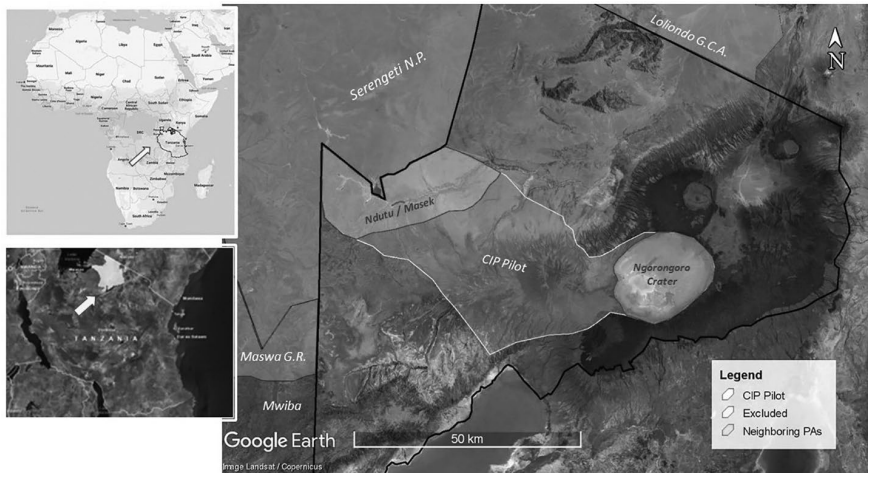

FIGURE 11.1 The Ngorongoro Conservation Area is a multiuse protected area and World Heritage Site located 180 km west of Arusha in northern Tanzania. The proposed area for piloting a conservation incentive payment program is situated between the Ngorongoro Crater in the east and the Ndutu/Masek area in the west.

make it one of Tanzania's premiere tourist destinations, drawing hundreds of thousands of tourists each year. However, the NCA is also home to approximately 100,000 people, the vast majority of whom are Maasai pastoralists, along with a smaller number of Datoga pastoralists and a few families of Hadzabe hunter-gatherers (NCA General Management Plan, 2006–2016).

Unique among Tanzania's protected areas, the NCA was formed for the joint purposes of conserving its natural resources, protecting the interests of the local people, and promoting tourism. Balancing these goals has proved challenging for the NCA Authority, the parastatal organization tasked with managing the area. While wildlife generate substantial revenue for the tourism industry, lions alone cause an estimated USD 70,000 to 75,000 in livestock losses per year, a significant burden on the NCA's residents, who rely largely on livestock for their livelihood and face rising levels of poverty. These losses often lead to retaliatory or preemptive killings, which (along with ritual killings) have caused lions to disappear from large parts of their historical range in the NCA. As a result, the lions of the Ngorongoro Crater have become increasingly isolated from the rest of the Serengeti ecosystem and have experienced a long history of close inbreeding (Kissui and Packer, 2004). In addition to the direct impact this conflict has had on local people and lions, it also has the potential to negatively impact the NCA's economy, since lions are an important driver of wildlife tourism in Africa (Willemen et al., 2015). Mitigating the NCA's human–lion conflict is thus essential for safeguarding the economic interests of the NCA's residents, conserving

the local lion population, and ensuring that the NCA remains one of Africa's premiere tourist destinations.

Concern about the decline and fragmentation of the NCA's lion population, along with a recognition of the costs lions and other carnivores impose on the NCA's pastoralists, led one of us (IJ) to co-found KopeLion, a community-based NGO aimed at fostering long-term human–lion coexistence in the NCA. KopeLion utilizes the Lion Guardians model (Hazzah et al., 2014), pursuant to which resident pastoralist warriors are employed to mitigate human–wildlife conflicts in their home-communities and to monitor and protect lions. KopeLion has also continued and expanded on a long-term monitoring survey of lion demography in the NCA, in which each lion is recognized and followed throughout its lifetime. While we have observed some signs of increased tolerance towards lions and documented increased lion presence and movements across the NCA's landscape, there is a growing concern about the prospects of long-term coexistence due to the substantial costs lions impose on local people.

Despite the obvious importance of addressing the NCA's human–lion conflict, the situation has come to resemble a traditional collective action problem (Ostrom, 1990), where the lack of collaboration and coordination among key stakeholders has led to persistent conflict and where the present governance regime seems to lack appropriate instruments to promote conflict resolution (Jansson et al., forthcoming). Accordingly, stakeholders in the area are actively searching for new solutions and there is a window of opportunity to explore the possibility of implementing an alternative policy and governance arrangement. Beginning in 2017, we examined the drivers of the NCA's human–lion conflict and the feasibility of piloting a CIP program as a new policy and governance approach to mitigating it.

Investigating the relationship between governance and policy in the NCA's human–lion conflict

To analyze the potential for piloting a CIP program in the NCA, we reviewed secondary sources (e.g., legal and policy documents) and engaged local stakeholders in three stages. First, from June to September 2017, we conducted a feasibility study, in which we conducted interviews and focus groups (n = 29) with members of four key stakeholder groups: the NCA Authority; NCA residents; the Ngorongoro Pastoral Council (an elected advisory body that represents the NCA's residents); and tourism operators. We held meetings with NCA residents from six villages in KopeLion's study area—Kayepus, Oloirobi, Misigiyo, Longojoo, Endulen, and Nasporiong'—and, in each village, we engaged five different stakeholder groups: members of the village council; traditional Maasai leaders; village elders; current and recently retired Maasai warriors; and general community members (with a particular emphasis on the inclusion of women). With each stakeholder group, we obtained views on conservation and human–lion conflict

in the NCA, opinions on the establishment of a lion CIP program, and preferences with respect to the design of such a program.

Second, following our feasibility study, in March 2018, we held a two-day joint-stakeholder workshop for the purpose of collaboratively outlining the framework for a potential pilot CIP program in the NCA. The workshop was attended by approximately 45 participants, including: 6 representatives from the NCA Authority; 4 representatives from the Ngorongoro Pastoral Council; 1 representative of the Ngorongoro District Council; 24 representatives from the villages engaged in our feasibility study; and 10 representatives from the tourism industry. The workshop was facilitated by several authors of this paper and a Maasai attorney. During the workshop, participants developed the framework for a potential lion CIP program in the NCA through a number of steps, including (1) identifying the most important issues to consider in establishing a CIP program, (2) developing various options for the design of a potential CIP program, and (3) conducting a SWOT (strength/weakness/opportunity/threat) analysis of the various options. Workshop participants interchangeably worked in small groups, designed to include participants from each stakeholder group, and presented their results in plenary sessions.

Third, based on the findings from our feasibility study and our workshop results, the NCA Authority conditionally approved the implementation of a pilot CIP program. Accordingly, we formed a CIP Design Committee consisting of representatives from all key stakeholder groups and held a second two-day workshop in April 2019 to collaboratively establish key terms and conditions of the pilot program.

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On the design and development of a CIP program

Dissatisfaction with governance is a key driver of the NCA's human–lion conflict

The NCA's current conflict is embedded in a long history of land-use conflict, unclear property rights, mistrust, and a lack of benefit sharing (Jansson et al., forthcoming; Rogers, 2009). Indeed, our interviews and focus groups revealed that the negative attitudes towards lions shared by many local people are a product of dissatisfaction with the politics, polity, and policy aspects of governance in the NCA. First, many focus group participants explained that, historically, they have been excluded from the decision-making process. As one village council-person explained, 'Previously, decisions have been made without prior consultation, for example, making the Crater a no-go area. The NCA Authority's approach is top-down, not participatory. They issue dos and don'ts; even the police are better at communication.'[1] As a result, many people feel that wildlife have been prioritized over people. For example, one elder complained that

> people get killed and eaten by lions and there is no response, but if you kill a lion, there is a harsh response on you. The authorities have prioritized wildlife over us for a long time, which has hurt our views on wildlife.

Second, many participants expressed the view that, because the 'rules of the game' have limited their participation in the NCA's natural resource governance, they have not benefited sufficiently from the area's wildlife. As one elder stated, 'Ngorongoro is our home, our land; it produces a lot of money, but we have not benefited enough from it.' Another echoed, 'When I was young, the NCA Authority used to tell us "just don't kill [wildlife]." We didn't get any benefits though.' Or, as a warrior put it, 'Lions are on the [Tanzanian national] currency, which shows that the government sees them as a benefit. We should see a benefit too if we are to tolerate them.' Notably, participants were not focused specifically on current practices but rather on various actions taken since the NCA was formed in the 1950s: 'The NCA Authority's mandate includes considering the interests of the pastoralists, which they have not done for 60-plus years' (Elder).

Thus, as one interviewee summed up the conflict,

> Animals have no problems, it is people who have problems. It is between the community and the Authority, that is where the real conflict lies. Lion killing doesn't reflect conflict between people and lions as much as it reflects animosity against the NCA Authority, and dissatisfaction with the NCA Authority's approach to issues.

CIPs have the potential to positively impact governance in the NCA

Our research showed that a traditional, top-down compensation system, in which local people are partially or fully reimbursed for losses caused by carnivores, is not a viable model for mitigating human–lion conflict the NCA due to problems with the verification of losses, transaction costs, fraud, and distrust between the NCA Authority and local residents. (In 2011, Tanzania adopted a policy of paying consolation (i.e., a small sum) for livestock losses caused by carnivores However, due to many of the complications noted above, that program was discontinued in the NCA.) Accordingly, stakeholders were nearly unanimous in the need for alternative policy options and open to the idea of CIPs. As one NCA Authority official explained,

> Compensation has failed. … We've been looking for a policy to help people for two to three years … There is clear viability [for a CIP program]; I see the NCA Authority supporting it. Incentive payments are a good way forward. … You don't fail until you stop trying.

Importantly, NCA Authority officials and community members alike recognized that not only would a CIP program allow the NCA's residents to profit from conserving lions, but it could also positively impact governance in the NCA in several ways. First, because a CIP program relies on (and rewards) people for their conservation efforts, it recognizes them as partners in conservation and important actors in the system. As one NCA Authority official explained, 'People should feel ownership of the wildlife—a CIP program can help do this.' Or, as

another NCA Authority official stated, 'A CIP program is good because it provides measurable commitments on the part of the communities.'

In addition, many community members also noted that one of the most important benefits a CIP program could provide would be improved relations with the NCA Authority and an increased role in the decision-making process:

> [A CIP program] comes with the possibility of negotiations and discussions with the NCA Authority, which is itself a benefit because we've always dealt with these issues [without engagement from the NCA Authority]
>
> *Elder*

> I think [a CIP program] is the right path forward. The most beneficial thing apart from the money is stakeholders coming together for a unified purpose
>
> *Warrior*

NCA Authority officials also echoed this sentiment:

> Improved communication is a benefit that can be derived from a CIP program
>
> *NCA Authority Official*

> This type of a program could start to mend the relationship between the communities and the NCA Authority
>
> *NCA Authority Official*

Finally, a CIP program would also contribute to the empowerment of local communities since they would be able to make their own decisions about benefit distribution and other features of the program:

> A CIP program is preferable for two reasons: (1) benefits can come as long as people accept not to kill lions, and if we do well at mitigation, we can have cows and benefits; (2) through the dividend the community gets, we can choose to compensate individuals if we want.
>
> *(Community member)*

Developing a CIP policy in light of the NCA's socioeconomic, political, and cultural context

As explained above, in establishing a community conservation initiative like a CIP program, it is essential to understand the issues in context and from the perspective of the stakeholders involved. Here, it became clear from our focus groups and interviews that much of the hostility towards lions and other carnivores in Ngorongoro was really a proxy for hostility towards the NCA Authority. As one respondent put it, 'The NCA Authority are strangers to our land and they have antagonized us with wildlife; so any hate we have to wildlife is really

because of the NCA Authority and not feeling unified with them' (Elder). Many respondents expressed that this sentiment has been building for decades, dating back to the removal of the Maasai from Serengeti National Park and the gazetting of the NCA in the 1950s: '[We're] concerned about what happened in Serengeti. White men came to conserve lions, then people got kicked out. This makes the pain fresh' (Village councilperson).

However, while many respondents expressed hostility towards the entity *officially* charged with conserving the NCA's wildlife, those feelings exist within the context of a strong conservation ethic shared by many of the NCA's residents. Indeed, despite feeling like they have benefited little from wildlife, many respondents expressed that they have conserved wildlife because of Maasai traditions and customs:

> Our people were the original conservationists. We lived here before it was gazetted. We conserve, we don't kill wildlife
>
> *Elder*

> [When there was a] rhino that came out of the Crater, the people herded it, called the NCA Authority, guarded it; they didn't try to kill it and take its horn. It showed that we are conservationists
>
> *Elder*

As a result, many respondents acknowledged the inherent value of human–wildlife coexistence in the NCA and the need for new solutions:

> It's not about whether we like [wildlife] or not, it's about everything deserving a place.
>
> *Traditional leader*

> Ngorongoro's uniqueness is because of people and wildlife. Our ancestors conserved, and we carry on with it despite the burden
>
> *Community member*

> We should not focus on *whether* Ngorongoro should be a mixed-use area, but focus on *ways* for coexistence. The eyes of the world are on us
>
> *Traditional leader*

Accordingly, our research showed that many local people have important relationships with and noneconomic reasons for valuing the environment, which should be taken into consideration in designing a CIP program.

Collaboratively designing a fair and equitable CIP policy

Although there was widespread enthusiasm for the potential benefits of introducing a CIP program in the NCA, participants raised a number of concerns about ensuring the fairness and equitability of the policy. In particular, these concerns

related primarily to (1) the conditions for earning benefits and (2) the manner in which benefits would be distributed and managed. However, each of these issues were collaboratively addressed by stakeholders, who developed agreed-on solutions during the joint-stakeholder CIP Design Committee workshop held in April 2019.

Conditions for earning benefits

Under the proposed CIP program, communities will earn benefits based on the presence of lions on ward land, as determined by KopeLion's continued lion monitoring activities, including the visual recognition of individual lions, the analysis of lion spoors (e.g., tracks, scat, hair), and the use of GPS collar data, lion call-ups, and motion-triggered camera traps. Benefit levels will be calculated based on the number of unique, individually recognized lions on ward land each month, with a substantial penalty for any lion killings (i.e., forfeiture of benefits for a certain number of months).

Community concerns with this proposed framework focused primarily on the possibility that they might not be credited for all lions observed on ward land each month. For example, with respect to the use of camera traps, one community member asked, 'How will the community know what the cameras are showing if only KopeLion gets to look at them?' A warrior put it more bluntly: 'How will we know we're not being cheated based on the number of lions?' In response, it was suggested by other respondents that each village could designate representatives to participate in the photo review process:

> As long as it's our person who reviews the pictures then we'll trust it. But if it was someone from far away, we wouldn't trust it necessarily
>
> *Community member*

> I would trust the process if we were involved in looking at the cameras
>
> *Village councilperson*

In addition, focus group participants generally agreed that, if they were involved in the verification process and no lions were observed on ward land during a given month, they would accept as fair that they would not receive a benefit for that month:

> [It's like] a cow, [which] usually gives birth once a year. Some years it doesn't, but you know you have the chance to get a calf the next year
>
> *Community member*

> This is completely reasonable; money shouldn't come for free. Cameras will show that good care of lions is being taken. A hard worker is always rewarded by his work
>
> *Community member*

Accordingly, at the CIP Design Committee workshop held in April 2019, it was agreed that each village participating in the CIP program would designate a certain number of CIP Community Liaisons whose responsibilities would include participating in the lion verification process. Not only did this solution address concerns about fairness, but the inclusion of community members in these biotic surveys and other aspects of program management also has the potential to reinforce support for the program (Emerson and Nabatchi, 2015; García et al., 2014; Gonzalez and Jentoft, 2011).

In addition to concerns with the benefit verification process, there was initial disagreement among community members about the proposed penalties for lion killings under the program. On the one hand, most respondents recognized that earning benefits under the proposed program entailed a commitment not to kill lions. As one community member noted, 'It is fair to require no lion killings [in exchange for benefits].' Indeed, several participants noted that if benefits under a CIP program were conditioned on a commitment not to kill lions, social pressure and cultural norms would limit such killings:

> The rest of the community would view a person badly if they defied the common purpose
>
> *Warrior*

> The advantage of incentives is that the community would not protect the person who killed a lion. It would also help people discourage hunts because the community will put pressure on those who want to hunt
>
> *Villager*

However, other community members raised concerns about the fairness of such a categorical prohibition. Specifically, a number of respondents emphasized the dangers that lions pose to people and livestock and urged that people should be permitted to defend themselves and their livestock without being penalized:

> To accept that there is no lion killing at all would mean that I couldn't kill a lion while I was right there to defend my livestock
>
> *Elder*

> If a lion attacks you, you have to defend yourself
>
> *Warrior*

Accordingly, a compromise was reached and approved by the CIP Design Committee whereby no penalty would be imposed for lion killings in cases of self-defense, that is, where the persons involved reasonably believed that the lion posed an immediate threat to the safety of any person, livestock, or other domestic animal. It was further agreed that, for purposes of the CIP program, the determination of whether any killing was in self-defense would be made by a majority determination of one representative of the NCA Authority, one representative of the community, and one representative of KopeLion.

Distributions of benefits

Discussions on how the benefits earned under the CIP program should be distributed and managed also focused on issues of fairness and equity. While people in positions of authority (village council members, traditional leaders) often suggested that funds earned under a CIP program should be managed by village leadership, others expressed concerns about corruption and transparency and suggested that benefits be given in the form of services or the direct funding of projects, so that CIP funds are not managed by local leaders:

> I would prefer that money be given in the form of a service, not money to the government because of corruption
>
> *Community member*

> We've experienced that money received never gets used for the intended purpose, so the receipt of services is better
>
> *Elder*

The question of individual versus communal benefits was also a central issue. While it was assumed that individual benefits would have the potential to reach most or all members of a community, it was recognized that they might be too insignificant to meaningfully impact people's lives. By contrast, communal benefits could be more impactful but might not be used or valued by all members of the community. Given these trade-offs, community members were split on the manner in which benefits should be provided. Those who favored individual benefits emphasized the individual nature of losses caused by lions. As one community member pointed out, 'a CIP program is a community thing, but what if I lose a cow and it was my only cow? How would a CIP program help me?'

Still, many others favored communal benefits that could bring meaningful projects to their village, especially since the benefits of such projects could be long-lasting:

> I would see it long-term. I would feel the pain [of livestock losses], but would recognize the long-term value of the benefits, and would support the program also because it is a community decision. Long-term benefits would outweigh short-term pain of losses
>
> *Village councilperson*

At the April 2019 workshop, the CIP Design Committee considered how to balance the interests of community self-determination with respect to the use of benefits, on the one hand, versus ensuring that benefits earned under the CIP pilot program are used in a manner that is both appropriate and impactful, on the other. Ultimately, a consensus was reached that (a) the memorandum of understanding (MOU) establishing the CIP pilot program should include a general framework for the permissible uses of funds earned under the program; (b) funds

should be disbursed directly to participating communities to be used in any manner consistent with the MOU; (c) participating communities should be required to account for all funds received under the program; and (d) a penalty (i.e., the forfeiture of future benefits) should be imposed if any funds are used in a manner inconsistent with the MOU.

In addition to these formal reporting requirements (e.g., the submission of budgets and receipts), recommendations for ensuring fairness and equity in the use of funds included requiring communities to publicly display how CIP funds were used; requiring communities to report on the use of CIP funds at public meetings; and, utilizing CIP Community Liaisons to survey and report back on community satisfaction with the use of CIP funds in their villages. If final approval to pilot the CIP program is granted, how participating communities resolve the question of individual versus communal benefits and whether communal benefits are sufficient to promote tolerance of lions in the face of individual livestock losses will be key issues to evaluate.

Institutional fit and funding of a CIP program

Designing a CIP policy for the NCA required recognition of the constraints imposed by funding limitations, administrative capacity and national law and policy. With respect to funding, NCA Authority officials expressed mixed views on the willingness of the NCA Authority Board of Directors to contribute funding for a CIP program. As one official noted, 'Money will be a hurdle, getting the NCA Authority on board. Money already goes to the PC [Pastoral Council], schools and other activities … Asking for more money will be difficult.' However, that the same official also suggested that the NCA Authority might be willing to relocate its budget for the suspended consolation program to support a CIP pilot instead. Indeed, in follow-up communications since our initial feasibility study, NCA Authority officials have increasingly asserted that, because it is the NCA Authority's responsibility to address the area's human–lion conflict, if a CIP program is to be piloted, it is incumbent on the NCA Authority to support the project both financially and administratively.

With respect to program administration, however, all stakeholders recognized that the communities' long history of distrust of the NCA Authority would limit faith in the program if it were managed by the agency. Likewise, many stakeholders recognized that the NCA Authority was not prepared to handle certain administrative activities, such as lion monitoring and verification, fundraising, external communications and dispute mediation. Accordingly, all stakeholders agreed that it would be necessary for some independent NGO to be involved in administering the program. However, as noted above, NCA Authority officials increasingly asserted the importance of the agency's participation in program administration. Likewise, stakeholders began to recognize the importance of communities' participation, not just by providing input in the program's design, but also in administering it as well. Accordingly, during

the April 2019 workshop, a consensus was reached that KopeLion should manage the day-to-day operations of the program and that the joint-stakeholder CIP Design Committee should serve as a permanent committee, to meet twice per year for the purpose of adaptively managing the program to address new and unforeseen challenges.

One final issue that was addressed concerning institutional fit was how to establish a CIP program within Tanzania's existing legal and policy framework. Because Tanzania's national policy is to pay consolation for livestock losses caused by wildlife, some NCA Authority officials expressed concern that the NCA Authority Board and/or the Ministry of Natural Resources and Tourism might oppose the establishment of an alternative program in the NCA:

> The Tanzanian government may not wish to see a double standard between the NCA and other areas
>
> *NCA Authority Official*

> The challenge will come from the parent ministry which may feel like it has its own policies already. It may not want the NCA Authority to come up with its own policies
>
> *NCA Authority Official*

However, through a review of the relevant statutes and regulations, it was determined that the establishment of a CIP program in the NCA would be consistent with Tanzanian law and policy. While Tanzania's Wildlife Conservation Act, 2009, provides that the government may implement a consolation program, that statute does not establish consolation payments as the only permissible means of promoting human–wildlife coexistence in Tanzania. Indeed, piloting a CIP program in the NCA would directly promote the national policy objectives to 'protect and conserve wildlife resources,' 'encourage, promote and facilitate active involvement and participation of local and traditional communities in the sustainable management, use and conservation of wildlife,' 'facilitate greater public awareness of the cultural, economic and social benefits for conserving wildlife,' and 'mitigate human-wildlife conflicts wherever they occur' Wildlife Conservation Act, 2009 § 5-(1)(a), (g), (j), and (k).

In fact, several officials noted that because of the NCA's unique status as the only Tanzanian protected area in which people live, the NCA Authority Board and the Ministry would be open to piloting a CIP program there.

> There are many national policies and political considerations … but the NCA is unique. This may be a reason to treat the NCA differently than other places. Any proposal would have to spell out clearly that it is a pilot and that the NCA is unique …. The NCA is seen as a model for other protected areas to try new things …
>
> *NCA Authority Official*

By the conclusion of the April 2019 workshop, it was generally agreed by the NCA Authority that its unique legal status provided the flexibility necessary to pilot a new policy instrument like a CIP program.

Insights from the policy literature for natural resource governance

The nexus between the three dimensions of governance, here illustrated in the context of a particular policy instrument—a CIP program—and its application to the case of the NCA, provides us with important lessons for the analysis of natural resource governance. First, the increasing complexity and dependencies between actors requires more coordination and collaboration to address complex governance problems, such as human–wildlife conflicts. This has, in turn, opened a window for the design of new policies and policy instruments that are dependent on participatory or inclusive modes of governance (Howlett and Mukherjee, 2017; Howlett and Rayner, 2007). Our case study shows that the co-design of a CIP program, which takes into account both historical and current political and sociocultural conditions, provides an opportunity to move from what can be characterized as a political deadlock, in our particular case, towards a more sustainable situation. However, to achieve long-term success, it is necessary to build capacity, that is, the ability of individuals and institutions to effectively make and implement decisions and perform various functions. Capacity building is needed at the individual level, to prepare the actors involved to meaningfully contribute to the development of the program; at the organizational level, to allow governmental and nongovernmental organizations to manage key resources, including leadership, information, and funding; and, finally, at the societal level, to empower local communities to support the program's development.

Second, although theories of public policy and theories of governance both focus on the relationships between policy making and its consequences, the links between the three dimensions of governance are rarely made explicit. Often, how these relationships impact on outputs and outcomes are not taken into account. Hence, both theoretical frameworks would benefit from adopting a multidimensional approach, giving consideration to all three dimensions of governance, that is, politics, polity, and policy. From an empirical perspective, a multidimensional perspective is equally important, since a pilot program like the one examined in our chapter needs to be continuously evaluated, not only to meet its overarching objectives but also to provide the information necessary for adaptive governance.

Finally, a CIP program is unlikely to be a 'silver bullet' solution to any particular human–wildlife conflict. While CIPs can help align the interests of local people with conservation goals, it is necessary to carefully consider the relationship between local people and conservation and the potentially negative impacts of external national and global conservation interests on local communities' rights and livelihoods. Optimally, consideration should be given to implementing CIP programs together with other measures that have the potential to strengthen and complement each other and improve both conservation and development goals.

Note

1 To promote a full and frank discussion during our interviews and focus groups, we advised all participants that we would not publish any personally identifiable information. Accordingly, we attribute quotes here based only on the respondent's stakeholder group ('traditional leader,' 'elder,' 'NCA Authority official,' etc.).

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This thesis investigates the complexities of human-lion coexistence and connectivity in the Ngorongoro Conservation Area, Tanzania, combining ecological, genetic, and socio-ecological analyses to address conservation challenges in a shared landscape. Key findings reveal behavioural adaptations by lions to avoid humans, ongoing conflicts over livestock predation, and genetic isolation of the Crater lion population, threatening its resilience. The study shows some promise for community-driven conservation efforts, such as the Lion Guardians and KopeLion programs, to sustain coexistence and mitigate conflicts amid increasing environmental and social pressures.

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